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The contribution of deep-sea macrohabitat heterogeneity to global nematode diversity

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Abstract:

The great variety of geological and hydrological conditions in the deep sea generates many different habitats. Some are only recently explored, although their true extent and geographical coverage are still not fully established. Both continental margins and mid-oceanic seafloors are much more complex ecologically, geologically, chemically and hydrodynamically than originally thought. As a result, fundamental patterns of species distribution first observed and explained in the context of relatively monotonous slopes and abyssal plains must now be re-evaluated in the light of this newly recognized habitat heterogeneity. Based on a global database of nematode genus composition, collected as part of the Census of Marine Life, we show that macrohabitat heterogeneity contributes significantly to total deep-sea nematode diversity on a global scale. Different deep-sea settings harbour specific nematode assemblages. Some of them, like coral rubble zones or nodule areas, are very diverse habitats. Factors such as increased substrate complexity in the case of nodules and corals seem to facilitate the co-existence of a large number of genera with different modes of life, ranging from sediment dwelling to epifaunal. Furthermore, strong biochemical gradients in the case of vents or seeps are responsible for the success of particular genera, which are not prominent in more typical soft sediments. Many nematode deep-sea genera are cosmopolitan, inhabiting a variety of deep-sea habitats and oceans, whereas only 21% of all deep-sea genera recorded are restricted to a single habitat. In addition to habitat heterogeneity, regional differences are important in structuring nematode assemblages. For instance, seeps from different regions yield different genera that thrive on the sulphidic sediments. This study also shows that many areas and habitats remain highly under-sampled, affecting our ability to understand fully the contribution of habitat heterogeneity versus regional differences to global nematode diversity.

Keywords: Biodiversity; census of marine life; deep sea; habitat heterogeneity; meiofauna; nematode genera

Introduction

The deep-sea floor has long been considered to be a relatively homogeneous environment on a large scale, comprising vast areas of soft well-oxygenated surface sediments. Mainly depth-related factors, such as food input, hydrodynamics and occasionally sediment composition, were assumed to be the main drivers of differences in benthic standing stock, biodiversity and community composition of the benthos (Grassle, 1989; Gage & Tyler, 1991). However, as a result of increasing exploration by means of bathymetric and visual mapping of habitats (Wefer *et al,* 2003), there is now a growing awareness of the true extent of habitat heterogeneity and associated biodiversity along continental margins and abyssal plains. Knowledge of the biological communities associated with particular, locally restricted habitats in the deep sea has significantly increased during the last decade, as has the understanding of how other interdependent variables such as substrate availability and type, biogeochemistry, nutrient input, productivity, hydrologic conditions and catastrophic events shape patterns of diversity on regional scales (Levin *et al,* 2001).

The increasing interest in particular deep-sea environments, such as cold seeps, hydrothermal vents, cold water corals, canyons and nodule areas, and the wider accessibility of ROV technology, have facilitated the direct sampling of these different habitats, which was often not possible using traditional remote coring techniques. Such studies have shown that they are occupied by benthic communities that are different from those living in surrounding areas of typical deep-sea floor (Wefer *et al,* 2003). However, the extent to which these special habitats contribute to the overall deep-sea biodiversity has never been investigated, since biodiversity studies focused on particular habitats were often restricted to comparisons between their biodiversity and that of the surrounding background environments on a local or occasionally regional scale (*e.g.* several papers from this volume). No comparisons have been made yet on a larger scale comprising different deep-sea habitats. This mainly reflects the lack of comprehensive databases required to determine if the high turnover between macrohabitats on these smaller scales also holds when data are compiled over ocean-basin or even global scales.

In this study, a large database containing quantitative data on nematode genus composition from different areas and habitats around the world was assembled, allowing a global comparison of nematode biodiversity to be made. This database was made possible through the global initiative, “The Census of Marine Life”, which aims to make a realistic estimation of currently known marine biodiversity by 2010, and to provide a better insight into the factors responsible for changes in biodiversity. Nematode data from several distinct deep-sea habitats, including soft sediments from different water depths, manganese nodules, coral, seamounts, cold seeps, hydrothermal vents, canyons and trenches, were included in this comparative analysis. Nematodes are among the most abundant and diverse benthic metazoan taxa. They are present from shallow water environments to the deep sea, and from oxygenated to anoxic, sulphidic sediments (Heip *et al,* 1985). They show a preference for soft sediment but also colonize hard substrates in close contact with deep-sea sediments, such as nodules and coral rubble. Since nematode data at the species level are scarce, and since the majority of deep-sea nematodes remain undescribed, we investigated patterns at the genus level. It has been shown that nematode community composition at the genus level reflects macro-ecological patterns (Vanreusel *et al,* 2000, Vanaverbeke *et al,* 1997, Fonseca & Soltwedel 2007) and thus provides an appropriate basis for comparisons of communities between habitats on a world-wide scale.

Based on this database of nematode genus assemblages collected within the Census of Marine Life projects CoMARGE and CeDAMar as well as the MarBef European network of Excellence, several hypotheses can be put forward. Inevitably the compilation of various datasets collected for multiple purposes by different researchers includes a high degree of heterogeneity partly generated by differences in temporal and spatial scales of sampling. Furthermore the sampling design is highly unbalanced leading to under-representation of different habitats and regions. Therefore caution is needed in the interpretation of the results taking into account the fragmented nature of the observations. With these restrictions in mind, the following three main testable hypotheses were identified. (1) Habitat heterogeneity contributes significantly to the total deep-sea nematode diversity when integrated over large scales. (2) Different deep-sea habitats harbour specific nematode assemblages. (3) Higher biodiversity is associated with particular deep-sea habitats compared with others.

Materials and methods

Data on nematode density and genus composition were obtained from 542 samples collected from the shelf to the hadal zone. In order to preserve the original composition and biodiversity estimates, data from replicate samples were kept separate and not pooled. Figure 1 shows all geographical areas (some including multiple samples) from which data were collected for this study. Since the focus was on the deep-sea, data obtained from shelf stations (< 200 m) were only included if these were part of a bathymetric transect that covered a significant part of the continental slope. Samples were always collected quantitatively (using different types of corers) and treated with standardized extraction procedures in order to guarantee the most comparable data (Heip *et al,* 1985). Literature datasets that did not provide complete taxonomic lists were not included, since the analyses required full genus counts and densities, including the rare taxa. Detailed sample information is available on request.

Data analysis was performed using the statistical package PRIMER v6.0. nMDS was combined with SIMPER and ANOSIM to identify differences in genus composition between habitats. A Bonferroni correction was applied in the case of multiple pairwise comparisons and a significance level of 5 % was used. Diversity indices were also calculated using the PRIMER v6.0 software. Genus richness was calculated as the total number of genera (Hill’s N_0; Hill , 1973). By analogy with the expected number of species (Hurlbert, 1971), we calculated the expected number of genera for theoretical samples of 51 [EG (51)] and 100 [EG (100)] individuals. In the case of seamount samples, the number of individuals was lower than 50 and no EG (51) was calculated. Samples were classified into 10 different macrohabitats (also referred to as habitats throughout the text) (Table 1) based on the following criteria: substrate composition (homogeneous soft sediment versus presence of manganese nodules or large biogenic substrate such as coral rubble and mussels), water depth, topography (canyon, trench and seamounts) and biochemistry (oxygen, methane and H_2S). Some macrohabitats were assumed to be more common than others, as indicated in Table 1. Also, the degree of connectivity between similar habitats differs as a function of their general distribution. Figure 2 shows some examples of visual habitat heterogeneity in the deep sea. The definition of the shelf, slope, abyssal plain and trench macrohabitats used here is rather arbitrary, being based on water depth and not considering differences in local or regional topography. For instance, the abyssal basins of the Mediterranean Sea are much shallower (3000–4000m) than elsewhere, and the shelf of the Weddell Sea margin extends out to a depth of 500 m. However, all the slopes identified in this paper have soft sediments from the depth zone between 200 and 4100 m, are from topographically regular settings, covered by well-oxygenated bottom waters and lack any indication of nearby flows of reduced chemical compounds. Some macrohabitats are characterized by considerable patchiness and comprise different micro- (or sub-) habitats. For instance, seeps includes both completely anoxic, sulphidic sediments as well as sediments that are well oxygenated at the surface but shows an increase in sulphide concentration below the surface. Similarly, the coral samples includes coral rubble and dead sponges as well as coralligeneous sediments. Temperature is not taken into account as a habitat characteristic, since the deep Mediterranean has much higher bottom temperatures than other oceans.

The number of samples per macrohabitat was unbalanced and ranged from three on seamounts to 355 from regular soft sediments along the slope (Table 2). Furthermore, the coral samples (NE Atlantic), the seamounts (NE Atlantic), the nodules (NE Pacific) and the trench samples (Atacama trench, NE Pacific) were all collected from within single regions, in contrast to samples from the slope, shelf, abyssal plains, seeps, canyons and hydrothermal vents, which covered different geographical regions. The slope sediments were geographically the best represented of all the macrohabitats and distributed in many parts of the World Ocean, although the majority of these samples were collected from the Atlantic including the Mediterranean Sea.

Results

Differences in nematode community composition between habitats

A total of 362 genera was recorded from the 542 samples (Table 2). The majority of these genera (about 90 %) were previously recorded from soft-bottomed, regular slope habitats, indicating that the additional habitat heterogeneity is only responsible for 10 % of the total genus pool recorded from deep-sea environments. The proportion of genera restricted to a single habitat within the total number of genera found in that habitat was highest in regular soft slope sediments (15%), followed by the nodule area (10%), the abyssal plains (8%), and the hydrothermal vents (6%). In the remaining habitats the proportion of genera restricted to the habitat was less than 2 %. Many of the dominant genera from soft-slope sediments were also represented in the other habitats, although in different proportions (Fig 3; Table 3). The highly abundant genera *Acantholaimus, Halalaimus, Thalassomonhystera*, but also *Desmodora, Desmoscolex* and *Theristus,* are the main ones showing wide distributions that include most of the investigated habitats.

Multivariate analysis, on the other hand, suggested that different deep-sea habitats harboured significantly different nematode communities (Fig. 4) (ANOSIM: R = 0.39; p < 0.01). According to the MDS ordination based on nematode genus composition (%), samples collected at seeps, hydrothermal vents, coral rubble, seamounts and nodule areas differed in genus composition from the majority of soft sediment samples collected on the shelf, slope and abyssal plains (Fig. 4). Within these three regular soft sediment habitats, shelf samples plotted mainly on one side of the central cluster of slope samples whereas the abyssal plains were grouped on the opposite side. Canyon and trench samples overlapped to a large extent with the slope samples. Nodule samples were clustered adjacent to the abyssal samples. The coral samples, as well as the seep, hydrothermal and seamount samples, were generally more separated from the central slope cluster, although samples from these specific habitats occasionally overlapped with slope samples in the MDS ordination. The pairwise comparison with Bonferroni correction (p< 0.05) showed that seeps (R = 0.367), hydrothermal vents (R = 0.759), corals (R = 0.336) and seamounts (R = 0.913) differed significantly in genus composition from the slope samples. Shelf communities also differed significantly from the slope communities (R = 0.426), whereas the communities from abyssal plains (R = -0.044), canyons (R = 0.095), nodules (R = 0.136) and trench samples (R = 0.197) were not significantly different from slope samples. All habitats also significantly differed from the abyssal plains (R > 0.377) except for the trench (R = 0.316) and slope samples (R = -0.044).

The average relative abundances of the dominant genera responsible for the similarity within each macrohabitat, as identified by a SIMPER analysis, are shown in Figure 5. This list of genera (also shown in Table 3) overlapped largely with the main genera responsible for the dissimilarity between each of the habitats and the slope. In general, slopes were characterized by several dominant genera (e.g. *Thalassomonhystera*, *Acantholaimus*, *Halalaimus*, *Daptonema* and *Sabatieria*) that occurred in similar proportions. The genus *Sabatieria,* however, declined in abundance below 2000 m and was absent from the abyssal plains and trenches. From this analysis it was also clear that the average communities at abyssal plain, canyon and trench sites shared several dominant genera with the slope communities. The other habitats were more distinct both in the composition of the dominant genera as well as in their diversity in terms of evenness. The highest dissimilarity with slope communities was found in the seamount samples, which were characterized by high abundances of the genera *Desmodora*, *Richtersia*, *Ceramonema* and *Desmoscolex,* and a low diversity. In contrast to the slope samples, *Thalassomonhystera*, *Sabatieria*, *Acantholaimus* and *Daptonema* were uncommon. However, the seamount assemblages were not representative of general patterns because of the low number of samples (3) and the restricted geographical coverage. The same was true for the trench habitat, which was represented only by 3 samples from the Atacama Trench.

Shelf and slope samples also differed in terms of the proportions of taxa; *Thalassomonhystera*, *Acantholaimus* and *Halalaimus* were abundant along the slope but found only occasionally on the shelf. *Sabatieria* was a dominant genus on the shelf and slope but, on average, less abundant along the slope compared with the shelf. Vent samples differed from slope samples in the increased dominance of the Monhysteridae (*Thalassomonhystera and Halomonhystera*), and the greater abundance of *Anticoma* and *Desmodora*, two genera that were rather rare on the slope. Seep samples differed from slope samples in the high dominance of *Halomonhystera* and *Sabatieria;* other typical slope genera, such as *Acantholaimus*, *Thalassomonhystera* and *Halalaimus*, were still present but reduced in abundance. Corals also showed a much reduced abundance of *Thalassomonhystera* and *Sabatieria* compared with soft sediments from similar depths, but were characterized by genera such as *Desmoscolex* and *Epsilonema*. However, the genera *Acantholaimus* and *Halalaimus* were still common. Some typical genera, such as *Theristus* and *Marisalbinema,* appeared in the nodule samples but were either not abundant or absent on slopes and in other abyssal samples.

Genus diversity per habitat

Sample diversity, expressed as the rarefaction index EG (51) (expected number of genera for 51 individuals), ranged from 1 to 33 over all habitats (Fig. 6). The highest values were recorded in the slope, shelf, nodule field and coral samples. However, whereas values from the shelf, and particularly from the slope, showed considerable variation, the coral and nodules estimates were always high (> 15). Generic diversity was always low in the samples from the hydrothermal vents. The seeps exhibited a range of diversity values from very low to medium. This variation reflected the high degree of small-scale heterogeneity (patchiness) within seeps, which encompass (micro-) habitats ranging from highly-sulphidic sediments with low nematode diversity to well-oxygenated surface sediments (*e.g.* in Siboglinidae tube worm fields) only influenced by seepage in deeper sediment layers and therefore characterized by higher nematode diversity. On average, diversity was lowest in the hydrothermal and seep samples.

Figure 7 shows the total diversity of pooled samples, combining each habitat respectively with the slope in order to illustrate the extent to which the different habitats contributed to overall slope diversity. Since the number of genera will depend on the number of samples analysed within a habitat, diversity is also expressed as EG(100) (Fig 7a & b). The abyssal plain and nodule habitats contributed particularly to the increased total genus richness of the slope (Fig. 7a). Except for the under-sampled seamounts and trenches, all other habitats added to the total genus pool but to a lesser extent (see also Table 2). In terms of expected number of genera (Fig 7b), the contribution of the abyssal plains and nodule areas became less pronounced due to the higher abundances of dominant taxa found in both these habitats. EG(100) values suggest that, except for the shelf samples, the coral habitat was mainly responsible for the increased diversity, as a result of greater evenness combined with the high number of genera present.

Discussion

Methodological problems

Several studies have addressed the importance of habitat heterogeneity at local or regional scales but no previous attempt has been made to determine whether the high turnover between macrohabitats on these smaller scales also holds for larger scales. However, investigating ecological patterns on larger scales requires the compilation of large databases, thereby increasing the heterogeneity of the data involved. The interpretation of the analyses is therefore not without risk (Soetaert & Heip 1995). Data compiled for this study were obtained using a number of different sampling gears, from small box corers (e.g. Muthumbi *et al,* 2004) to larger box-corers (e.g. Netto *et al,* 2005), multiple corers (e.g. Fonseca & Soltwedel 2007), ROV push cores (Van Gaever *et al,* this volume) or even mussel pots (Flint *et al,* 2006), for which sampling efficiency is known to vary especially for the surface sediment layers (Bett *et al,* 1994). Differences in sample processing (sieve size and extraction procedures), and the inherent small-scale and temporal variability, may have added some uncertainties to the comparison. Identification problems can occur since several genera are differentiated by relatively small differences, possibly subject to personal interpretation. However, potential misidentifications of dominant genera were carefully checked by the different data-providers. As already indicated, the main limitation of the dataset is the unbalanced design in terms of sampling intensity within different habitats and regions. The slope is clearly over-represented compared with all other habitats both in terms of number of samples and geographical coverage. For these reasons, all comparisons between macrohabitats were focussed on the slope; in other words we investigated the extent to which macrohabitats differed in composition and diversity from those of typical slope sediments.

In general the patterns observed in our analyses were robust across the data set and the different habitats were represented by a multitude of characteristic genera. We are confident, therefore, that the approach used in this study is the only way to overcome the problems involved in conducting extensive sampling campaigns in order to detect large-scale patterns in deep-sea nematode communities.

Importance of habitat heterogeneity for deep-sea nematode biodiversity at different spatial scales

At the local scale (diversity per individual sample: Fig 6), nematode diversity varied significantly within and between habitats. In some habitats, the coexistence of genera was always relatively high, especially in corals and nodules areas, two habitats characterized by an increased substrate complexity owing to the presence of coral rubble, sponge skeletons or manganese nodules on top of the soft sediments. These observations suggest that increased substrate heterogeneity plays an important role in structuring local nematode diversity and are in accordance with the small-scale habitat heterogeneity hypothesis (Bazzaz, 1975). This hypothesis, proposed for terrestrial systems, assumes that structurally complex habitats provide more diverse ways for exploiting environmental resources, thereby increasing diversity.

In contrast, the coexistence of genera was occasionally very low in reduced habitats (e.g. seeps and hydrothermal vents), although some seep samples also showed high diversity. In reduced environments, harsh biochemical conditions led to reduced diversity, despite the high food availability. Some opportunistic genera take advantage of the increased organic load associated with seeps or vents and dominate these communities, while the more common deep-sea genera disappear. The high variability in diversity estimates within the seep habitat was due to differences in surface biochemical conditions between different seep microhabitats. Soft sediments along the slope also showed high variability in local diversity from very genus rich (33) to extremely poor (< 5). The low values were often associated with oligotrophic areas with low densities, such as part of the Brazilian margin.

At the large scale, i.e. considering all samples from a given habitat as one (Fig 7), it was the abyssal habitats which increased the genus richness the most when combined with the slope, contradicting the source sink hypothesis that the abyss only acts as a sink for typical bathyal species (Rex *et al*, 2005). This is in accordance with previous observations for abyssal copepods (Bagulay *et al,* 2006). Corals increased the total slope diversity through increased evenness, whereas the nodules, an exclusively abyssal habitat, also increased total abyssal diversity. These results suggest that habitat heterogeneity plays an important role in maintaining the regional diversity of deep-sea environments by preserving taxa that are usually rare in soft sediments.

Habitat specific nematode assemblages

The most striking result emerging from the combination of all these independent datasets was that several nematode genera are cosmopolitan, inhabiting a variety of deep-sea habitats and oceans, while only a few genera are restricted to a single habitat. In fact, only a minority of genera (about 21% of the total genera) seem to be restricted to one particular habitat. Most of these were encountered in soft slope sediments, which may be partly explained by the higher number of samples collected in these settings (65% of all samples). All other habitats combined only contributed 10% of the genus richness. Most of these habitat-restricted genera were uncommon, suggesting that their absence from other habitats may also reflect (1) under-sampling, (2) misidentifications or (3) random colonisation of the specific habitat. Most genera have the potential to colonize a variety of deep-sea substrates, although some that are dominant in one habitat are not found in others (*e.g. Sabatieria* is not found in the abyss) or become rather rare *(Acantholaimus* and *Halalaimus* in vents). The eurytopic, cosmopolitan character of most genera does not necessarily apply to species since the few studies done at species level have shown that, while there may be some widespread nematode species, many are restricted in their distribution (Vermeeren *et al,* 2004, Ingels *et al,* 2006; Fonseca & Soltwedel 2007, Fonseca *et al,* 2007).

This analysis demonstrates that each habitat hosts certain nematode genera that are usually rare in 'typical' bathyal and abyssal sediments. This is mainly because such habitats have completely different sedimentary and biochemical characteristics compared to the adjacent sediments. For instance, the 3-dimensional structure of deep-sea corals enhances the abundance of non-burrowing, interstitital or epifaunal forms such as epsilonematids, while the gravel sediments of the seamounts favours nematodes with coarsely ornamented cuticle, such as *Ceramonema, Richtersia* and *Desmodora*. Habitats rich in sulphide and hydrothermal vents had higher abundances of *Terschellingia, Sabatieria* and *Halomonhystera,* genera that are better known from organically-enriched, shallow-water environments than from other deep-sea habitats.

Corals The nematode communities associated with cold-water coral habitats included in this analysis were previously described by Raes & Vanreusel (2006) and Raes *et al,* (2008) from the Belgica Mound region of the Porcupine Seabight (NE Atlantic), at a depth of approximately 1000m. Here, a series of seabed mounds occurs that support cold-water coral banks and their degradation zones; these zones originate from the progressive degradation of dead coral thickets until only small-sized coral debris remains. Samples were collected in sediment-clogged coral framework (Freiwald *et al,* 2002), a three-dimensionally complex habitat composed of (1) dead *Lophelia pertusa* (Linnaeus, 1758) thickets, (2) glass sponges of the species *Aphrocallistes bocagei* (Scultze, 1886) and their skeletons, and (3) sediment**.** It seems that the 3-dimensional micro-structure of deep-sea coral fragments and sponges enhances the abundance of epifaunal nematodes, such as members of the Epsilonematide and Draconematidae (for details see Raes & Vanreusel 2006 and Raes *et al,* 2008), which are unusual for ocean margins (Decraemer *et al,* 2001). Coral fragments and sponges are relatively unprotected on the ocean margin seabed and their associated fauna is therefore subject to stronger current activity, typical of areas with *Lophelia* reefs (White, 2007). Taxa that are specially adapted to crawl on larger surfaces and to withstand this physical stress may have a competitive advantage in such habitats. Epsilonematidae and Draconematidae are characterised by the presence of unique locomotory structures. Most Epsilonematidae have ambulatory setae on the ventral side of their posterior body and Draconematidae have both cephalic and posterior adhesion tubes (Gourbault & Decraemer, 1996; Decraemer *et al*, 1997). Together with the caudal glands, these structures enable the nematodes to attach themselves to a large substratum and/or crawl over its surface in a fashion that is similar to that of a geometrid caterpillar (Stauffer, 1924; Lorenzen, 1973). A comparable mode of locomotion was observed in *Desmoscolex* (Stauffer, 1924), another dominant genus on coral fragments and sponge skeletons.

Seamounts Interestingly, higher abundances of *Desmoscolex*, together with *Desmodora*, *Richtersia* and *Ceramonema,* were also observed on the seamounts included in this analysis (Great Meteor and Sedlo seamounts). In addition, members of the Epsilonematidae and Draconematidae were found here although in low abundances. The Great Meteor Seamount is characterized by coarse biogenic sediments composed of corals and mollusc shells, and by strong current activity (Gad 2004; Gad & Schminke 2004). These environmental conditions could be comparable to those in cold-water coral degradation zones as described above. Indeed, Gad (2004) stated that the nearest congeners of some Epsilonematidae species on the Great Meteor Seamount are found in cold-water coral habitats along the North-Atlantic continental margin. In addition to their distinct locomotory behaviour, the stout body shape together with the thick cuticle are additional morphological features that may bestow advantages for survival in such physically harsh environments. This comparison suggests that the intricate physical micro-structure of the substrate may be one of the most important factors structuring nematode assemblages. Unfortunately, little detailed information is available on the biology of the genera *Desmodora*, *Richtersia* and *Ceramonema* on the deep-sea floor.

Nodules Polymetallic nodule deposits on the abyssal seafloor also represent a unique habitat type in which nematode assemblages inhabit both the hard nodule substratum (Mullineaux, 1987; Veillette *et al,* 2007a, b), including the sediment accumulated in crevices on the nodule surface (Thiel *et al,* 1993), and the soft sediment that underly the nodules and in which the nodules are partly submerged. Data from two nodule areas in the Clarion-Clipperton Fracture Zone (CCFZ) were analysed: the eastern area (CCFZ-E) (Radziejewska, 2002) at depths of about 4300-4400 m and the central area (CCFZ-C) at depths of about 4950-5050 m (Miljutina unpublished). In both areas, samples were collected, using a multiple corer, from nodule-bearing and nodule-free patches. In the eastern area (CCFZ-E), *Desmoscolex* and *Pareudesmoscolex* were among the dominant groups, suggesting again that the presence of hard substrate favours genera with distinct locomotory behaviour. However, in the central area (CCFZ-C), the dominant genera were thread-like interstitial forms such as the Monhysteridae, *Acantholaimus*, and *Theristus*, These genera were also common in soft sediments from around the World Ocean. Nevertheless, the analysis showed that 22 genera were unique for the nodulised seafloor; furthermore none of these genera was common to the two CCFZ areas. The differences between these two areas were further accentuated by different dominant genera. In particular, *Marisalbinema* was one of the characteristic and dominant genera in the CCFZ-C. Also remarkable was the fact that the composition of the nematode fauna in the CCFZ-E differed significantly from all the other deep-sea samples included in this analysis. Owing to the dominance of *Terschellingia,* these samples showed the highest similarity with seep habitats (Nordic margin) and shelf samples. This observation suggests that the CCFZ-E environment is controlled by some factor(s) in addition to the presence of nodules and may not represent a typical nodule area. Therefore the CCFZ-E samples were not included in the MDS analysis. It is possible that the distinctly different nature of the CCFZ-E nematode fauna (low abundance of abyssal genera such as *Acantholaimus* and *Thalassomonhystera* and the high abundance of genera such as *Terschellingia*) is related to hydrothermal venting, the signature of which, in the form of elevated metal contents in the water column, has been reported from the area (Tkatchenko *et al*, 1997). *Terschellingia* dominates cold seep communities on the Nordic margin) (Van Gaever *et al*, 2009) and is also reported to be abundant in sulphidic, shallow-water habitats (Heip *et al*, 1985; Vranken *et al*, 1988). Apparently, nematode of this genus are tolerant of harsh biochemical conditions that are often lethal to other meiofaunal organisms. In addition, nematode assemblages in the CCFZ-E area showed a distinct temporal shift in the suite of dominants, from *Terschellingia* in samples from the first (1995) campaign to Desmoscolecidae in the subsequent (1997) sampling programme. This was probably a response to a phytodetritus sedimentation event, the signature of which was detected in the sediment (Radziejewska, 2002).

Seeps and hydrothermal vents Relatively high abundances of certain nematode genera was occasionally observed at hydrothermal vents and more commonly at seeps. In particular, the Nordic cold seep was characterized by higher densities of *Halomonhystera* (Van Gaever *et al*, 2006) as well as by *Terschellingia,* although at lower densities (Van Gaever *et al*, 2009). The cold seep in the Gulf of Guinea was characterized by the dominance of *Sabatieria* (Van Gaever *et al*, in press). High densities of *Thalassomonhyster*a, *Halomonhystera* and *Anticoma* were particularly characteristic of hydrothermal vents. *Thalassomonhystera* is a typical soft bottom deep-sea genus, but the other genera are mostly rare in deep-sea sediments and are known to attain high abundance and dominance in shallow waters (Heip *et al* 1985). In particular, *Sabatieria* occurs at higher abundances along the shelf and upper slope but gradually disappears almost completely in well-oxygenated soft sediments below 2000 m, corresponding with a decreasing flux of organic matter (Soetaert & Heip 1995; Vanaverbeke *et al*, 1997). There are different possible explanations for their presence in the reduced conditions of a seep environment; for example, their relatively larger body size may be an advantage for tolerating low oxygen availability (Jensen, 1987). As already observed for other marine nematode genera (Ott *et al*, 2004), symbioses with sulphur-oxidizing chemoautotrophic bacteria are another adaptation for survival in seeps and hydrothermal vents. However, there is presently little evidence of symbiosis in deep-sea nematodes associated with reduced environments.

Some seep microhabitats, in particular the well-oxygenated sediment underneath siboglinid tubeworm patches, are inhabited by a genus-rich nematode assemblage composed of genera similar to those of the slope sediments. Here, genera such as *Acantholaimus, Halalaimus* and *Thalassomonhystera* are present in high numbers. Cold seeps therefore harbor a wide variety of nematode assemblages.

Canyons These large-scale geomorphological features disrupt the monotony of the seafloor and create another source of spatial heterogeneity in the deep sea.. Canyon samples included in this analysis covered the Western Iberian Margin (Nazaré Canyon) (Ingels *et al*, 2009), the Mediterranean Sea (Samaria Canyon) (Lampadariou, unpubl) and the West-African coast (Zaire Canyon) (Van Gaever *et al*, in press). Canyons are normally characterized by an extraordinary topographic and hydrodynamic complexity, which is peculiar to each site and time scale (de Stigter *et al*, 2007). Highly active axes and the relatively undisturbed areas, such as the terraces beside the active channels, result in very contrasting environmental conditions (see also Ingels *et al*, 2009). We might expect that nematode assemblages would respond to the conditions prevailing in each sub-habitat and hence exhibit considerable variability. From the present study, it was indeed clear that heterogeneity in canyons is high, as illustrated by the low similarity value of 27.9 %, reflecting their extreme environmental complexity that drives variability on various spatial and temporal scales (Canals *et al*, 2006; de Stigter *et al*, 2007). In particular, the highly active canyon axes and the more undisturbed terraces yield nematode communities that are very different in terms of their abundance, composition and diversity (Ingels *et al*, 2009; Garcia et al, 2007). This is consistent with the ANOSIM tests indicating that canyon assemblages differed significantly from those of the other habitats, except for the slope. Although there was a strong overlap between canyons and slope communities, nematode assemblages in canyons were characterised by a larger number of dominant genera such as *Daptonema* (4.5%), *Paralongicyatholaimus* (4.3%), *Pomponema* (3.5%), *Dichromadora* (3.5%), *Elzalia* (3.3%), *Halalaimus* (3.1%) and *Acantholaimus* (3.0%). This probably reflects the generally harsh canyon conditions, which lead to an increase in dominance and lower evenness. In contrast to sediments from coral rubbles, sponges, seamounts and nodules areas, the sedimentary properties in canyons are more similar to those of soft, regular sediments.

Trenches Only data from the Atacama Trench (Gambi *et al*, 2003) were used in this analysis. This is an atypical hadal system, characterized by close proximity to the continent (ca 80 km) and a location directly beneath one of the largest upwelling regions (Peru-Chile upwelling system). This specific geographic setting imparts the characteristics of a eutrophic system, with extremely high concentrations of nutritionally-rich organic matter (i.e. chlorophyll-a and proteins; Danovaro *et al*, 2002, 2003)**.** It is therefore too early to attempt to establish a general pattern for nematodes in trenches. For example, nematode assemblage composition (not included here) has been analysed from only two other hadal systems (the Puerto Rico and the South Sandwich trenches). While genus richness decreased significantly from the slope to hadal depths in all three trenches (Tietjen 1989; Gambi *et al*, 2003; Vanhove *et al*, 2004), genus composition varied significantly and each system was characterized by different dominant genera (Gambi *et al*, 2003). Studies carried out in the Venezuela Basin and Puerto Rico Trench suggest that the decrease in nematode biodiversity at hadal depths reflected, in addition to the reduced food availability, lower heterogeneity in sediment texture (Tietjen, 1984; 1989). The more heterogeneous substrates at bathyal depths could be responsible for a higher number of microhabitats and hence an increase of nematode diversity (Tietjen 1984). The role of microhabitat heterogeneity is potentially important also in the Atacama Trench, where the rather homogeneous sediments at hadal depths hosted approximately 40% fewer genera than at bathyal sites, where sediments were more heterogeneous (Gambi *et al,* 2003). The inaccessibility of hadal sediments makes fine-scale spatial studies, and a detailed analysis of microhabitat heterogeneity, difficult. Further studies are needed to clarify the influence of habitat heterogeneity on nematode biodiversity at hadal depths.

Abyssal In comparison to the slope environment, the vast abyss also represents a peculiar habitat for the fauna (Rex *et al,* 2005; Smith *et al,* 2008). The abyss mainly differs from the other habitats considered here in having low current velocity, sediments consisting mainly of fine sand and clay, and habitat heterogeneity created by biogenic structures, such as the tests of giant protozoans and the burrows, mounds and tracks of megabenthos (for review see Smith *et al*, 2008). The abyss is normally characterized by a distinct macro- and mega-faunal community structure (Rex *et al*, 2005, Brandt *et al,* 2007, Smith *et al,* 2008). For nematodes, this is only partly true since the ANOSIM did not show that the abyssal assemblages differed significantly from slope assemblages. However, the abyssal samples contained several (16) additional genera not yet recorded from the slope. Nematode assemblages in this habitat are dominated by deposit-feeding genera. In most of the abyssal areas studied (Arctic Ocean, North Atlantic, Northeast tropical Atlantic, Southeast tropical Atlantic, Southern Atlantic, Northeast tropical Pacific), the dominant taxa are the Monhysteridae (including *Thalassomonhystera, Monhystrella*), *Halalaimus* and *Acantholaimus.* Apart from the unvarying dominance of Monhysterids, the identity of sub-dominant abyssal nematode taxa seems to be related to the surface primary production. It has already been observed that higher fluxes of particulate-organic carbon promote changes in polychaetes and nematode assemblages in the equatorial Pacific (Smith *et al,* 1997, Lambshead *et al,* 2002). However, primary productivity is not the sole factor since we also observed that areas characterized by similar primary production levels (Northeast tropical Atlantic and Northwest tropical Atlantic) showed different sets of dominant and subdominant nematode genera. In this case, other environmental factors may be involved.

Conclusions

It is apparent from this study that habitat heterogeneity in the deep sea is important for global nematode diversity. However, the question of the extent to which habitat heterogeneity contributes to global diversity has no single answer. It was confirmed by this analysis that many deep-sea nematode genera are cosmopolitan, inhabiting a variety of deep-sea habitats and oceans, while only 21 % of all deep-sea genera recorded are restricted to a single habitat. Furthermore the genera restricted to one habitat are never dominant or generally present in all samples within a habitat, suggesting that their presence or absence may be random rather than a selective colonization of particular habitats. On the other hand different habitats, such as cold seeps, hydrothermal vents, cold water corals and nodule areas, do show typical nematode assemblages with dominant genera that are rare in other habitats.

Factors such as increased substrate complexity in the case of nodules and corals, or strong biochemical gradients in the case of vents or seeps, seem to be responsible for the success of particular genera, which are not prominent in ‘normal’ soft sediments. Furthermore, clear shifts in the relative proportions of the dominant genera were observed between soft-sediment habitats from the shelf to hadal depths. In this case we can conclude that different deep-sea habitats harbour specific nematode assemblages, but that few genera are restricted to one habitat. The soft sediments of the slope are responsible for more than 60 % of all the habitat-restricted genera. However, it must be born in mind that many other habitats, including nodule areas, corals, seamounts, canyons and trenches, remain under-sampled. In terms of local diversity, the nodule areas and coral rubble samples emerge as habitats where most genera co-exist in equal proportions. In both cases, the added complexity of the substrate facilitates the occurrence of sediment-dwelling as well as epifaunal taxa in the same environment.

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Fig. 1. World map showing location of the sampling areas classified according to macrohabitat

Fig. 2. Overview of deep-sea habitat diversity. (A) soft sediment in the Nazaré Canyon; (B) cold-water corals; (C) *Beggiatoa* mats at the Håkon Mosby Mud Volcano (© Ifremer Vicking 2006); (D) pingo colonised by siboglinid tube worms at Nyegga (© If remer Vicking 2006); (E,F) manganese nodule areas (E and F; © Ifremer Nodinaut 2004).

Fig 3 Average relative abundances of genera present in more than 8 macrohabitats and dominant (>5 %) in at least one of the habitats

Fig. 4. MDS ordination of 542 samples based on nematode genus percentage abundance using the Bray Curtis similarity index, with symbols indicating the designated macrohabitats

Fig. 5. Average relative abundances (%) of the main genera responsible for the similarity within a habitat and the dissimalirity between each habitat and the slope, as identified by SIMPER analysis. HV = hydrothermal vents.

Fig 6: Expected number of genera (EG(51)) per sample (black dots). Averages and standard deviations shown by the vertical bars with error bars (for number of samples per macrohabitat see Table 2)

Fig. 7 (A): Total genus diversity. (B): Expected number of genera (EG(100)) of the slope habitat and the slope combined with each of the other macrohabitats. All samples per macrohabitat are pooled.

References

Baguley J.G., Montagna P.A., Lee W., Hyde L.J., Rowe G.T. (2006) Spatial and bathymetric trends in Harpacticoida (Copepoda) community structure in the northern Gulf of Mexico deep sea. *Journal of Experimental Marine Biology and Ecology* **330**, 327-341.

Bazzaz F.A. (1975) Plant Species Diversity in Old-Field Successional Ecosystems in Southern Illinois *Ecology*, **56**, 485-488

Bett B.J., Vanreusel A., Vincx M., Soltwedel T., Pfannkuche O., Lambshead P.J.D., Gooday A.J., Ferrero T., Dinet A. (1994) Sampler bias in the quantitative study of deep-sea meiobenthos. *Marine Ecology Progress Series*, **104**, 197–203.

Brandt A., Gooday A.J., Brandão S.N., Brix S, Brökeland W, Cedhagen T, Choudhury M., Cornelius N., Danis B., De Mesel I., Diaz R. J., Gillan D.C., Ebbe B., Howe J.A., Janussen D., Kaiser S., Linse K., Malyutina1 M., Pawlowski J., Raupach M. & Vanreusel A. (2007). First insights into the biodiversity and biogeography of the Southern Ocean deep sea. Nature 447, 307-311

Canals, M., Puig, P., de Madron, X.D., Heussner, S., Palanques, A., Fabres, J., 2006. Flushing submarine canyons. Nature 444, 354-357.

Danovaro R., Gambi C., Della Croce N. (2002) Meiofauna hotspot in the Atacama Trench (Southern Pacific Ocean). Deep-Sea Research I, 49, 843–857.

Danovaro R., Della Croce N., Dell'Anno A., Pusceddu A. (2003) A depocenter of organic matter at 7800 m depth in the SE Pacific Ocean. Deep-Sea Research I, 50, 1411–1420.

Decraemer W., Gourbault N., Backeljau T. (1997) Marine nematodes of the family Draconematidae (Nemata): a synthesis with phylogenetic relationships. Hydrobiologia, 357, 185–202.

Decraemer, W., Gourbault, N. & Helléouet, M.-N. (2001) Cosmopolitanism among nematodes: examples from Epsilonematidae. *Vie et Milieu*, **51**, 11–19.

de Stigter, H.C., Boer, W., Mendes, P., Jesus, C.C., Thomsen, L., van den Bergh, G.D., van Weering, T.C.E., 2007. Recent sediment transport and deposition in the Nazare Canyon, Portuguese continental margin. *Marine Geology* **246** (2-4), 144-164.

Flint H.C., Copley J.T.P., Ferrero T.J., Van Dover C.L. (2006) Patterns of nematode diversity at hydrothermal vents on the East Pacific Rise. *Cahiers de Biologie Marine*, **47**, 365–370.

Fonseca G., Soltwedel (2007) Deep-sea meiobenthic communities underneath the marginal ice zone off Eastern Greenland. *Polar Biology*, **30**, 607–618.

Fonseca G., Muthumbi A.W., Vanreusel A. (2007) Species richness of the genus *Molgolaimus* (Nematoda) from local to ocean scale along continental slopes. *Marine Ecology – An Evolutionary Perspective*, **28**, 446–459.

Freiwald A., Hühnerbach V., Lindberg B., Wilson J.B., Campbell J. (2002) The Sula Reef Complex, Norwegian Shelf. *Facies*, **47**, 179–200.

Gad G. (2004) Diversity and assumed origin of the Epsilonematidae (Nematoda) of the plateau of the Great Meteor Seamount. *Archive of Fishery and Marine Research*, **51**, 30-42.

Gad G., Schminke H.K. (2004) How important are seamounts for the dispersal of interstitial meiofauna? *Archive of Fishery and Marine Research*, **51**, 43-54.

Gage JD , PA Tyler (1991) Deep-sea Biology Cambridge Univerity press 504pp

Gambi C., Vanreusel A., Danovaro R. (2003) Biodiversity of nematode assemblages from deep-sea sediments of the Atacama Slope and Trench (Southern Pacific Ocean). *Deep-Sea Research I*, **50**, 103–117.

Garcia, R., Koho, K.A., De Stigter, H.C., Epping, E., Koning, E., Thomsen, L. 2007. Distribution of meiobenthos in the Nazare canyon and adjacent slope (western Iberian Margin) in relation to sedimentary composition. *Marine Ecology-Progress Serie,s* **340**, 207-220.

Gourbault N., Decraemer W. (1996) Marine nematodes of the family Epsilonematidae: a synthesis with phylogenetic relationships. *Nematologica*, **42**, 133–158.

Grassle, J.F. 1989. Species diversity in deep-sea communities. *Trends in Ecology and Evolution*, **4.** 12-15.

Heip C., Vincx M., Vranken G. (1985) The ecology of marine nematodes. *Oceanography and Marine Biology – An Annual Review*, **23**, 399–489.

Hill MO. (1973) Diversity and eveness: a unifying notation and its consequences. *Ecology* **54**, 427-432

Hurlbert SH (1971) The Nonconcept of Species Diversity: A Critique and Alternative Parameters *Ecology***,** **52**, 577-586

Ingels J., Vanhove S., De Mesel I., Vanreusel A. (2006) The biodiversity and biogeography of the free-living nematode genera *Desmodora* and *Desmodorella* (family Desmodoridae) at both sides of the Scotia Arc. *Polar Biology*, **29**, 936–949.

Ingels, J., Kiriakoulakis, K., Wolff, G.A., Vanreusel, A., (2009). Nematode diversity and its relation to quantity and quality of sedimentary organic matter in the Nazaré Canyon, Western Iberian Margin. *Deep Sea Research Part I*. **56,**1521-1539

Jensen P (1987) Differences in microhabitat, abundance, biomass and body size between oxybiotic and thiobiotic free-living marine nematodes. *Oecologia,* **71**, 1432-1939

Lambshead P.J.D, Brown C.J, Ferrero T.J, Mitchell N.J, Smith C.R, Hawkins L.E, Tietjen J (2002) Latitudinal diversity patterns of deep-sea marine nematodes and organic fluxes: a test from the central equatorial Pacific. *Marine Ecology Progress Series*. **236,** 129-135

Levin, L.A. Etter R.J, Rex M.A, Gooday A.J, Smith C.R, Pineda J., Stuart C.T, Hessler R.R, Pawson D. (2001). Environmental Influences on Regional Deep-Sea species diversity. *Ann. Rev. Ecol. Syst.* **132**, 51-93

Lorenzen S. (1973) Die Familie Epsilonematidae (Nematodes). *Mikrofauna Meeresboden*, **25**, 411–494.

Mullineaux L.S. (1987) Organisms living on manganese nodules and crusts: distribution and abundance at three North Pacific sites. *Deep-Sea Research*, **34**, 165–184.

Muthumbi A.W., Vanreusel A., Duineveld G., Soetaert K., Vincx M. (2004) Nematode community structure along the continental slope off the Kenyan Coast, Western Indian Ocean. *International Review of Hydrobiology*, **89**, 188–205.

Netto S.A., Gallucci F., Fonseca G.F.C. (2005) Meiofaunal communities of continental slope and deep-sea sites off SE Brazil. *Deep-Sea Research I*, **52**, 845–859.

Ott J., Bright M. & Bulgheresi S. (2004). Symbioses between marine nematodes and sulfur-oxidizing chemoautotrophic bacteria. *Symbiosis,* **36**,103-126.

Radziejewska T. (2002) Responses of deep-sea meiobenthic communities to sediment disturbance simulating effects of polymetallic nodule mining. *International Review of Hydrobiology*, **87**, 457–4779.

Raes M., Vanreusel A. (2006) Microhabitat type determines the composition of nematode communities associated with sediment-clogged cold-water coral framework in the Porcupine Seabight (NE Atlantic). *Deep-Sea Research I*, **53**, 1880–1894.

Raes M., Decraemer W., Vanreusel A. (2008) Walking with Worms: coral-associated epifaunal nematodes. *Journal of Biogeography*, **35**, 2207–2222.

Rex M.A, McClain C.R, Johnson N.A, Etter R.J, Allen J.A, Bouchet P, Waren A (2005) A source-sink hypothesis for abyssal biodiversity. *American Naturalist*. **165**, 163-178

Smith C.R, Berelson W, Demaster D.J, Dobbs F.C, Hammond D, Hoover D.J, Pope R.H, Stephens M (1997) Latitudinal variations in benthic processes in the abyssal equatorial Pacific: control by biogenic particle flux. *Deep-Sea Research II*, **44**, 2295-2317.

Smith C R., De Leo F C., , Bernardino A. F. , Sweetman A. K. , &. Martinez Arbizu P (2008) Abyssal food limitation, ecosystem structure and climate change *Trends in Ecology & Evolution* ***23****,518-528*

Soetaert K., Heip C. (1995) Nematode assemblages of deep-sea and shelf break sites in the North Atlantic and Mediterranean Sea. *Marine Ecology Progress Series*, **125**, 171–183.

Stauffer H. (1924) Die Lokomotion der Nematoden. Beiträge zur Kausalmorphologie der Fadenwürmer. *Zool. Jb.*, **49**, 1–118.

Thiel H., Schriever G., Bussau C., Borowski C. (1993) Manganese nodule crevice fauna. *Deep-Sea Research I*, **40**, 419–423.

Tietjen J.H. (1984) Distribution and species diversity of deep-sea nematodes in the Venezuela basin. *Deep-Sea Research A*, **31**, 119–132.

Tietjen J.H. (1989) Ecology of deep-sea nematodes from the Puerto Rico Trench area and Hatteras Abyssal Plain. *Deep-Sea Research I*, **36**, 1579–1594.

Tkatchenko G., Kotlinski R., Stoyanova V., Lian D., Zhang G., Huang Y. (1997) On the role of geologic factors in determining peculiarities of water mass structure in the Clarion-Clipperton ore field. In: Chung J.S., Das B.M., Matsui T.M., Thiel H. (Eds*). Proceedings of the 7th (1997) International Offshore and Polar Engineering Conference, Honolulu, USA,* Vol. 1: 959–961.

Vanaverbeke J., Soetaert K., Heip C., Vanreusel A. (1997) The metazoan meiobenthos along the continental slope of the Goban Spur (NE Atlantic). *Journal of Sea Research*, **38**, 93–107.

Van Gaever S., Moodley L., de Beer D., Vanreusel A. (2006) Meiobenthos at the Arctic Håkon Mosby Mud Volcano with a parental caring nematode thriving in sulphide-rich sediments. *Marine Ecology Progress Series*, **321**, 143–155.

Van Gaever S., Olu K., Derycke S., Vanreusel A. (2009) Metazoan meiofaunal communities at cold seeps along the Norwegian margin: influence of habitat heterogeneity and evidence for connection with shallow-water habitats. *Deep-Sea Research I*. **56**, 772-785

Van Gaever S., Galéron J., Sibuet M., Vanreusel A. (in press) Deep-sea habitat heterogeneity influence on meiofaunal communities in the Gulf of Guinea. *Deep-Sea Research II*.

Van Gaever S, Raes M, Pasotti F, Vanreusel, A (this volume) Spatial scale and habitat-dependent diversity patterns in nematode communities in three seepage related sites along the Norwegian margin. *Marine Ecology – An Evolutionary Perspective*

Vanhove S., Vermeeren H., Vanreusel A. (2004) Meiofauna towards the South Sandwich trench (750-6300 m) focus on nematodes. *Deep-Sea Research II,* **51**, 1665–1687.

Vanreusel A., Clough L., Jacobsen K., Ambrose W., Jivaluk J., Ryheul V., Herman R., Vincx. M. (2000) Meiobenthos of the central Arctic Ocean with special emphasis on the nematode community structure. *Deep-Sea Research I,* **47**, 1855–1879.

Veillette J., Sarrazin J., Gooday A.J., Galéron J., Caprais J.-C., Vangriesheim A., Etoubleau J., Christian J.R., Juniper S.K. (2007a) Ferromanganese nodule fauna in the Tropical North Pacific Ocean: species richness, faunal cover and spatial distribution. *Deep-Sea Research I,* **54**, 1912–1935.

Veillette J., Juniper S.K., Gooday A.J., Sarrazin J. (2007b) Influence of surface texture and microhabitat heterogeneity in structuring nodule faunal communities. *Deep-Sea Research I,* **54**, 1936–1943.

Vermeeren H., Vanreusel A., Vanhove S. (2004) Species distributions within the free-living marine nematode genus Dichromadora in the Weddell Sea and adjacent areas. *Deep-Sea Research II,* **51**, 1643–1664.

Vranken G., Herman P.M.J., Heip C. (1988) Studies of the life-history and energetics of marine and brackish-water nematodes. I. Demography of Monhystera disjuncta at different temperature and feeding conditions. *Oecologia,* 77, 296–301.

Wefer, G, Billett D., Hebbeln D., Jorgensen BB, Schlüter M., van Weering TCE (2003) Ocean Margin Systems; Springer 495 pp

White M. (2007) Benthic dynamics at the carbonate mound regions of the Porcupine Sea Bight continental margin. *International Journal of Earth Sciences*, **96**, 1–9.

Habitat	Substrate	Topography	Biochemistry	Depth	Connectivity	Distribution
Shelf	Soft sediments	Flat		< 200m	High	Common
Slope	Soft sediments	Regular		200–4100m	High	Common
Abyssal	Soft sediments	Flat		> 4100m	High	Common
Nodules	Mn nodules on sediments	Flat		> 4100m	Low	Rare
Corals	Coral and other biogenic rubble	Mounds			Low	Medium
Canyons	Sediments	Channel and terraces			Low	Common
Seeps	Soft sediments	Pockmarks or mud volcanoes	Sulphidic and methanic		Low	Rare
Hydrothermal vents	Sediments, Mussel beds	Ridge or rise	Sulphidic		Low	Rare
Seamounts	Sediments	Mounts			Medium	Medium
Trenches	Sediments			> 6000 m	Extreme low	Rare

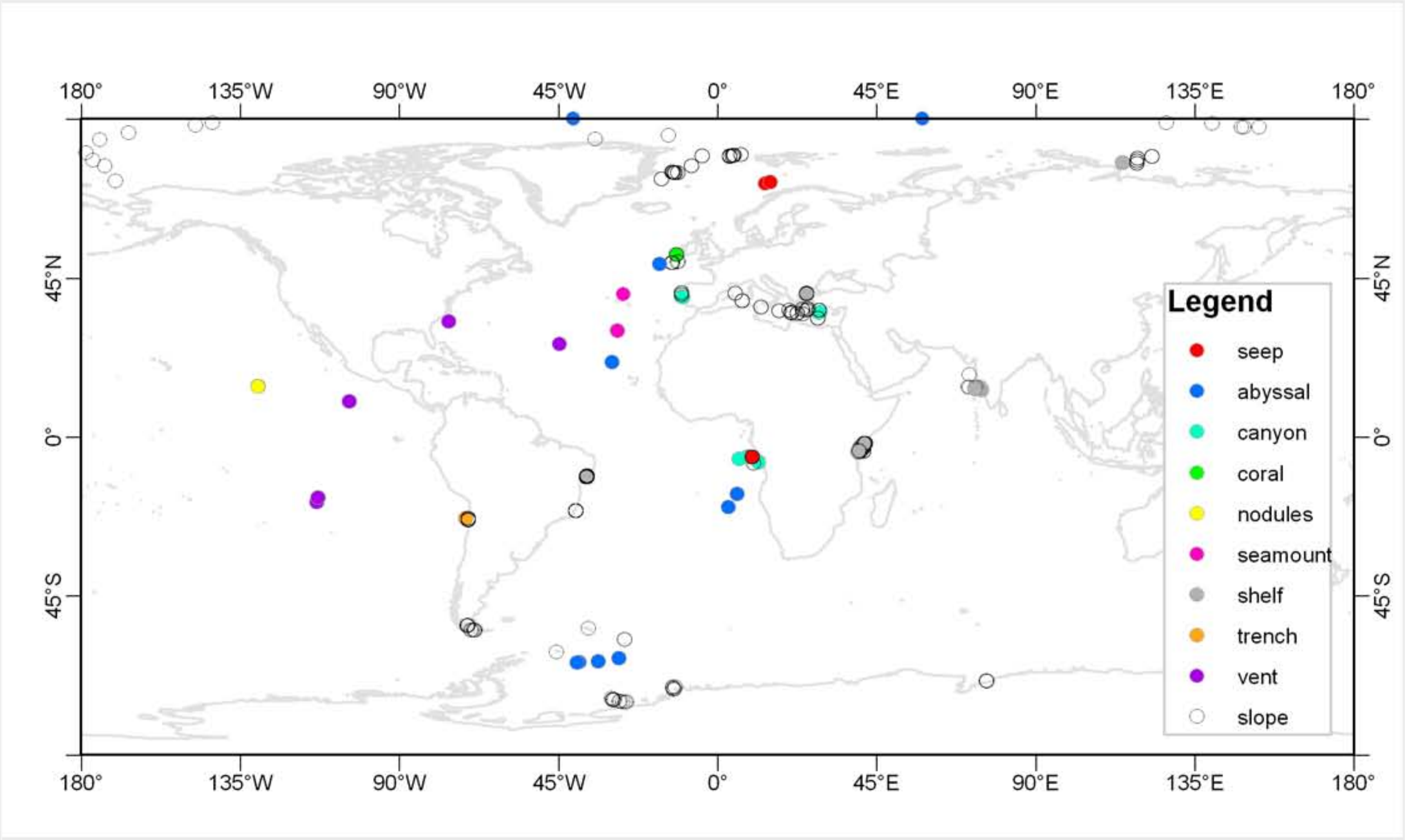
Table 1: Basic criteria used to identify the 10 main macrohabitats.

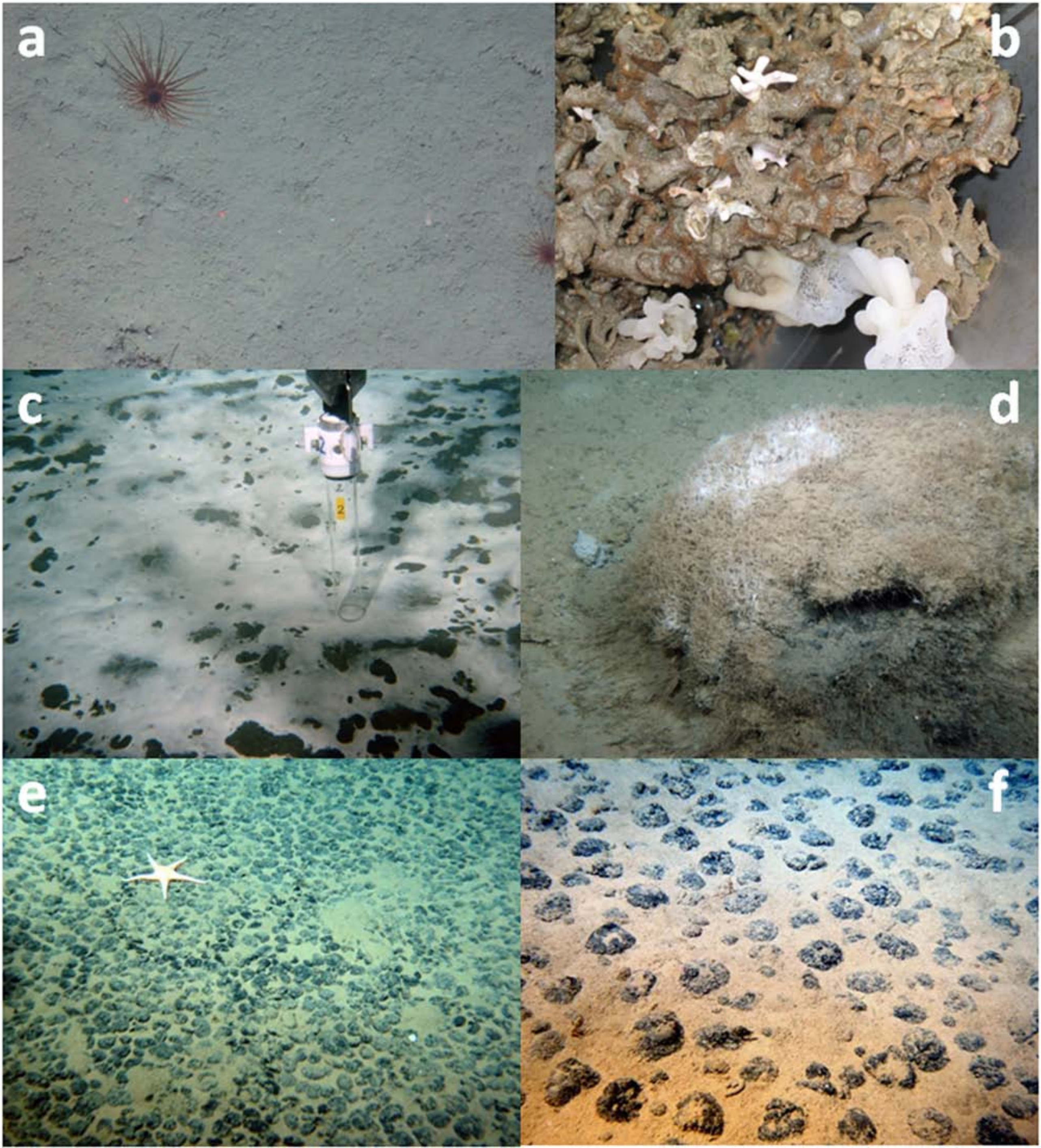
Habitat	**Total nr of genera**	**Nr of habitat-restricted genera**	**Nr of samples analysed**
Shelf	210	2	43
Slope	325	48	355
Abyssal	143	11	25
Nodules	90	9	14
Corals	112	2	22
Canyons	130	2	15
Seeps	120	1	26
Vents	31	2	36
Seamounts	33	0	3
Trenches	27	0	3
Total	362		

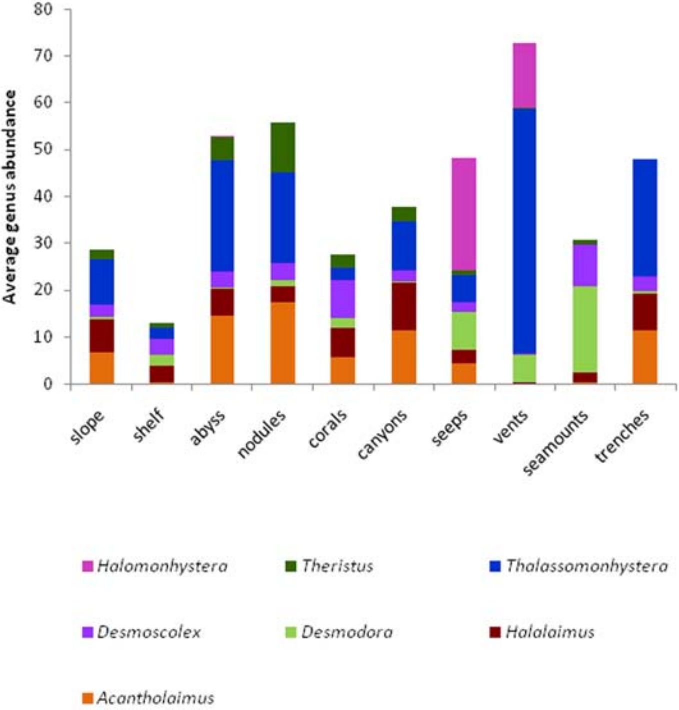
Table 2 : Total number of genera, number of habitat-restricted genera recorded, and number of samples analysed for the each of the 10 macrohabitats

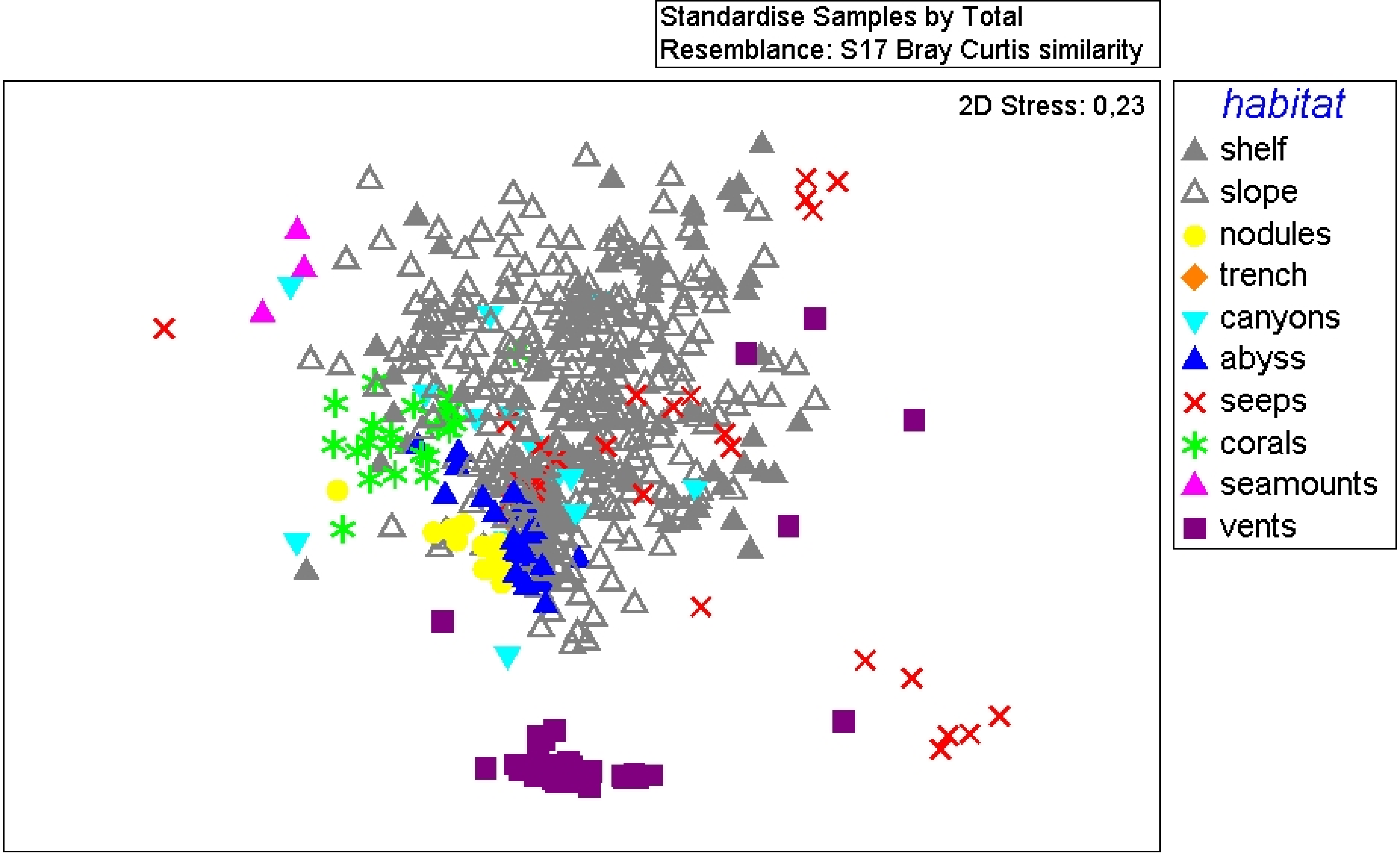
	slope	**shelf**	**abyss**	**nodules**	**corals**	**canyons**	**seeps**	**vents**	**seamounts**	**trenches**
Acantholaimus	6,67	0,65	14,49	17,44	5,62	11,57	4,32	0,54	0,53	11,57
Halalaimus	7,20	3,22	5,72	3,43	6,37	10,06	3,08	0,08	2,15	7,77
Desmodora	0,55	2,27	0,50	1,28	2,03	0,18	7,95	5,66	18,19	0,36
Desmoscolex	2,59	3,51	3,30	3,54	8,14	2,36	2,00	0,24	8,87	3,30
Thalassomonhystera	9,65	2,21	23,80	19,47	2,52	10,38	5,80	52,39		24,85
Theristus	1,99	1,10	4,91	10,67	3,07	3,27	0,98	0,05	0,97	
Microlaimus	2,48	4,13	7,91	1,79	1,30	7,87	4,46			8,84
Daptonema	5,51	4,67	2,69	1,23	0,51	3,13	2,29			6,24
Ceramonema	0,13	0,16	0,10	0,32	3,55	0,02			9,49	
Sabatieria	8,71	11,32			1,91	2,40	12,97	2,37		
Anticoma	0,22			0,67	4,44		0,23	9,05		
Richtersia	0,27	0,88			0,23	0,40			10,88	
Epsilonema	0,04	0,00			4,70	0,89	0,55		0,85	
Halomonhystera			0,06				24,08	13,67		
Marisalbinema			0,01	4,83			0,02			

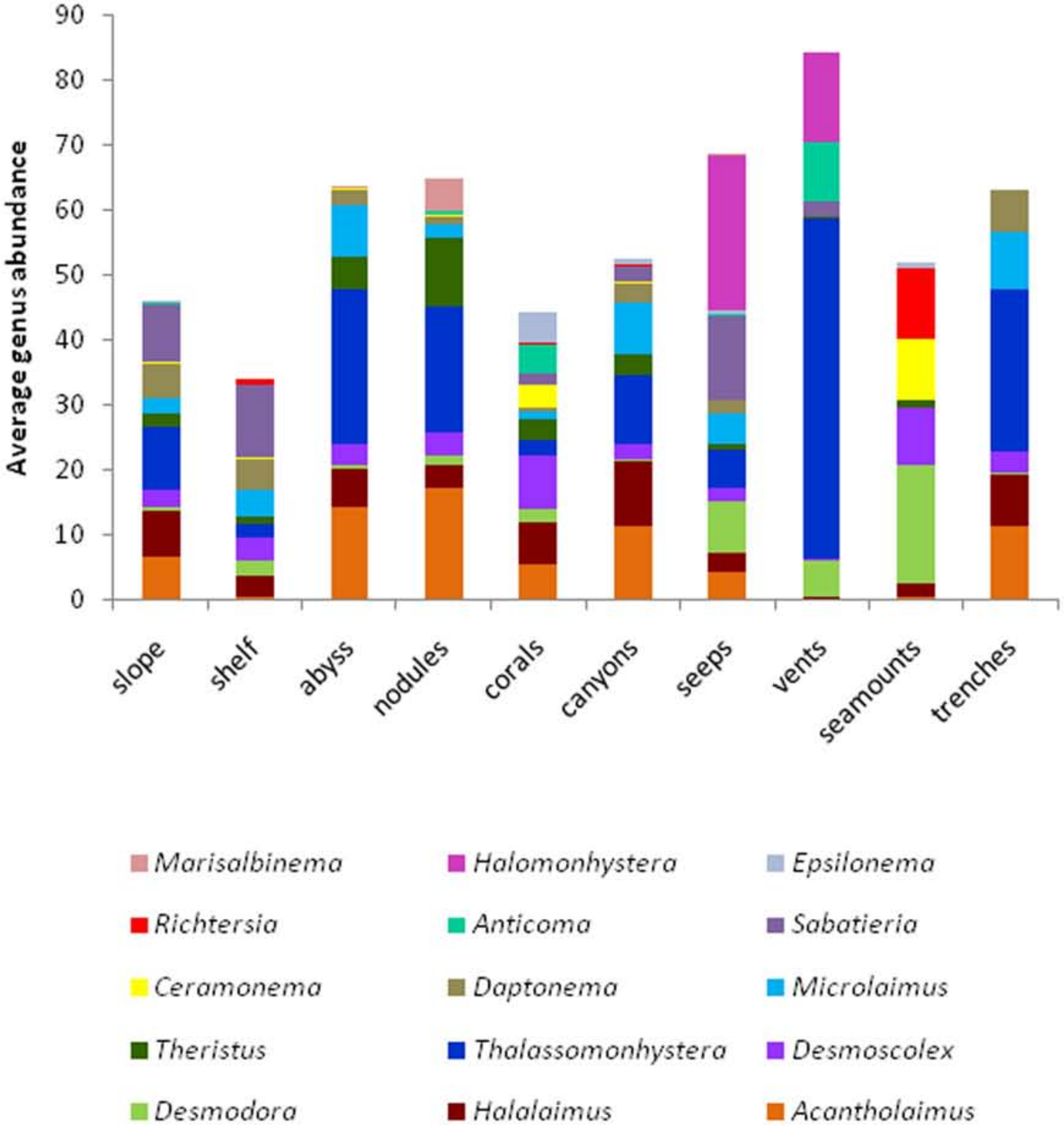
Table 3: Average relative abundances (%) per habitat of the genera dominantly responsible for the similarities within habitats and the dissimilarity between each macrohabitat and the slope habitat based on a SIMPER analysis.


180°
135°W
90°W
45°W
0°
45°E
90°E
135°E
180°
45°N
0°
45°S
Legend
seep
abyssal
canyon
coral
nodules
seamount
shelf
trench
vent
slope

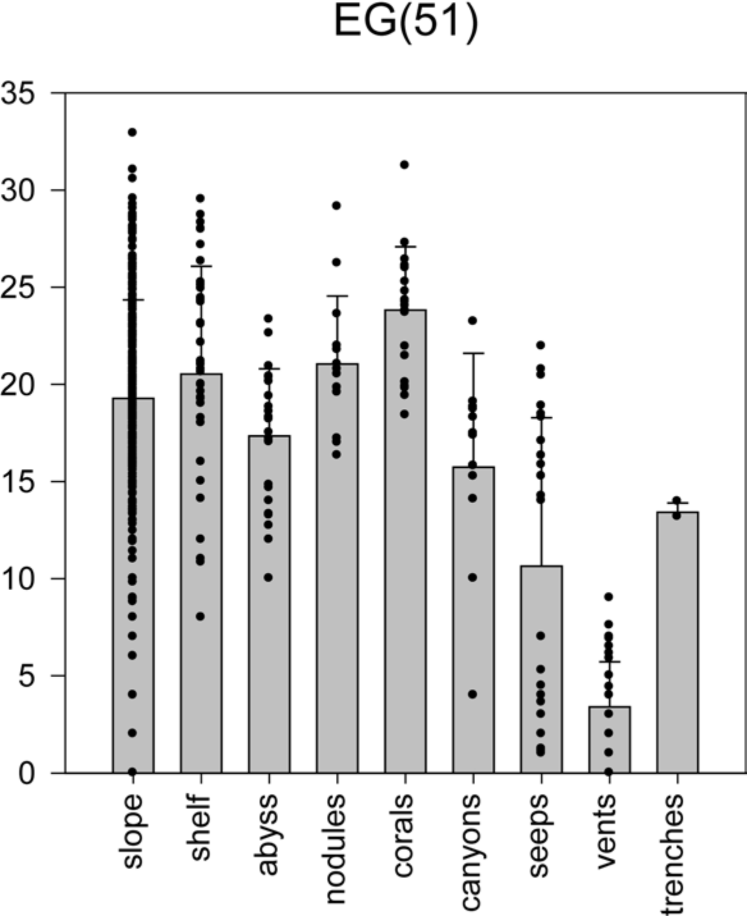

a
b
c
d
e
f

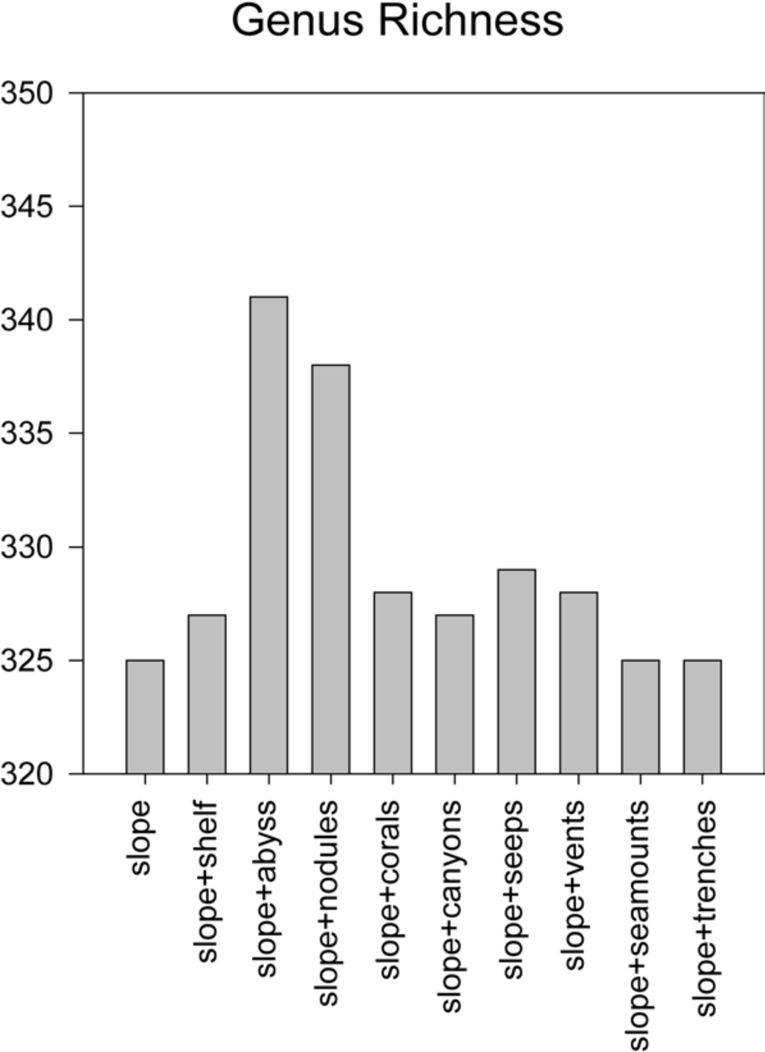

Average genus abundance
80
70
60
50
40
30
20
10
0
slope
shelf
abyss
nodules
corals
canyons
seeps
vents
seamounts
trenches
Halomonhystera
Theristus
Thalassomonhystera
Desmoscolex
Desmodora
Halalaimus
Acantholaimus

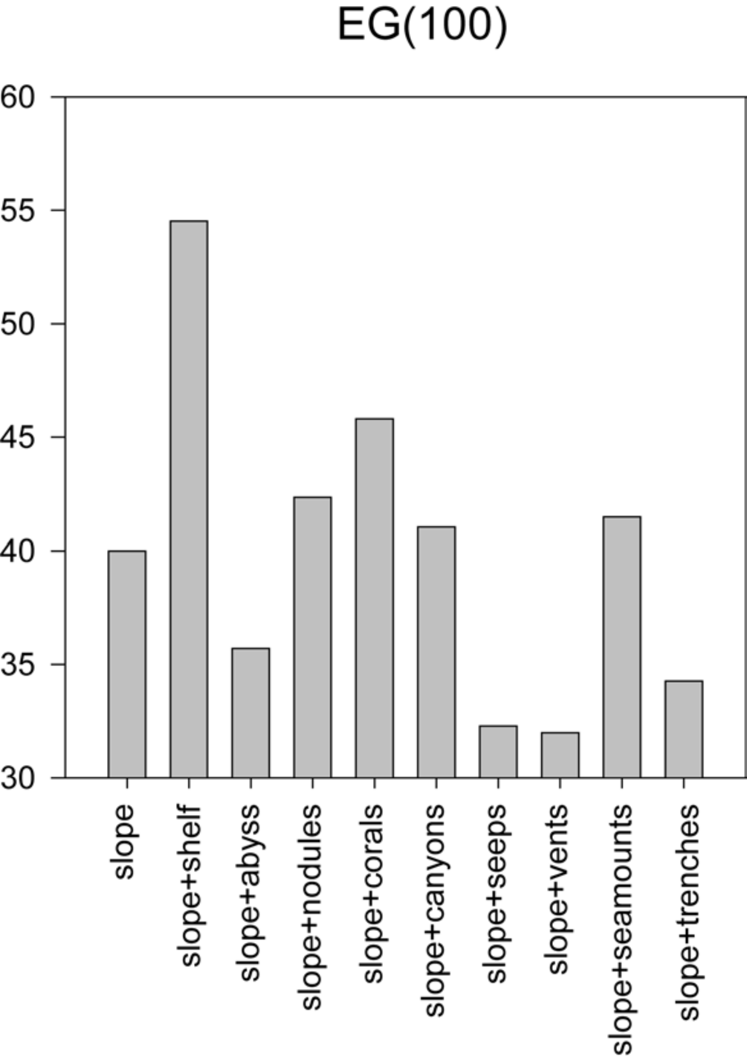

Standardise Samples by Total
Resemblance: S17 Bray Curtis similarity
2D Stress: 0,23
habitat
shelf
slope
nodules
trench
canyons
abyss
seeps
corals
seamounts
vents



Average genus abundance
0
10
20
30
40
50
60
70
80
90
slope
shelf
abyss
nodules
corals
canyons
seeps
vents
seamounts
trenches
Marisalbinema
Halomonhystera
Epsilonema
Richtersia
Anticoma
Sabatieria
Ceramonema
Daptonema
Microlaimus
Theristus
Thalassomonhystera
Desmoscolex
Desmodora
Halalaimus
Acantholaimus


EG(51)
35
30
25
20
15
10
5
0
slope
shelf
abyss
nodules
corals
canyons
seeps
vents
trenches


Genus Richness
350
345
340
335
330
325
320
slope
slope+shelf
slope+abyss
slope+nodules
slope+corals
slope+canyons
slope+seeps
slope+vents
slope+seamounts
slope+trenches


EG(100)
60
55
50
45
40
35
30
slope
slope+shelf
slope+abyss
slope+nodules
slope+corals
slope+canyons
slope+seeps
slope+vents
slope+seamounts
slope+trenches