Deep-water scleractinian corals promote higher biodiversity in deep-sea meiofaunal assemblages along continental margins

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Submitted to Biological Conservation

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Abstract

Deep-water coral ecosystems are hot spots of biodiversity and provide habitats and refuges for several deep-sea species. However, their role in shaping the biodiversity of the surrounding open slopes is still poorly known. We investigated how meiofaunal biodiversity varies with and is related to the occurrence of deep-water living scleractinian corals and coral rubble in two deep-sea areas (the Rockall Bank, north-eastern Atlantic) and the Santa Maria di Leuca (central Mediterranean). In both areas, replicated sampling on alive and dead coral areas and from the adjacent slope sediments without corals (at the same and increasing depths) allowed us to demonstrate that sediments surrounding the living corals and coral rubble were characterised by higher meiofaunal biodiversity (as number of higher taxa, and nematode species richness) than the slope sediments. Despite the soft sediments surrounding the living coral having a higher nutritional value than those not associated with corals, with the opposite seen for coral rubble, the presence of both alive and dead corals had a significant effect on nematode assemblages. Our data suggest that, due particularly to the effects on habitat heterogeneity/complexity, both living coral and coral rubble promoted higher biodiversity levels than in surrounding slope sediments. We conclude that the protection of deep-water corals can be crucial to preserve the biodiversity of surrounding open slopes, and that the protection of dead corals, a so-far almost neglected habitat in terms of biological conservation, can further contribute to the maintenance of a high deep-sea biodiversity along continental margins.

Keywords. Deep-water scleractinian corals, coral rubble, nematode diversity, deep-sea conservation, north-eastern Atlantic, Mediterranean Sea.

1. Introduction

Deep-water corals are common along the continental margins at depths typically ranging from 200 m to more than 1,000 m (Freiwald et al., 2004; Huvenne et al., 2005; Roberts et al., 2006). Among these, scleractinian corals form biogenic reefs, which are large and complex three-dimensional structures that can entrap soft sediments and provide a wide variety of microhabitats and niches for deep-sea fauna (Rogers, 1999; Huvenne et al., 2005; Roberts et al., 2006; Henry and Roberts, 2007). Habitat heterogeneity is also high at the edges of deep-sea coral reefs (the so-called coral degradation zones), being created by the accumulation of dead coral fragments (coral rubble) derived from the erosion and break-down of coral colonies (Raes and Vanreusel, 2005; 2006; Roberts et al., 2006).

Deep-water reefs host highly diverse faunal communities characterised by high abundance and biomass, which are similar to some extent to those typically encountered in shallow tropical coral reefs (Jensen and Frederiksen, 1992; Mortensen et al., 1995; Rogers, 1999; Tursi et al., 2004; Auster, 2005; Cerrano et al., 2010). The characteristics of these habitats (e.g., local circulation patterns, larval retention, and provision of refugees from predation) along with the reefs' longevity, have been suggested to support specific biological assemblages (Rogers, 2004; Roberts et al., 2006). Moreover, deep-water corals have been shown to serve as nursery and are areas of spawning and feeding for several commercially important deep-sea species (Jensen and Frederiksen, 1992; Mortensen et al., 1995; Fosså et al., 2002; Husebø et al., 2002; Rogers, 2004; Roberts et al., 2008; D'Onghia et al., 2010).

In the last decades intensive bottom trawling has been documented to cause destruction to deep-coral ecosystems worldwide (Althaus et al., 2009; Fowler, 2003; Bruckner 2009; Heifetz et al., 2009), thus extending the areas characterised by the presence of coral rubble. Deep-water corals are also potentially highly vulnerable to other direct (e.g., mining, waste dumping) and indirect (e.g., ocean acidification) impacts (Fosså et al., 2002; Hall-Spencer et al., 2002; Freiwald et al., 2004; Guinotte et al., 2006; Davies et al., 2007; Turley et al., 2007). Deep-water corals biology and their distribution in world oceans will almost certainly be influenced also by climate change and ocean acidification (e.g., Fautin et al. 2009).

Despite these increasing concerns, the development of new strategies for the proper conservation and management of deep-sea coral habitats has fallen behind other terrestrial and shallow marine ecosystems (Davies et al., 2007). Major difficulties encountered to define relevant conservation policies have been either political or practical. Often sites of interest are located outside single national jurisdiction (high seas) which make more difficult the application of conservation regulations (Armstrong and van den Hove, 2008). In addition, although the scientific knowledge of deep-sea habitats is progressively improving, deep-water coral reefs are not easily accessible environments and there is much more to learn in terms of their distribution, connectivity with the adjacent systems and beta-diversity. Unfortunately, this information is essential for the proper planning of reliable and effective protection measures (Davies et al., 2007; Roberts et al., 2008).

Habitats characterised by the presence of dead coral fragments (coral rubble) in tropical reefs host high levels of biodiversity (Meesters et al., 1991; Raes et al., 2007 and literature therein). At temperate latitudes, persistent biogenic structures, like mollusc shell

debris, by creating patches of spatial heterogeneity, can contribute to maintain beta diversity (Hewitt et al., 2005). Deep-sea coral rubble systems are also characterised by high biodiversity (Raes and Vanreusel, 2005; 2006; Raes et al., 2008; Roberts et al., 2008). The presence of different types of *Lophelia pertusa* macrohabitats (e.g., framework versus coral rubble) is also an important factor that creates beta diversity in the associated macrofauna (Henry et al., 2010). However only minor conservation concerns and protection plans and/or measures have been conceived so far for these habitats. This is also due to the lack of enough comparative information on biodiversity of the adjacent slope systems. It is therefore clear that a better knowledge of the importance of deep-water reefs and coral rubble habitats on deep-sea biodiversity and ecosystem functioning is a priority for improving measures of preservation of the biodiversity, goods and services provided by deep-sea ecosystems (Davies et al., 2007; Armstrong and Van den Hove, 2008; Game et al., 2009).

In order to cope with these gaps of knowledge and provide new insights on the effects of biological conservation of deep-water scleractinian corals and/or their debris, we investigated meiofaunal higher taxa and nematode diversity, as well as their abundances and biomasses, in the Mediterranean Sea and in the north-eastern Atlantic. We compared the biodiversity associated with coral rubble (Mediterranean Sea) and living corals (Atlantic Ocean) with that of the neighbouring slope bare sediments, both at similar depths and across a bathymetric transect along the slope (from 500 m to 2,500 m in depth).

The aims of the present study are: i) to evaluate how meiofaunal biodiversity varies between deep-water (both living and dead) scleractinian coral systems and adjacent bare sediments and ii) to test the significance of the relationships between nematode species

composition and the occurrence of alive coral and coral rubble habitats. Specifically we tested two null hypotheses: i) meiofaunal (nematode) biodiversity levels in sediments surrounding living coral and coral rubble are not significantly different from those far from the coral bank/coral rubble area; and ii) the presence of living or dead corals does not explain the nematode species composition in the neighbouring slope sediments.

2. Materials and methods

2.1 Sampling

We collected sediment samples in the proximity of coral mounds and in slope sites (far from the coral and characterised by the presence of bare sediments). Sampling activities were carried out in two distinct biogeographic regions: the central Mediterranean Sea (southern Adriatic margin, the Santa Maria di Leuca Bank) and the north-eastern Atlantic Ocean (Rockall Bank; Fig. 1).

The investigated Mediterranean area is located ca. 25 miles south of Cape Santa Maria di Leuca, where the presence of living *Lophelia pertusa* and *Madrepora oculata* has been documented (Tursi et al., 2004; Taviani et al., 2005; Carlier et al., 2009; Freiwald et al., 2009; Fig. 1). This area is characterised by relatively high bottom-water temperatures (slightly above 13°C) and by the presence of coral mounds that are composed of sub-fossil deposits and dominated by the presence of fragments of dead coral (i.e., coral rubble). Sediment samples were collected between April and May 2006, aboard the R/V Urania, at three sites located within a narrow depth range (1,084-1,276 m). Two sites (Sites 19 and 33) were located at the edge of a coral bank in the reef degradation zone (hereafter referred

to as the coral rubble sediments), whilst the third site (Site 77) was located in bare sediments (Fig. 1, Table 1).

The area located in the south-east flank of Rockall Bank (west of Ireland, north-eastern Atlantic; Fig. 1) is characterised by the presence of living colonies of *L. pertusa* (Kenyon et al., 2003). Sampling was carried out between June and July 2006, aboard the R/V Pelagia. Sediment samples were collected at four sites on the top of the Haas mounds (Sites 4, 5, 6 and 7, ranging from 567 m to 657 m in depth; hereafter referred to as the living coral sediments) and at one site located along the slope (Site 2, 469m depth), which was characterised by the presence of bare sediments.

To assess the variation in benthic biodiversity with increasing distance (and depth) from the deep-water coral along the slope, a bathymetric transect was identified across the Rockall Bank area, which included Site 2, plus Sites 1, 3, 9 and 10, located at depths ranging from 1,091 m to 2,459 m (Fig. 1, Table 1).

A visual characterisation of the four habitat types investigated (living coral and bare sediments of the north-eastern Atlantic and coral rubble and bare sediments adjacent to coral rubble in the Mediterranean Sea) is illustrated in Figure 2 (a-d).

At all of the sampling sites, sediments were collected by three independent deployments of a box corer (NIOZ, 0.30 m^2), and once on board, the collected sediments were sub-sampled with PVC cores (3.6 cm internal diameter).

For analysis of the biochemical compositions of the organic matter and of the prokaryote abundance, the top 1 cm of the three replicated cores (each from an independent box-corer deployment) were stored at -20 °C until analysis. For meiofauna variables (abundance, biomass and community structure) and nematode diversity, the three replicated

cores were sliced into five sediment layers (0-1, 1-3, 3-5, 5-10 and 10-15 cm), preserved in 4% buffered formalin, and stained with Rose Bengal until analysis.

2.2 Analysis of the potential food sources of meiofauna and sediment water content

Chlorophyll-a (Chl a) and phaeopigment analyses were carried out after 90% acetone extractions (Pusceddu et al., 2009a). Phaeopigment concentrations were determinated after acidification with 200 µl 0.1 N HCl. The total phytopigment concentration was defined as the sum of the chlorophyll-a and pheopigment concentrations. Protein, carbohydrate and lipid concentrations were analysed spectrophotometrically (Pusceddu et al., 2009a) and expressed as bovine serum albumin, glucose and tripalmitine equivalents, respectively. For each assay, blanks were obtained using pre-combusted sediments (450 °C for 4 h). The carbohydrate, protein, and lipid concentrations were converted into carbon (C) equivalents using the conversion factors of 0.40, 0.49 and 0.75 mg C mg^{-1}, respectively, and their sum is referred to as the biopolymeric organic C (BPC; Pusceddu et al., 2009a). The algal C contribution to the BPC was calculated as the percentage of phytopigment-to-BPC concentrations, after converting the phytopigment concentrations into C equivalents using a mean value of 40 µg C $µg^{-1}$ Chl a (Pusceddu et al., 2009a). Sediment water content was calculated as the difference between wet weight and dry weight (after 60 °C for 24 h), and expressed as a percentage of sediment wet weight.

Prokaryote counts were carried out as described by Luna et al. (2002). Samples were stained with SYBR Green and filtered onto 0.2-µm polycarbonate filters. The filters were then analysed using epifluorescence microscopy (Zeiss Axioplan; magnification 1,000×), by examining at least 10 to 20 microscope fields and 200 prokaryotes, for each filter.

2.3 Meiofaunal abundance, biomass and the richness of higher taxa

For meiofauna extraction, the sediments previously sieved through a 1.0mm mesh were passed through a 20.0-µm mesh to retain the smallest meiofaunal organisms. The fraction remaining on the latter sieve was resuspended and centrifuged three times with Ludox HS 40 (density adjusted to 1.18 g cm^{-3}), as described by Heip et al. (1985). The remaining sediment after the three steps of centrifugation was observed under the stereomicroscope to check for the presence of non-extracted meiofaunal individuals. The efficiency of the procedure including 3-steps of extraction was >99%. All of the metazoans were counted and classified per taxon under a stereomicroscope, after staining with Rose Bengal (0.5 g l^{-1}). The meiofaunal abundance was integrated from the surface sediments down to 15 cm. The richness of the higher meiofaunal taxa was determined as the number of taxa identified from all of the replicate samples from each site, after counting at least 1,000 meiofaunal individuals. Due to possible bias in identifying formalin-preserved samples, some fresh samples were analysed immediately after sampling. All soft-body organisms from the preserved samples were mounted on slides and viewed at 1,000× magnification.

Nematode biomass was calculated from the biovolume, which was estimated from at least 100-120 specimens per replicate (for a total of more than 300 specimens per site) using the formula from Andrassy (1956). The biovolumes of all of the other taxa were measured for all of the specimens encountered. Body volumes were derived from measurements of body length (L; in mm) and width (W; in mm) using the formula $V = L \times W^2 \times C^*$; where C* is the approximate conversion factor for each meiofaunal taxon

(Higgins and Thiel, 1988). The body volume was multiplied by an average density (1.13 g cm^{-3}) to obtain the biomass (µg dry weight), and the C content was considered to be 40% of the dry weight (Higgins and Thiel, 1988).

2.4 Nematode diversity

From each replicate sample, 100 nematodes were withdrawn from the top 1 cm of the sediment layer and following the formalin-ethanol-glycerol technique to prevent dehydration, they were mounted on slides. The nematodes were identified to the species level according to Platt and Warwick (1983; 1988), Warwick et al. (1998) and the recent literature dealing with new nematode genera and species (NeMys database, Deprez et al., 2005).. The species richness was calculated as the total number of species collected at each site. The Margalef index (D) was estimated as D = (S-1)/ln N; where S is the number of species and N is the number of individuals in the sample (Margalef, 1958). The Shannon–Wiener diversity index (H') was calculated using $\log_2$ as $H' = -p_i\Sigma_i (\log_2 p_i)$, where p_i is the relative abundance of the i^{th} species in a sample. Pielou's evenness (J') was estimated as $J' = H'_{obs} / H'_{max}$, where $H'_{obs} = H'$ and H'_{max} is the highest possible if all of the species are equally abundant (Pielou, 1975). At each site, the species data were converted into rarefaction diversity indices (Sanders, 1968, as modified by Hurlbert, 1971). The expected number of species for a theoretical sample of 51 specimens, ES(51), was selected.

The feeding habits of the deep-sea nematodes were identified according to Wieser (1953). Each single nematode was assigned to one of the following groups: (1A) no buccal cavity or fine tubular one - selective feeders; (1B) large but unarmed buccal cavity - non-

selective deposit feeders; (2A) buccal cavity with scraping tooth or teeth - epistrate or epigrowth (diatom) feeders (in case of deep-sea habitats, referred to organisms feeding on vegetal detritus and phytoplankton settled from the photic zone); and (2B) buccal cavity with large teeth - predators/ omnivores. This classification was preferred to the others that are available (Moens and Vincx, 1997), to allow a wider comparison with the deep-sea literature. The Index of Trophic Diversity (ITD) was calculated as $ITD = \Sigma\theta^2$, where θ is the contribution of each trophic group to the total nematode abundance (Danovaro et al., 2008b). The ITD ranges from 0.25 (highest trophic diversity; i.e., the four trophic guilds account for 25% each) to 1.0 (lowest diversity; i.e., one trophic guild accounts for 100% of nematode abundance).

2.5 Statistical analyses

The two hypotheses of this study were tested using uni- and multivariate analysis of variance coupled with analysis of Bray Curtis dissimilarity and using canonical partitioning of spatial variation of community composition data by means of canonical correspondence analysis, respectively. Moreover, the two hypotheses were also tested after the removal and/or weighting (variance partitioning analysis) of the effects associated with changes in the amount of food available for meiofauna.

Differences in quantity of organic matter, prokaryote abundance, meiofaunal abundance and biomass and nematode diversity, between living coral (or coral rubble) and adjacent bare sediments were tested by one-way analysis of variance (ANOVA), separately for the two study areas (Mediterranean Sea and north-east Atlantic). Changes in these

variables among different depths along the north-eastern Atlantic slope were also analysed by one-way ANOVA. When significant differences were seen, a *post-hoc* HSD-Tukey test was carried out. Before the analyses, the homogeneity of the variances was checked using Cochran's test, and the data not-normally distributed were appropriately transformed to meet this assumption.

A permutational analysis of variance (PERMANOVA) was also carried out to analyse differences in meiofaunal abundance and biomass, and nematode diversity (ES[51] and ITD indices) between sites, after removing the effects of environmental variables (water depth, sediment water content, phytopigment and BPC concentrations), treated as covariables. This analysis is based on Euclidean distances of untransformed data, and it was carried out using 4,999 random permutations of the appropriate units under a reduced model, by means of the PERMANOVA.exe program (Anderson and ter Braak, 2003; Anderson 2005). We also used analysis of similarities (ANOSIM) to assess significant differences in nematode assemblage structure between living coral, coral rubble and bare sediments. For this, a ranked matrix of Bray-Curtis similarities was constructed using a presence-absence raw matrix. Since ANOSIM revealed significant differences among the four habitats, the matrix was then used to produce a non-metric, multidimensional scaling (nMDS) plot of the nematode assemblages. Coefficients of dissimilarity and species responsible for the clustering were determined by means of SIMPER analysis. ANOSIM, nMDS plots and SIMPER analyses were carried out with PRIMER v5.0 (Plymouth Marine Laboratory, UK; Clarke 1993).

Analysis of dissimilarity (SIMPER), based on Bray Curtis dissimilarity matrixes, was used to measure beta-diversity (i.e., species turnover in the sites investigated) of the

nematode assemblages in the deep-sea sediments. This analysis was done using presence/absence transformed data to give equal weight to rare taxa (Clarke, 1993).

One of the aims of the present study was to verify whether the observed assemblage structures (and thus the beta-diversity) could be related with the presence of the alive corals and coral rubble. To achieve this objective, we adopted the raw-data approach proposed by Legendre et al. (2005), based on the canonical partitioning of spatial variation of community composition data. Such a technique is indeed suitable to test hypotheses about the origin of beta diversity. This approach has been recently applied to a *Lophelia pertusa* setting in the Mingulay Reef Complex in the outer Hebrides off the west coast of Scotland in the northeast Atlantic (Henry et al. 2010). As living organisms often show unimodal responses to the environmental gradients of their biotopes, the analyses were made using canonical correspondence analysis (CCA), separately for the two regions. CCA partitions the variance in community composition due to constrained variables of interest and unconstrained residual inertia. The constrained variance was then further partitioned into three fractions of pure environmental, pure spatial and spatially structured environmental effects (Legendre 2008). These were estimated using partial CCA (pCCA; Borcard et al., 1992) as the variance explained by: i) the matrix of environmental variables, the matrix of the spatial variables, the environmental matrix (with co-varying spatial variables) and the spatial matrix (with spatial variables co-varying). The latter two represent the contribution of purely environmental (or spatial) effects uncoupled from spatial (or environmental) effects.

The response variables were species presence–absence data, from which species occurring in only one grab were excluded from the CCA and pCCA analyses, as these

disproportionately inflate the effects of rare species on canonical ordinations (Legendre and Gallagher 2001). The explanatory matrixes included either spatial (latitude and longitude) and environmental (the presence/absence of alive corals or coral rubble , water depth, and the water, phytopigment and biopolymeric C contents in the sediment) variables.

3. Results

3.1 Biochemical composition of sediments, and potential food sources of meiofauna.

The biochemical composition of the organic matter and the prokaryote abundance in the deep-sea habitats investigated (coral rubble sediments and bare sediments in the Mediterranean Sea, and living coral sediments and bare sediments of the north-eastern Atlantic) are reported in Table 1. In the Mediterranean Sea, phytopigment, protein, carbohydrate, lipid and BPC concentrations were significantly higher in bare sediments than in coral rubble sediments (Table 2). In the north-eastern Atlantic, living coral sediments had significantly higher phytopigment, protein, carbohydrate, lipid and BPC concentrations than those in bare sediments (Table 2). The concentrations of phytopigment, protein, carbohydrate, lipid and BPC were highest in the deepest sites (Table 2).

3.2 Richness of higher taxa, and meiofaunal abundance and biomass

The meiofaunal abundance, biomass and number of taxa in all of the regions, habitats and sites investigated are reported in Table 3. In the deep-Mediterranean Sea, coral rubble sediments contained 5-8 meiofaunal taxa, whilst only 4 taxa were encountered in bare sediments. At all of the Mediterranean sites, meiofaunal abundance was dominated by nematodes (83%-93% of total meiofaunal abundance), followed by copepods and

tardigrades (6%-12% and 0.6%-7.0%, respectively) and other rare taxa (altogether representing <1.4% of total meiofaunal abundance; Fig. 3a). Among the rare taxa, polychaetes, gastrotrichs, isopods, hydrozoans, acharins and ostracods were exclusively encountered in coral rubble (Fig. 3b). Only one of the two coral rubble sites (Site 19) showed significantly higher meiofaunal abundance than in bare sediments (Table 4). The total meiofaunal biomass was generally dominated by nematodes (33%-92%), followed by copepods (8%-43%), which did not show any significant differences among sampling sites (Table 4).

In the north-eastern Atlantic, living coral sediments contained 7-10 taxa, whilst only 5 were encountered in bare sediments, and 3 to 6 were found in sites sampled along the bathymetric transect (Table 3). At all of the sites, nematodes represented the dominant taxon (>90% of total meiofaunal abundance), followed by copepods and tardigrades (ranging from 1.0% to 5.9%, and from 0.7% to 3.2%, respectively; Fig. 3a). When pooled together, all of the other rare taxa again represented <1.4% of total meiofaunal abundance (Fig. 3a). Among the rare taxa, gastrotrichs, amphipods, nemerteans, kinorhynchs and loriciferans were exclusively found in sediments associated with living coral (Fig. 3b). Significant differences were also seen for meiofaunal abundance among the sites, although these were not related to the presence of coral (Table 4). No significant differences in total meiofaunal biomass were seen in comparing living coral and bare sediment sites. Along the bathymetric transect, meiofaunal abundance and biomass were significantly higher in bare sediment (Site 2) and at deeper depths (Site 10, Table 4).

3.3 Alpha-diversity of nematode assemblages

The nematode species richness, the Shannon-Wiener's, Margalef's, Pielou's and trophic diversity indices, as well as the expected numbers of nematode species, for all of the regions, habitats and sites investigated are reported in Table 3. In the deepMediterranean Sea, nematode species richness was higher in sediments surrounding coral rubble than in bare sediments (Table 3). Overall, 22 nematode families, 70 genera and 124 species were identified. Only 10 nematode families were consistently found at all of the sites. Seven families (Aegialoalaimidae, Anoplostomatidae, Cyatholaimidae, Diplopeltidae, Draconematidae, Monhysteridae and Selachinematidae) were exclusively encountered within coral rubble, while only Linhomoeidae was exclusively found in adjacent bare sediments. A total of 60 genera and 104 species were encountered within coral rubble sediments, while only 35 genera and 52 species were encountered in adjacent bare sediments. About half of the nematode genera (n = 33) were exclusively encountered in coral rubble sediments, and five of these (*Pierrickia*, *Paralongicyatholaimus*, *Bathyepsilonema*, *Elzalia* and *Hapalomus*) were relatively abundant, with each one accounting for >2% of total nematode abundance. In contrast, only 10 genera were exclusively found in bare sediments.

In the north-eastern Atlantic, species richness was higher in bare sediment than in sediments associated to living corals (Table 3). A total of 119 nematode genera (belonging to 32 families) and 231 species were identified. Sixty-nine genera and 104 species were encountered within sediments associated with coral, while 47 genera and 75 species were encountered in bare sediments. Thirty-seven genera were exclusively found in coral, while 17 were found in bare sediments. Seven families (Aegialoalaimidae, Anoplostomatidae, Anticomidae, Draconematidae, Enchelidiidae, Leptosomatidae and Meyliidae) were

exclusively found within living coral sediments, while only one family (Thoracostomopsidae) was exclusively seen in bare sediments.

3.4 Beta-diversity of nematode assemblages

The ANOSIM test performed on the nematode species composition revealed significant differences among the four habitat types (living coral sediments and bare sediments of the north-eastern Atlantic, coral rubble sediments and bare sediments adjacent to coral rubble in the Mediterranean Sea; $R = 0.92$, $p < 0.01$). The pair-wise test showed the presence of significant differences in nematode species compositions comparing living coral and bare sediments ($R = 0.96$, $p < 0.01$), coral rubble and bare sediment ($R = 0.6$, $p < 0.05$) and coral rubble and living coral sediments ($R = 0.93$, $p < 0.001$). The non-metric multi-dimensional scaling (nMDS) plot allowed four distinct clusters to be distinguished (Fig. 4). The SIMPER analysis revealed a high coefficient of dissimilarity between sediments associated with living coral and bare sediments in the north-eastern Atlantic, and between sediments associated with coral rubble and bare sediments in the Mediterranean Sea (74% and 77%, respectively). A dissimilarity of 79% was seen between nematode assemblages associated to living colonies (north-east Atlantic) and those associated to coral rubble sediments (central Mediterranean). Lower dissimilarities (54% and 67%) were seen within sites in the living coral and the coral rubble areas, respectively (Fig. 4).

Overall, analysis of nematode biodiversity along the bathymetric transect revealed the presence of 91 genera and 152 species. The ANOSIM revealed significant differences in nematode genera composition (as presence/ absence) between living coral sediments and sediments of all of the other sites along the bathymetric transect ($R = 0.82$, $p < 0.001$). The

SIMPER analysis revealed a dissimilarity ranging from 61% to 70% between living corals and all of the other non-coral sites. The genera that were responsible for these high dissimilarities between coral and bare sediments were *Pareudesmoscolex* (exclusively reported in coral sediments, accounting for 6.5% of total nematode abundance), and *Rhynchonema* (exclusive to bare sediments, accounting for 5.7% of total nematode abundance).

When comparing nematode beta-diversity (i.e. species turnover) in sediments collected within and outside the coral bank in the north-eastern Atlantic, ANOSIM revealed a significant difference among these groups ($R = 0.9$, $p < 0.001$). Significant differences were seen between the sediments associated with corals and each of the sites along the bathymetric transect (pairwise test, $p < 0.01$), while no significant differences were seen among the sites of the bathymetric transects. The nMDS plot allows sediments surrounding the coral to be clearly distinguished from sediments outside the coral bank (Fig. 5).

3.5 Functional diversity of nematode assemblages

At all of the sites investigated, the relative contribution of predator/ omnivore nematodes to total nematode abundance increased from coral rubble to live coral (Fig. 6). Moreover, the percentage of predator/ omnivore increased with increasing distance from the coral bank (from 12% to 34% of total nematode abundance; Fig. 6). In the Mediterranean Sea, selective and non-selective deposit feeders accounted together for >65% of total nematode abundance (Fig. 6). Bare sediments contained a lower proportion of non-selective deposit feeders and a higher fraction of epistrate feeders and predator omnivores compared to coral rubble sediments. In the north-eastern Atlantic, living coral

sediments had a dominance of selective deposit feeders (i.e., bacterivorous nematodes, comprising 34%-54% of total nematode abundance), followed by non-selective deposit feeders (25%-28%; Fig. 6). Sediments collected along the bathymetric transect had a dominance of epistrate feeders (39%). No significant differences among the sites were observed in terms of the ITD, in both areas (Table 4).

3.6 Effects of living coral and coral rubble habitats on nematode assemblages

In the north-eastern Atlantic, the CCA revealed that linear combinations of the tested explanatory variables (i.e., latitude and longitude, the presence/absence of alive corals or coral rubble, water depth, and the water, phytopigment and biopolymeric C contents in the sediment) explained significantly ($P<0.001$) 46.3% of the variation in nematode assemblage composition (Fig. 7a). The outputs of the partial CCA revealed that pure environmental effects explained 23.6% of the variation, though this was not statistically significant at $\alpha=0.05$ ($P = 0.160$). Pure spatial effects accounted for 4.3% of the nematode species assemblage, and this also was not statistically significant ($P=0.99$). The effects of spatially structured environmental effects, for which a significance test does not exist (Borcard et al. 1992; Henry et al. 2010), accounted for an additional 21.6%, with a residual unexplained variance of 53.8%.

In the Mediterranean Sea, linear combinations of the tested explanatory variables explained significantly ($P=0.007$) 85.8% of the variation in nematode assemblage composition (Fig. 7b). The outputs of the partial CCA revealed that pure environmental effects explained 57.1% of the variation, though this was not statistically significant at

α=0.05 (P = 0.672). Pure spatial effects accounted for only 1% of the nematode species assemblage, and this also was not statistically significant (P=0.99). The effects of spatially structured environmental effects accounted for an additional 27.7% (no significant test available), with a residual unexplained variance of 14.2%.

4. Discussion

Studies on benthic biodiversity close to deep-water corals have been so far mainly focused on macro- and mega-fauna (Jensen and Frederiksen, 1992; Mortensen et al., 1995; Rogers, 1999; Jonsson et al., 2004; Reed, 2004; Tursi et al., 2004; Reed et al., 2006; Henry and Roberts, 2007; Cordes et al., 2008; Henry et al., 2008; Roberts et al., 2008; D'Onghia et al., 2010; Freiwald et al., 2009; Mastrototaro et al., 2010), while the information available on meiofaunal assemblages are limited to the Porcupine Seabight coral area or focused on epifaunal or specific meiofaunal taxa (Raes and Vanreusel, 2005; 2006; Raes et al., 2008; Gheerardyn et al., 2009 and literature therein). Meiofauna have key roles in the functioning of deep-sea benthic ecosystems, as they can serve as a link between the microbial component and the larger macro-megafauna (Danovaro et al., 2008a, and literature therein). Meiofauna are largely dominated by nematodes, which, in the deep sea, typically represent ca. 90% of the total metazoan faunal abundance. Nematodes are an ideal component for investigating the effects of habitat heterogeneity at different spatial scales as they are characterised by very high species richness, recognizable feeding types and life-history strategies that allow for an assessment of functional diversity in these communities (Danovaro et al., 2008a; b and literature therein).

4.1 Effects of deep-water coral habitats on richness of meiofaunal taxa and on nematode alpha-diversity

Deep-water coral reefs have been reported to host a great abundance and diversity of deep-sea fauna (Jensen and Frederiksen, 1992; Mortesen et al., 1995; Rogers, 1999; Raes and Vanreusel, 2006; Henry and Roberts, 2007; Roberts et al., 2008 and associated literatures). However, only a limited number of studies have investigated the roles of living coral or of their dead fragments (i.e., coral rubble) on the community structure and biodiversity of adjacent deep-sea benthic assemblages (Jonsson et al., 2004; Henry and Roberts, 2007; Soest et al., 2007; Roberts et al., 2008; Henry et al., 2010). Results from the present study have revealed a general lack of significant differences in terms of meiofaunal abundance and biomass between living coral or coral rubble sites and the adjacent areas characterised by the presence of bare sediments. This suggests that presumably these variables are not directly influenced by the presence of deep-water coral reefs. However, in both investigated regions, "coral habitats" (i.e., either living coral or coral rubble) contained a higher number of rare meiofaunal taxa (i.e., taxa accounting for less than 1% of total meiofaunal abundance), as well as the presence of taxa exclusively associated to these habitat types. Moreover, sediments in both coral rubble in the Mediterranean Sea and living corals in the north-eastern Atlantic Ocean hosted a large number of nematode families, genera and species, that were exclusive to these habitats (i.e., absent in adjacent bare sediments). The presence of rare epifaunal taxa in nematode assemblages of deep-water coral dead fragments has been also reported in the Porcupine Seabight (NE Atlantic; Raes and Vanreusel, 2006). The presence of specific meiofaunal assemblages associated with the

deep-water coral habitats was apparently the cause of the significantly higher dissimilarity in nematode species assemblages seen comparing living coral and bare sediments (in the north-eastern Atlantic), and comparing coral rubble and bare sediments (in the Mediterranean Sea). This suggests that deep-water coral environments can promote meiofaunal biodiversity (even at the highest taxonomic level) as seen for the other larger benthic components (Jensen and Frederiksen, 1992; Mortensen et al., 1995; Jonsson et al., 2004; Henry and Roberts, 2007; Roberts et al., 2008).

Among the several factors potentially influencing the distribution of meiofaunal biomass and their diversity in deep-sea sediments, the quality and quantity of the potentially available food sources and the sedimentary/ textural characteristics are amongst the best documented (Galéron et al., 2001; Danovaro et al., 2002, Baguley et al., 2006; Gambi and Danovaro, 2006; Pusceddu et al., 2009b). The results reported in the present study indicate that sediments beneath the living coral of the north-eastern Atlantic displayed higher quantity and greater nutritional quality of organic matter that is potentially available to benthic consumers (e.g., BPC, phytopigment and protein concentrations) than the adjacent bare sediments. This finding is consistent with our expectations, as altering of bottom currents by deep-water coral reefs can entrap food particles in the sediments beneath the coral structure (Duineveld et al., 2004; Cerrano et al., 2010). Another explanation for the accumulation of a significant amount of bioavailable organic matter could be the production of mucus by living corals (Wild et al., 2004; 2009). In the north-eastern Atlantic, the high organic matter quality and quantity in living-coral sediments were associated with a greater richness of higher meiofaunal taxa and a greater nematode diversity. In the Mediterranean Sea, despite a lower food availability, coral rubble

displayed a greater richness of higher meiofaunal taxa and the nematode species richness than bare sediments (Table 3).

The differences seen in nematode diversity between coral and bare sediments might be the result of indirect effects generated by the three-dimensional structure of the living coral or the coral rubble on the general characteristics of the sediments. The PERMANOVA analysis revealed that relevant proportions of the differences between coral and bare sediments in terms of meiofaunal abundance and biomass in the Mediterranean Sea were indeed explained by environmental covariables (including biopolymeric C and phytopigments concentrations, water depth and sediment water content), but also that the differences remained significant after removal of the covariables effects (Table 5). In the Mediterranean Sea, the effects of coral rubble on nematode trophic biodiversity (ITD) appeared to be mediated by differences in environmental conditions (used as covariables in the statistical analysis). In the north-eastern Atlantic (including the bathymetric transect), differences in meiofaunal abundance and biomass between living coral and bare sediments were almost entirely related to differences in environmental characteristics. In contrast, differences in the expected number of nematode species and their functional diversity remained significant also after removal of the effects of environmental covariables.

The CCA revealed that the presence of either living corals and coral rubble habitats, and their environmental features, explained a significant fraction of the variation in nematode assemblages. These findings support the conclusion that coral habitats influence significantly the biodiversity of the surrounding soft sediments. Altogether, these results suggest that living coral or coral rubble habitats promote higher values of beta-diversity, thus supporting overall higher values of biodiversity along continental margins.

The CCA analyses revealed also that i) species and environmental data have similar spatial structures, ii) a large fraction of the nematode species assemblages variation remained unexplained for both coral habitats, and iii) this unexplained fraction was higher in coral rubble than in living coral sediments (Fig. 8). Our sampling design did not allow us to discriminate between the factors contributing to the unexplained variation of nematode assemblages in the two systems. Previous studies identified microbial abundance and metabolism as factors potentially responsible for the observed differences (Allers et al., 2008; Neulinger et al., 2008; Wild et al., 2009 and literature therein). However, in both sampling areas, no significant differences in prokaryotic abundance between living/dead corals and adjacent sediments were observed.

Differences in habitat complexity were also partially reflected by changes in the nematode functional diversity (measured as trophic structure), as in both areas the fraction of predator/ omnivore associated to bare sediments was significantly higher than in living coral or coral rubble sediments. We hypothesise that these differences are related to a lower availability of refuges for potential preys in bare sediments, with the consequent lower possibility of escaping from predation, with respect to the structurally complex (living and dead) coral habitats. Our results are opposite to those found for macro- and megafauna in a *L. pertusa* reef off the Swedish west coast by Jonsson and colleagues (2004). Such a discrepancy, again, is likely to be related to the limited sampling strategy we adopted in this study and suggests that additional studies are needed to test our hypothesis.

Overall, this comparative analysis of the results from these two regions allow us to conclude that differences in structural and functional biodiversity are mostly related to the presence of three-dimensional biogenic structures created by the coral, both in the form of

living coral and as dead coral rubble. These structures, that are characterised by a large habitat complexity and heterogeneity, provide additional spatial niches and protect the fauna from erosion, bottom currents and potential predators (Raes and Vanreusel, 2006).

4.2 Effects of living coral and coral rubble on beta-diversity of nematode assemblages

Even when they are associated with low values of alpha-diversity, high values of beta-diversity can have profound implications on the regional diversity and on the identification of factors controlling the spatial distribution of deep-sea biodiversity at the large spatial scale (Gray, 2000; Harborne et al., 2006).

In both studied areas, ANOSIM revealed the presence of a dissimilarity in nematode species composition (expressed as percentages of non-shared species) between living coral and adjacent bare sediments and between coral rubble and the adjacent sediments much higher than between the living corals and coral rubble habitats (Fig. 4).

In deep-sea ecosystems, depth differences are key drivers of observed patterns of abundance, biomass and diversity distribution (Rowe et al., 1982; Soltwedel, 2000; Rex et al., 2006; Danovaro et al., 2008b). However, in the north-eastern Atlantic the dissimilarity among nematode species between coral and adjacent bare sediments, and between coral and bare sediment at different depths along the slope, were almost invariant (typically >70%), and did not show clear patterns with increasing depth (ranging from 72% to 80%; Fig. 5).

Some of the nematode genera were found exclusively in coral sediments (i.e., absent in bare sediments at similar depths, and in other sites at increasing depths), while others (such as *Pareudesmoscolex, Sphaerolaimus, Quadricoma, Anticoma, Prochromodorella, Disconema and Southerniella*) were encountered in both coral sediments and in other sites

along the bathymetric transect, but not in bare sediments adjacent to coral habitats. The sampling design used here does not allow us to determine whether deep-water reefs are ”hot-spots” of biodiversity, acting through a spill-over effect as distributors of biodiversity towards the adjacent deep basin (Fosså et al., 2002; Tursi et al., 2004; D'Onghia et al., 2010), or whether they act as refuges for species which find a suitable habitat for their survival within the reef. Data reported here, however, allow hypothesising that deep-water reefs can have a pivotal role in modulating beta-diversity in the surrounding of the reefs.

4.3 Implications for deep-sea biodiversity conservation

Living coral colonies and their dead fragments (coral rubble) contribute to increase local habitat heterogeneity by creating complex three-dimensional structures interspersed in a more homogeneous surrounding environment made of soft incoherent sediments. Our results provide evidence that sediments associated to deep-water living corals and coral rubble can be characterised by a greater meiofaunal diversity (in particular a higher number of rare taxa) than the surrounding bare sediments. Since higher deep-sea diversity values are associated with an exponentially higher ecosystem functioning (Danovaro et al. 2008a), the conservation of "coral habitats" can contribute to maintain higher levels of the deep-sea ecosystem functions.

Deep-water corals have been shown to be highly diverse and, at the same time, to be highly vulnerable to increasing anthropogenic threats (Fosså et al., 2002; Hall-Spencer et al., 2002; Freiwald et al., 2004; Davies et al., 2007; Roberts et al., 2008). For these reasons, the classifications of deep-sea protected areas or networks of deep-sea protected areas adopted to date (e.g. EUNIS habitat classification for the deep sea;

http://www.eunis.eea.europa.eu/01/06/09) or recently proposed (Howell, 2010) include either *Lophelia pertusa* reefs (EUNIS category A6.611) or areas with coral debris (EUNIS category A6.22) as crucial levels of categorization. In 2006 the United Nations General Assembly (Resolution A/RES/61/105) in an attempt to protect vulnerable marine ecosystems (VMEs) from destructive fishing practices in international waters specifically included coldwater corals. As a result, some deep-sea corals have gained the status of protected species because of the closure of seamounts to fishing (Miller et al. 2009).

Nonetheless, to date, only few deep-sea areas including deep coral reefs have been granted permanent protected status (see examples reported in Davies et al., 2007) and works focusing on conservation aspects of these environments are at a pioneer stage (Davies et al., 2007; Morgan et al., 2007; Armstrong and van den Hove, 2008). Moreover, the census of the presence and distribution of deep-water corals in both the Mediterranean Sea and Atlantic Ocean is largely incomplete.

As a result of the recognition of the impact of trawling and, to a lesser extent, of other fishing gears on the deep-water coral banks, in January 2006 the General Fisheries Commission for the Mediterranean (GFCM) decided on recommendations concerning the prohibition of towed gears (dredges and trawl nets) in the deep-water coral banks of Santa Maria di Leuca, thus creating the new legal category of "Deep-sea fisheries restricted area" (Rec. GFCM/2005/1 and GFCM/2006/3). Results reported in the present study indicate that the policy issues adopted for the protection of deep-water corals and the surrounding habitats are needed for a proper management not only for the conservation of the *L. pertusa* but also of the natural resources of these systems.

However, our results also suggest that the application of the conservation measures adopted in 2006 should be extended also to coral rubble habitats, whose location is outside the boundaries of the "Deep-sea fisheries restricted area". Both in Santa Maria di Leuca and other deep-water coral areas, the fishermen continue their activities on coral rubble, as they still provide high fishing yields (D'Onghia et al., 2010). The risk we could face (not only in the Mediterranean Sea) is that fishermen, by trawling close to or on deep-water reefs, could destroy the living corals, transforming them to coral rubble. In these areas fishermen could continue their fishing activities without any legal constraint. This negative feedback mechanism is potentially analogous to the deliberate forest fires documented for terrestrial ecosystems in order to extend the land use (see for instance Serrão and Homma, 1993). Moreover, since coral rubble habitats have been suggested to function as reserves for coral reefs, providing a "recruitment pool" that can accelerate the recovery of coral-reef biodiversity after intense disturbances (Meesters et al., 1991 and literature therein), besides the protection of deep-water coral reefs, the protection of coral rubble habitats is a measure that is certainly needed for deep-sea biodiversity conservation at a regional scale.

Acknowledgements

This study was conducted in the framework of the HERMES (Hot Spot Ecosystem Research on the Margins of European Seas) and HERMIONE (Hotspot Ecosystem Research and Man's Impact on European Seas) projects funded by the European Commission (FPVI, Contract N° GOCE-CT-2005-511234-1; and FP7-ENV-2008-1 Contract N° 226354). Partial founding was also provided by the BIOCORAL grant (Italian Ministry of Environment). This is ISMAR-CNR Scientific contribution n. 1637. The

authors are indebted to Daniela Zeppilli (DISMAR, Italy), Gerard Duineveld (NIOZ, The Netherlands), Fabio Trincardi (CNR-ISMAR, Italy) for support in the sampling activities, and to the crews of the R/Vs *Urania* (Italy) and *Pelagia* (The Netherlands) for their valuable help during the sea-going activities.

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Figures legends

Figure 1. Sampling sites in the north-eastern Atlantic Ocean and the Mediterranean Sea. The white dots are the sampling sites within the living coral and coral rubble areas, while the grey dots show the sampling sites located outside the coral at comparable depths (bare sediments), and in the north-eastern Atlantic sites along a bathymetric transect.

Figure 2. Sediment samples collected from different deep-sea habitats. **(a)** living coral sediment from the north-eastern Atlantic; **(b)** bare sediment from areas adjacent to the coral bank in the north-eastern Atlantic; **(c)** coral rubble sediment from the central Mediterranean; **(d)** bare sediment adjacent to the coral rubble area in the central Mediterranean.

Figure 3. (a) Meiofaunal assemblage structure, and **(b)** rare taxa assemblage structure in the Mediterranean Sea and the north-eastern Atlantic. *Inc. sedis*, incertae sedis (of uncertain taxonomic position).

Figure 4. Multidimensional scaling (nMDS) of nematode species taxonomic composition in living coral, coral rubble and bare sediments in the Mediterranean Sea and north-eastern Atlantic. Species abundance is presence/ absence transformed. Percentages indicate the dissimilarity between habitats.

Figure 5. Multidimensional scaling (nMDS) of nematode species taxonomic composition sediments associated with living coral and sediments not influenced by coral (bare and bathymetric transect sediments) in the north-eastern Atlantic. Species abundance is presence/ absence transformed. Percentages indicate percentage of dissimilarity among sites.

Figure 6. Trophic structure of the nematode assemblage in the Mediterranean Sea and north-eastern Atlantic. The percentage contributions are reported for selective deposit feeders (1A), non-selective deposit feeders (1B), epistrate feeders (2A), and predators/omnivores (2B).

Figure 7. Two-dimensional canonical biplots of constrained inertia with ordination of sites (living corals or coral rubble and bare sediments) along the first two canonical axes (percentage of constrained variance explained given in parentheses) in the North-Eastern Atlantic (a: living corals) and in the Mediterranean Sea (b: coral rubble).

Figure 8. Variation partitioning of the nematode assemblages in living coral and coral rubble sediments. Reported are percentages of variation explained by the pure environmental matrix (including the presence of alive corals or coral rubble, water depth, sediment water content and quantity of organic matter in the sediment, with co-varying geolocation), the pure spatial matrix (including geographical coordinates with co-varying environmental variables), the spatially structured variation and the unexplained variation.

Table 1. Biochemical composition of the organic matter and the prokaryote abundance in the deep-sea habitats investigated in the present study, as means ± standard deviation (n=3).

Area	Site	Habitat	Latitude N	Longitude W	Depth m	Protein mg g $^{-1}$	Carbohydrate mg g $^{-1}$	Lipid mg g $^{-1}$	Phytopigment µg g $^{-1}$	Biopolymeric C mg g $^{-1}$	Prokaryotes ×10 ^{8} cells g $^{-1}$
Mediterranean	19	Coral rubble	39°50.67'	17°37.72'	1084	0.43 ±0.09	0.38 ±0.02	0.36 ±0.05	3.94 ±0.99	0.63 ±0.09	0.81±0.05
	33	Coral rubble	39°49.58'	17°36.48'	1276	0.58 ±0.13	0.34 ±0.06	0.36 ±0.09	5.19 ±0.80	0.69 ±0.15	3.29 ±0.85
	77	Bare sediment	39°44.98'	19°11.38'	1096	1.12 ±0.19	0.81 ±0.29	0.61 ±0.08	11.02 ±0.56	1.33 ±0.27	1.82 ±0.19
North-eastern Atlantic	4	Living coral	55°30.21'	15°47.15'	657	0.62 ±0.07	3.13 ±1.15	0.68 ±0.05	5.86 ±1.71	2.06 ±0.53	4.31 ±0.48
	5	Living coral	55°30.01'	15°47.92'	591	0.62 ±0.15	2.60 ±0.66	0.59 ±0.09	14.7 ±4.38	1.78 ±0.41	5.77 ±0.59
	6	Living coral	55°29.87'	15°48.61'	588	0.45 ±0.07	1.11 ±0.11	0.26 ±0.04	7.85 ±1.17	0.86 ±0.07	1.35 ±0.26
	7	Living coral	55°29.71'	15°48.56'	567	0.72 ±0.01	0.80 ±0.00	1.06 ±0.18	25.49 ±2.77	1.47 ±0.14	1.95 ±0.39
	2	Bare sediment	55°39.00'	15°56.00'	469	0.19 ±0.02	0.80 ±0.08	0.24 ±0.05	2.88 ±0.69	0.59 ±0.08	5.96 ±0.52
	1	Bath. transect	55°27.11'	15°45.97'	1091	0.14 ±0.01	0.62 ±0.09	0.18 ±0.02	2.01 ±0.61	0.45 ±0.06	19.70 ±2.01
	3	Bath. transect	55°22.41'	15°39.19'	1488	0.05 ±0.00	0.39 ±0.01	0.18 ±0.02	1.87±0.25	0.32 ±0.02	3.12 ±0.14
	9	Bath. transect	55°12.45'	15°46.76'	1958	0.21 ±0.06	0.78 ±0.01	0.45 ±0.08	6.20 ±1.54	0.75 ±0.09	1.67 ±0.47
	10	Bath. transect	55°04.92'	15°46.33'	2459	1.33 ±0.22	2.36 ±0.29	1.00 ±0.08	52.69 ±15.98	2.35 ±0.29	4.59 ±0.72

Table 2. One way analysis of variance (ANOVA) testing for the differences between sites in sediment organic matter biochemical composition, content, and prokaryote abundance. Data on prokaryotic abundance were log-transformed prior to the analyses.

Mediterranean Sea (coral rubble and bare sediment)

Variables	df	MS	F	*p*	*post-hoc* HSD-Tukey test	*p*
Protein	2	0.40	19.52	**	bare > c. rubble (33,19)[#]	**
Carbohydrate	2	0.20	7.00	*	bare > c. rubble (33,19)	*
Lipid	2	0.06	10.74	*	bare > c. rubble (33,19)	*
Phytopigment	2	42.83	66.90	***	bare > c. rubble (33,19)	***
Biopolymeric C	2	0.45	31.58	**	bare > c. rubble (33,19)	**
Prokaryote abundance	2	1.431	50.18	***	c. rubble (33) > bare > c. rubble (19)	*

North-eastern Atlantic (living coral and bare sediment)

Variables	df	MS	F	*p*	*post-hoc* HSD-Tukey test	*p*
Protein	4	0.13	21.86	***	coral (4,5,6,7) > bare	**
Carbohydrate	4	3.61	10.24	**	coral (4,5) > bare	**
Lipid	4	0.34	34.70	***	coral (7) > (5,4) > bare	**
Phytopigment	4	255.59	40.45	***	coral (7) > (5) > bare	**
Biopolymeric C	4	1.15	11.80	**	coral (4, 5, 7) > bare	**
Prokaryote abundance	4	1.377	62.14	***	bare > corals (4, 6, 7)	**

North-eastern Atlantic (bathymetric transect)[§]

Variables	df	MS	F	*p*	*post-hoc* HSD-Tukey test	*p*
Protein	4	0.85	78.71	***	site (10) > other sites	*
Carbohydrate	4	1.84	94.53	***	site (10) > other sites	*
Lipid	4	0.36	115.87	***	sites (10, 9) > other sites	*
Phytopigment	4	1476.20	28.54	***	site (10) > other sites	*
Biopolymeric C	4	2.06	103.02	***	sites (10, 9) > other sites	*
Prokaryote abundance	4	2.544	98.11	***	sites (10, 2) > site (1)	*

df, degree of freedom; MS, mean square; F, F statistic; *p*, probability level; bare, bare sediments; c., coral

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

[#] in brackets, relevant site numbers

[§] site 2 of the bathymetric transect corresponding to north-eastern Atlantic bare sediments.

Table 3. Meiofaunal abundance, biomass, taxon richness and indices of nematode diversity of samples in the present study, as means ±standard deviation (n=3).

Area	Site	Habitat	Meiofaunal abundance ind 10 cm^{-2}	Meiofaunal biomass µgC 10 cm^{-2}	No. taxa	SR	H'	D	J	ES (51)	ITD
Mediterranean	19	Coral rubble	181.70 ±48.88	12.21 ±11.99	8	76	4.72 ±0.17	8.04 ±0.38	0.91 ±0.02	28.07 ±1.26	0.35 ±0.10
	33	Coral rubble	121.57 ±18.70	6.47 ±5.74	5	65	4.45 ±0.70	7.34 ±1.92	0.89 ±0.07	26.91 ±5.89	0.36 ±0.10
	77	Bare sediments	91.50 ±6.53	2.61 ±0.59	4	52	4.33 ±0.09	6.29 ±0.35	0.94 ±0.02	24.00 ±0.00	0.32 ±0.10
North-eastern	4	Living corals	597.71 ±80.49	25.84 ±17.28	7	40	4.02 ±0.44	5.26 ±1.47	0.89 ±0.02	19.71 ±4.24	0.38 ±0.13
Atlantic	5	Living corals	818.95 ±315.67	818.95 ±315.67	8	41	4.17 ±0.20	5.70 ±0.54	0.89 ±0.03	21.33 ±2.17	0.34 ±0.08
	6	Living corals	486.27 ±89.90	37.04 ±11.32	10	57	4.38 ±0.36	6.73 ±1.65	0.90 ±0.01	24.28 ±4.66	0.29 ±0.05
	7	Living corals	907.52 ±84.28	26.07 ±5.89	9	62	4.50 ±0.12	7.37 ±0.37	0.89 ±0.02	25.56 ±0.83	0.37 ±0.12
	2	Bare sediments	451.63 ±164.79	20.64 ±5.66	5	75	4.94 ±0.22	8.72 ±0.77	0.93 ±0.03	29.98 ±3.62	0.30 ±0.06
	1	Bath. transect	125.49 ±16.72	6.60 ±2.27	4	59	4.49 ±0.34	6.91 ±1.70	0.92 ±0.02	25.62 ±4.44	0.27 ±0.03
	3	Bath. transect	25.16 ±7.36	0.81 ±0.38	3	nd	nd	nd	nd	nd	nd
	9	Bath. transect	138.89 ±37.80	4.47 ±1.30	3	66	4.73 ±0.32	7.89 ±1.19	0.93 ±0.03	29.77 ±4.62	0.28 ±0.05
	10	Bath. transect	338.24 ±81.97	22.61 ±8.85	6	67	4.75 ±0.15	8.05 ±0.27	0.92 ±0.02	28.82 ±1.04	0.31 ±0.08

SR, nematode species richness; H', Shannon index; D, Margalef index; J, Pielou index; ES (51), expected number of species; ITD, index of trophic diversity; nd, not determined.

Table 4. One way analysis of variance (ANOVA) testing for the differences between sites in meiofaunal abundance, biomass and nematode diversity indices. Data of meiofaunal abundance were log-transformed prior to the analyses.

Mediterranean Sea (coral rubble and bare sediment)

Variables	df	MS	F	*p*	*post-hoc* HSD-Tukey test	*p*
Meiofaunal abundance	2	6327.48	6.93	*	c. rubble (19)[#] > bare	*
Meiofaunal biomass	2	70.13	1.19	ns	na	na
H'	2	0.12	0.67	ns	na	na
D	2	2.34	1.31	ns	na	na
J	2	0.002	1.15	ns	na	na
ES(51)	2	13.21	1.09	ns	na	na
ITD	2	0.001	0.10	ns	na	na

North-eastern Atlantic (living coral and bare sediment)

Variables	df	MS	F	*p*	*post-hoc* HSD-Tukey test	*p*
Meiofaunal abundance	4	122790.05	4.14	*	na	ns
Meiofaunal biomass	4	197.16	1.99	ns	na	na
H'	4	0.37	4.44	*	bare > coral (4)	*
D	4	5.68	4.81	*	bare > coral (5, 4)	*
J	4	0.001	2.37	ns	na	na
ES(51)	4	47.74	4.10	*	bare > coral (4)	*
ITD	4	0.005	0.60	ns	na	na

North-eastern Atlantic (bathymetric transect)[§]

Variables	df	MS	F	*p*	*post-hoc* HSD-Tukey test	*p*
Meiofaunal abundance	4	90766.15	12.73	***	sites (2, 10) > other sites	*
Meiofaunal biomass	4	295.20	12.59	***	sites (2, 10) > other sites	*
H'	3	0.10	1.44	ns		na
D	3	1.68	1.35	ns		na
J	3	0.002	0.17	ns		na
ES(51)	3	12.17	0.88	ns		na
ITD	3	0.001	0.29	ns		na

H', Shannon index; D, Margalef index; J, Pielou index; ES(51), expected species number; ITD, index of trophic diversity; ns, not significant; na, not applicable; df, degree of freedom; MS, mean square; F, F statistic; *p*, probability level; bare, bare sediments; c., coral
* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$
[#] in brackets, relevant site numbers
[§] site 2 of the bathymetric transect corresponds to north-eastern Atlantic bare sediments

Table 5. Results of the permutational multivariate analysis of variance (PERMANOVA) on the differences between the sites investigated in the present study

Mediterranean Sea (coral rubble and bare sediment)

Meiofaunal abundance					**Meiofaunal biomass**					**Nematode ES(51)**					**Nematode ITD**				
Source	df	MS	F	*p*	Source	df	MS	F	*p*	Source	df	MS	F	*p*	Source	df	MS	F	*p*
Covariables[†]	4	3772.62	12.40	*	Covariables	4	161.4	17.43	*	Covariables	4	16.48	1.14	ns	Covariables	4	0.01	21.67	**
Site	2	978.17	4.22	*	Site	2	17.03	3.94	*	Site	2	1.38	0.09	ns	Site	2	0.00	11.24	*
Residual	2	231.84			Residual	2	8.65	4.32		Residual	2	14.73			Residual	2	0.06		
Total	8				Total	8				Total	8				Total	8			

North-eastern Atlantic (living coral and bare sediment)

Meiofaunal abundance					**Meiofaunal biomass**					**Nematode ES(51)**					**Nematode ITD**				
Source	df	MS	F	*p*	Source	df	MS	F	*p*	Source	df	MS	F	*p*	Source	df	MS	F	*p*
Covariables	4	147249.31	8.56	**	Covariables	4	311.95	6.27	*	Covariables	4	49.66	4.73	*	Covariables	4	0.02	12.6	**
Site	4	315.31	0.02	ns	Site	4	58.00	1.17	ns	Site	4	57.81	6.75	*	Site	4	0.03	27.95	**
Residual	6	97252.56	16208.76		Residual	6	50.39			Residual	6	8.56			Residual	6	0.11		
Total	14				Total	14				Total	14				Total	14			

North-eastern Atlantic (bathymetric transect)

Meiofaunal abundance					**Meiofaunal biomass**					**Nematode ES(51)**					**Nematode ITD**				
Source	df	MS	F	*p*	Source	df	MS	F	*p*	Source	df	MS	F	*p*	Source	df	MS	F	*p*
Covariables	4	91703.53	581.37	**	Covariables	4	338.04	127.92	**	Covariables	4	6.85	0.24	ns	Covariables	4	0.001	3.51	ns
Site	4	9371.54	1.83	ns	Site	4	9.39	2.32	ns	Site	3	25.92	1.31	ns	Site	3	0.003	3.05	*
Residual	6	5110.36			Residual	6	4.03			Residual	4	19.83			Residual	4	0.001		
Total	14				Total	14				Total	11				Total	11			

ES(51), expected species number; ITD, index of trophic diversity; ns, not significant; df, degree of freedom; MS, mean square; F, F statistic; *p*, probability level.* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; [†] covariables considered were phytopigments, BPC, water depth and sediment water content.

Figure 1

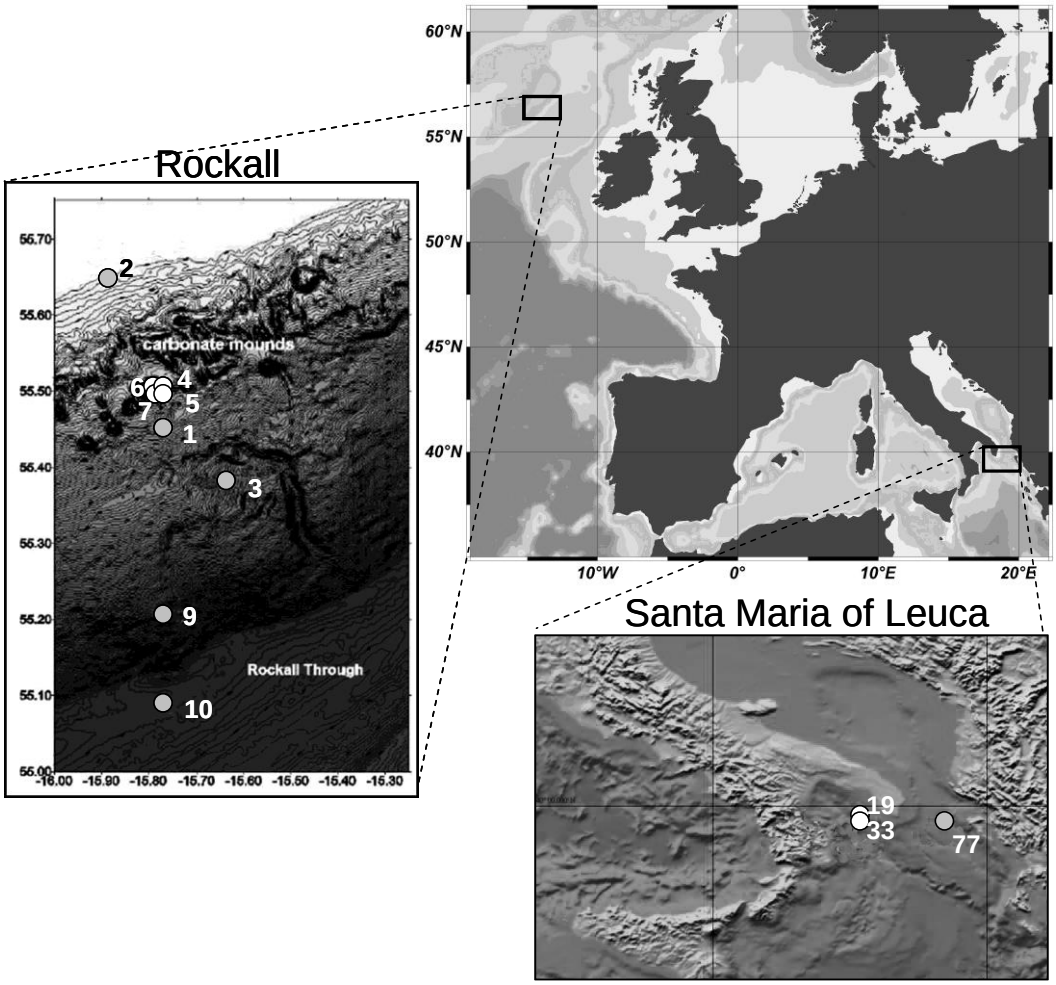
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Figure 2

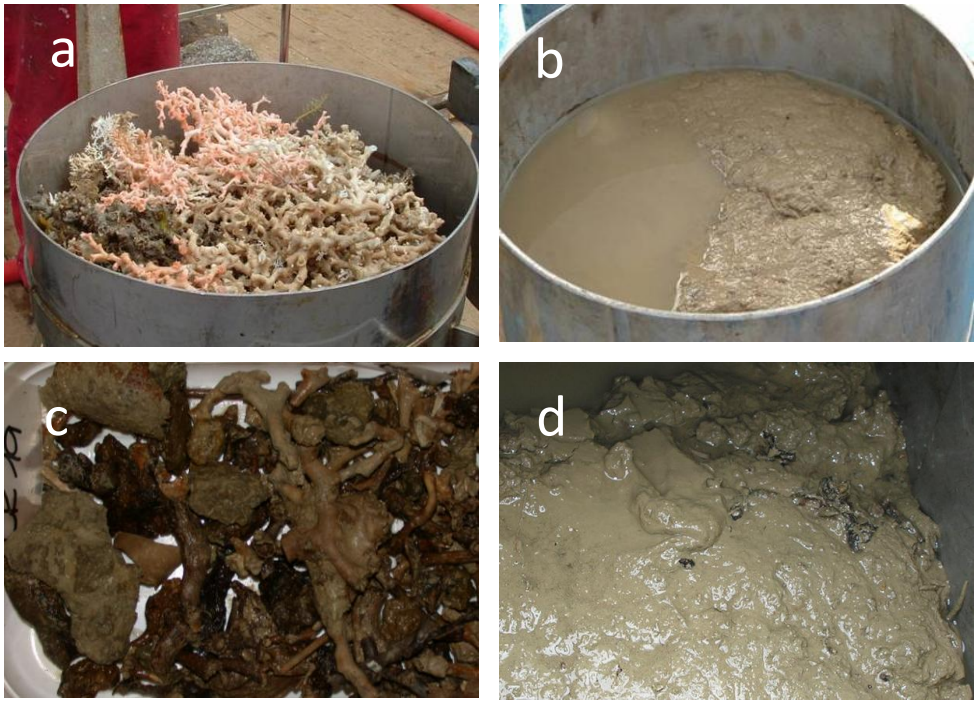
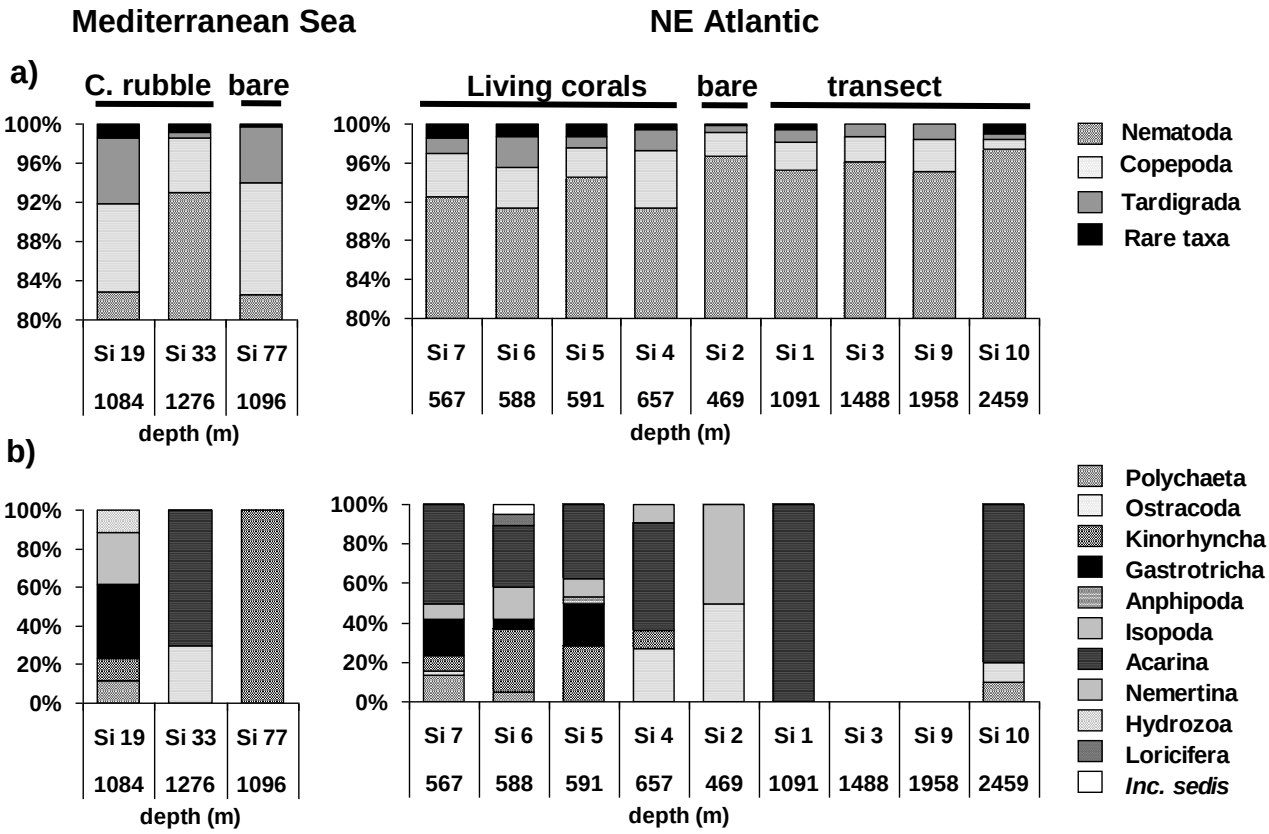


Figure 3


Mediterranean Sea
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a)
C. rubble
bare
Living corals
bare
transect
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96%
92%
88%
84%
80%
Si 19
Si 33
Si 77
1084
1276
1096
depth (m)
Si 7
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Si 5
Si 4
Si 2
Si 1
Si 3
Si 9
Si 10
567
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591
657
469
1091
1488
1958
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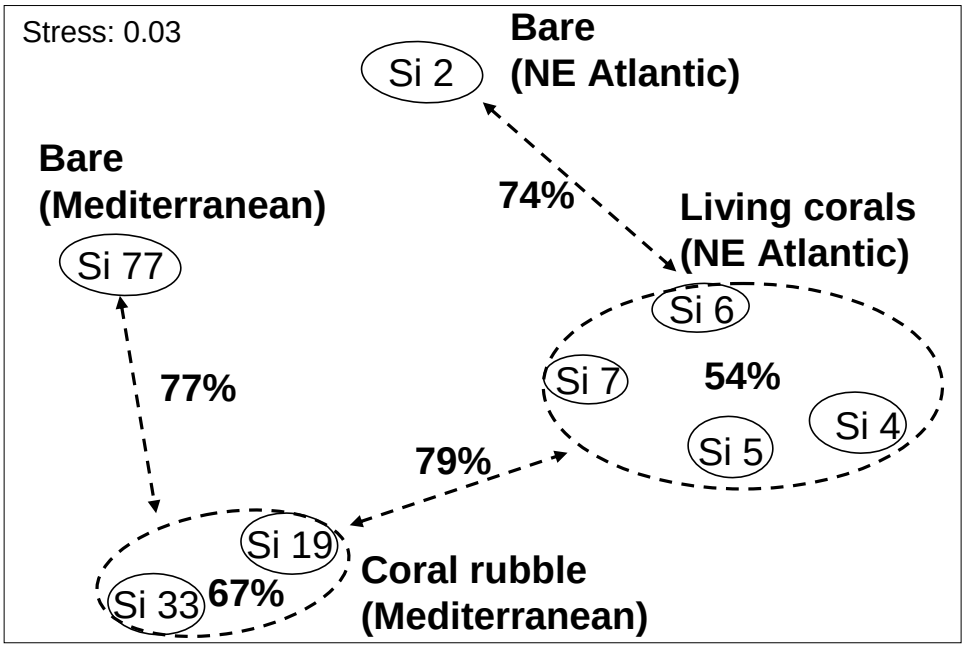
depth (m)
Nematoda
Copepoda
Tardigrada
Rare taxa
b)
100%
80%
60%
40%
20%
0%
Polychaeta
Ostracoda
Kinorhyncha
Gastrotricha
Anphipoda
Isopoda
Acarina
Nemertina
Hydrozoa
Loricifera
Inc. sedis

Figure 4


Stress: 0.03
Si 2
Bare
(NE Atlantic)
74%
Bare
(Mediterranean)
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Living corals
(NE Atlantic)
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Si 19
Si 33
67%
Coral rubble
(Mediterranean)

Figure 5

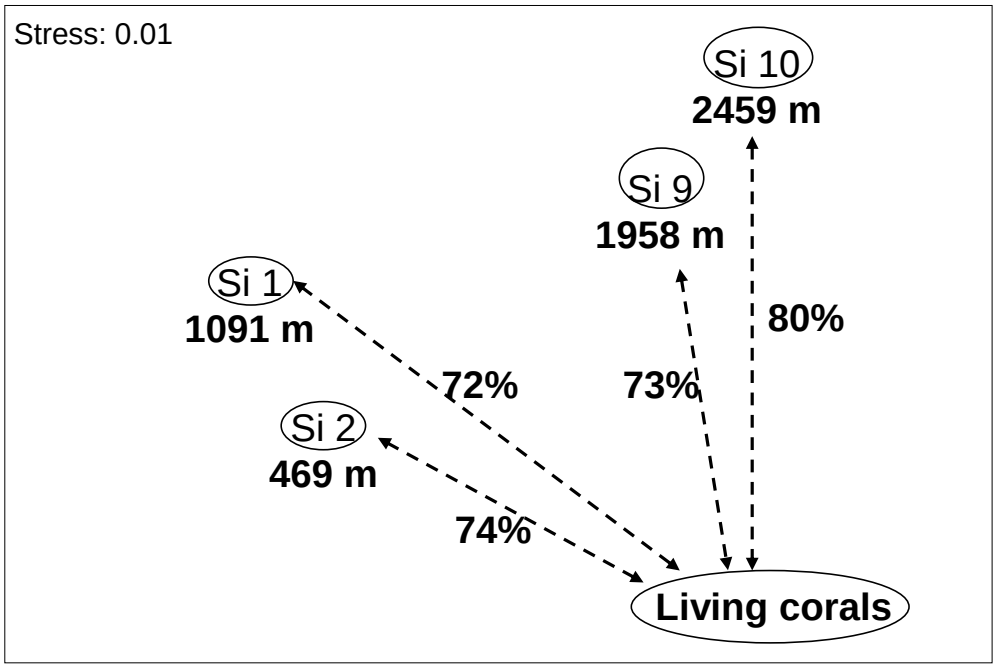
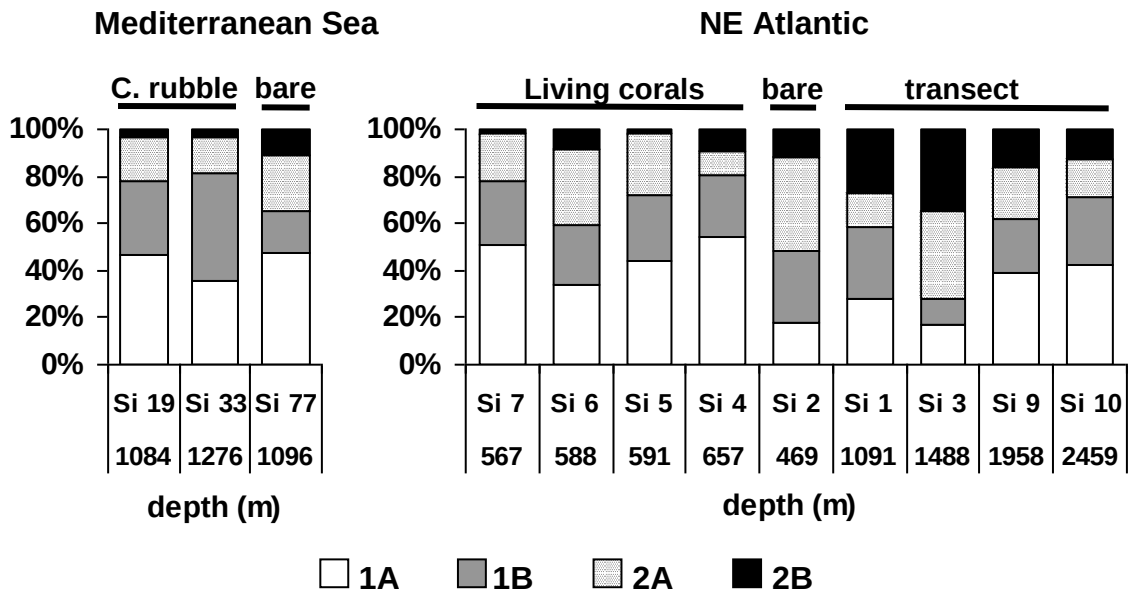

Stress: 0.01
Si 10
2459 m
Si 9
1958 m
Si 1
1091 m
Si 2
469 m
80%
73%
72%
74%
Living corals

Figure 6


Mediterranean Sea
NE Atlantic
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bare
Living corals
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Si 33
Si 77
1084
1276
1096
Si 7
Si 6
Si 5
Si 4
Si 2
Si 1
Si 3
Si 9
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Figure 7

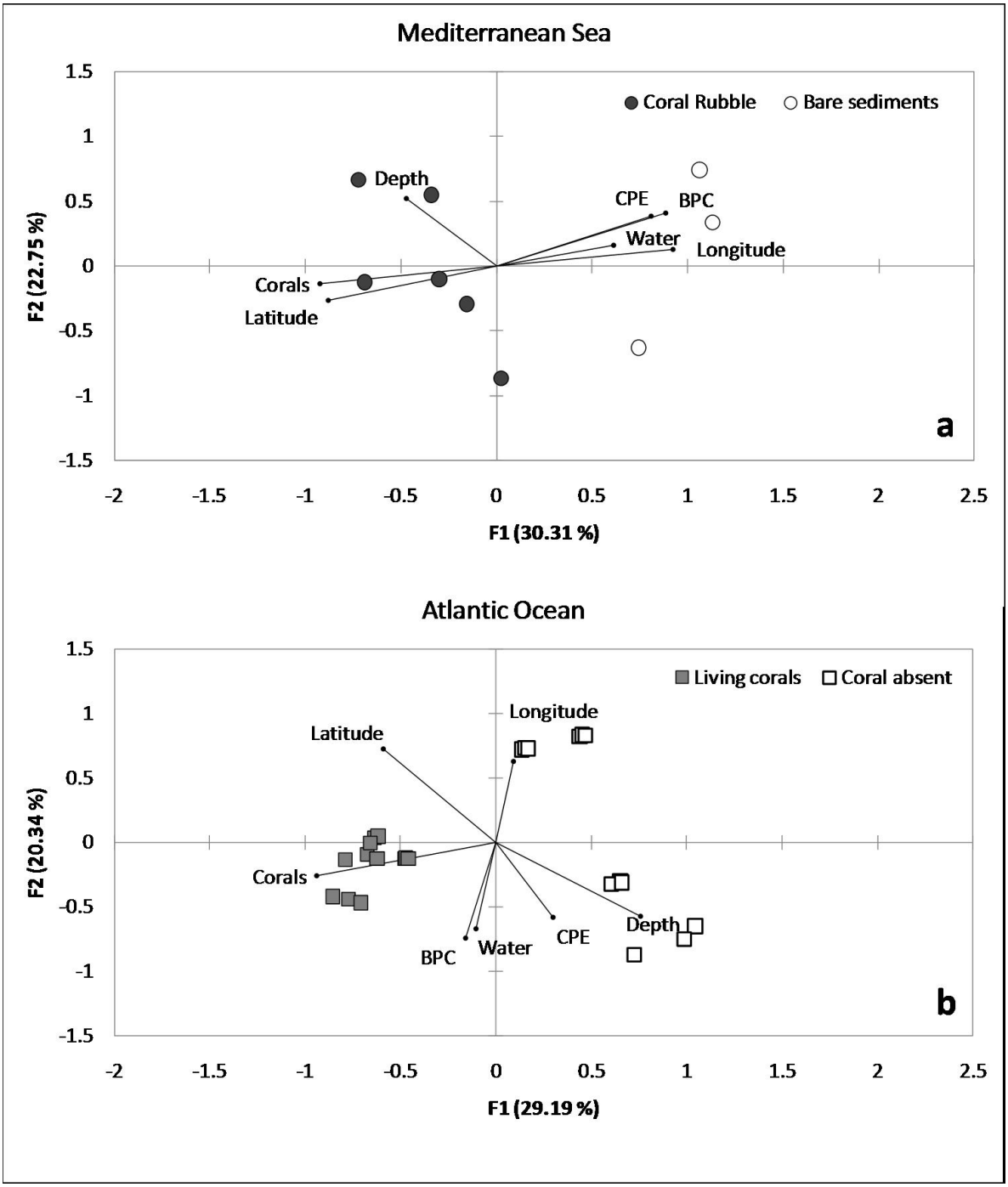
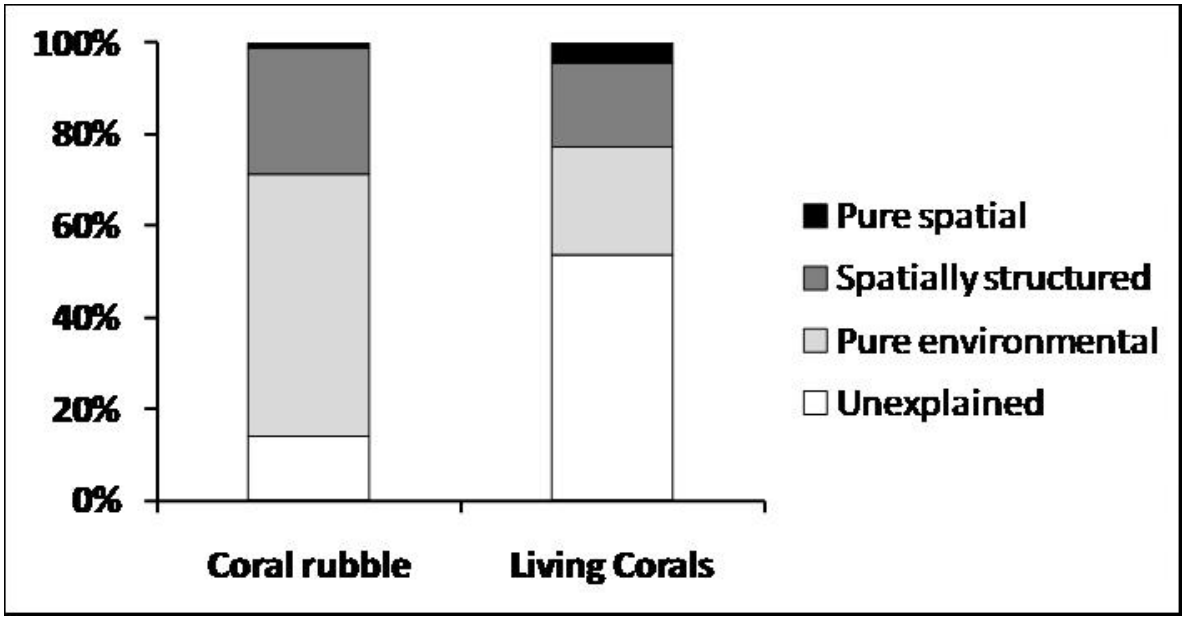

Mediterranean Sea
Coral Rubble
Bare sediments
Depth
CPE
BPC
Water
Longitude
Corals
Latitude
a
F2 (22.75 %)
F1 (30.31 %)
Atlantic Ocean
Living corals
Coral absent
Longitude
Latitude
Corals
Depth
CPE
BPC
Water
b
F2 (20.34 %)
F1 (29.19 %)

Figure 8


100%
80%
60%
40%
20%
0%
Coral rubble
Living Corals
Pure spatial
Spatially structured
Pure environmental
Unexplained