

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

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**Abstract :**

The great variety of geological and hydrological settings in the deep-sea generates many different habitats, some of them only recently explored whereas their true extent and geographical coverage is not yet fully established until today. Both continental margins and mid-oceanic seafloors are much more complex ecologically, geologically, chemically, and hydrodynamically, than originally thought, such that 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 light of the newly recognized habitat heterogeneity. Based on a global database on nematode genus composition collected within the initiative of Census of Marine life it was shown that habitat heterogeneity contributes significantly to the total deep-sea nematode diversity. Different deep-sea habitats harbour specific nematode assemblages, whereas some of them like coral rubble zones or nodule areas can be identified as local hot spots of biodiversity. Factors such as increased substrate complexity in the case of nodules and corals seem to facilitate the co-existence of a high number of genera with different modes of life 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 regular soft sediments. However many nematode deep-sea genera are cosmopolitan inhabiting a variety of deep-sea habitats and oceans, while only 25 % of all deep-sea genera recorded are restricted to a single habitat. In addition to habitat heterogeneity, also regional differences are important in structuring nematode assemblages, as shown for instance by seeps from different regions where each time different genera thrive on the sulphidic sediments. Finally this study also showed that many areas and habitats remain under-sampled in order to fully understand the contribution of habitat heterogeneity versus regional differences to global nematode diversity.

**Keywords:** deep-sea, habitat heterogeneity, nematodes, biodiversity, census of marine life

## **Problem**

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 driving factors for differences in benthic standing stock, biodiversity and community composition of the benthos (Grassle, 1989; Gage and Tyler, 1991). However, through increasing exploration by means of bathymetric and visual mapping of habitats (Wefer et al, 2000), there is now a growing awareness of the true extent of habitat heterogeneity and the 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 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, has allowed for the direct sampling of these different habitats, which was not possible by the traditional remote coring techniques. Such studies have showed that these habitats were inhabited by benthic communities that were different from the surrounding regular deep-sea floor (Wefer et al, 2000). However, the extent to which these special habitats contribute to the overall deep-sea biodiversity has never been investigated, since studies on the biodiversity of particular deep-sea habitats were often restricted to comparisons between specific habitats and their background environments on a local or occasionally regional scale. No comparisons have been made yet on a larger scale comprising different deep-sea habitats, mainly due to the lack of comprehensive databases allowing research to be conducted on large-scale patterns.

In this study a large database containing quantitative data on nematode genus composition from different areas and habitats around the world was compiled, allowing for a global comparison on the 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 a better insight in the factors responsible for trends in biodiversity changes. 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 on 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 before that nematode community composition at the genus level reflects macro-ecological patterns

(Vanreusel et al. 2000, Vanaverbeke et al. 1997, Fonseca and Soltwedel 2007) and thus, it allows for a comparison of communities between habitats on a world-wide scale.

Based on a global database of nematode genus assemblages collected within the Census of Marine life projects CoMarge and CeDAMar and the MarBef European network of Excellence, the following hypotheses were tested: (1) Habitat heterogeneity contributes significantly to total deep-sea nematode diversity (2) Different deep-sea habitats harbour specific nematode assemblages (3) Particular deep-sea habitats can be identified as hot spots of biodiversity (4) Turnover in genus composition between habitats is more important than turnover between geographical regions.

## **Material and methods**

Data on nematode density and genus composition were collected from 542 samples from the shelf to the hadal (Fig. 1). Since the focus of this study was on the deep-sea, data obtained from shelf stations (< 200 m) were only included if these were part of a bathymetric transect which covered a significant part of the continental slope. Samples were 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). Datasets that are known from literature, but which were not available as complete taxonomic lists, were not included, since the analyses were done on full genus counts and densities, including the rare taxa. Detailed Sample information is available online or 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. 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). The expected number of genera for theoretical samples of 51 and 100 individuals,  $EG(51)$  and  $EG(100)$ , were calculated as analogous to the expected number of species (Hurlbert, 1971).

Turnover (1) between habitats within the same region and (2) between regions for the same habitat was measured (based on genus presence/absence data) and visualized in a ternary plot (Koleff *et al.*, 2003). The values of  $a'$ ,  $b'$  and  $c'$  (*i.e.* the percentage of shared species  $a$ , of species exclusively present in the neighbouring sample  $b$  and of species exclusively present in the focal sample  $c$ ) were plotted against a background of  $\beta_{sim}$ -values (Lennon *et al.*, 2001). The darkest areas on the bottom of the triangular plot represent highest turnover.

Samples were classified into 10 different habitats (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  $H_2S$ ). Fig 2 shows some examples of visual habitat heterogeneity in the deep-sea. The definition of the habitats shelf, slope, abyssal plain and trench used here is rather arbitrary 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 than elsewhere (3000–4000m), and the shelf at the Weddell Sea

margin extends out to a depth of 500 m. However, all the slopes identified here have soft sediments from the depth zone between 200 and 4100 m, from topographically regular settings, covered by well oxygenated bottom waters and without any indication of nearby flows of reduced chemical compounds. Some habitats are characterized by high patchiness and comprise different micro- (or sub-) habitats. For instance, seep includes both completely anoxic, sulphidic sediments as well as sediments which are well oxygenated at the surface but shows an increase in sulphide concentration at the subsurface. Similarly, the coral samples included coral rubble and dead sponges as well as coralligenous sediments.

The number of samples per habitat was unbalanced: 25 from the abyssal soft sediments, 15 from canyons, 22 from corals, 14 from nodules, 3 from seamounts, 26 from seeps, 43 from the shelf, 355 from soft sediments along the slope, 3 from trenches and 36 hydrothermal vent samples. 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 soft slope sediments were geographically the best represented of all the habitats and covered many world oceans, although the majority of samples were collected from the Atlantic including the Mediterranean Sea.

## Results

In total 362 genera were recorded over the 542 samples (Table 2); The majority of these genera (about 90 %) have previously been 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 unique genera within a 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 number of genera restricted to the habitat is 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). Mainly the highly abundant genera *Acantholaimus*, *Halalaimus*, *Thalassomonhystera*, but also *Desmodora*, *Desmoscolex* and *Theristus* showed a wide distribution including the majority of the investigated habitats.

Multivariate analysis, however, showed that different deep-sea habitats harboured significantly different nematode communities (Fig. 4) (ANOSIM:  $R = 0.39$ ;  $p < 0.01$ ). The MDS ordination based on nematode genus composition (%) showed that 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 were plotted mainly on one side of the central cluster of slope samples whereas the abyssal plains were grouped at the opposite side. Canyon and trench samples were overlapping, largely with the slope samples. Nodules 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 occasionally, samples from these specific habitats overlapped with slope samples in the MDS

ordination. The pairwise comparison showed that seeps, hydrothermal vents, corals, seamounts and nodules differed significantly in genus composition from the slope samples. Shelf communities also differed significantly from the slope communities, whereas the communities from abyssal plains, canyons and trench samples were not different from those from the slopes. All habitats also differed from the abyssal plains except for the trench samples. Mainly due to the high number of samples, the MDS ordination showed a high stress value (0.23). The stress value was significantly reduced (0.18) when the analysis was done at the 3D level. However the 2D ordination remains more illustrative, since the 3D representation needs to be rotated continuously in order to fully represent the pattern and the main patterns are consistent for both ordinations.

Figure 5 shows for each habitat, the average relative abundances of the main genera responsible for the similarity within habitats as identified by a SIMPER analysis. 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 represented by similar proportions such as Monhysteridae (mainly *Thalassomonhystera*), *Acantholaimus*, *Halalaimus*, *Daptonema* and *Sabatieria*. The genus *Sabatieria*, however, declined in abundance from depths deeper than 2000m and was absent from the abyssal plains and in trenches. From this analysis it was also clear that the average communities at abyssal plains, canyons and trenches shared several dominant genera with the slope communities. The other habitats were more different both in composition of the dominant genera as well as in their diversity in terms of evenness. The highest dissimilarity was found in the seamount samples which were characterized by high abundances of the genera *Desmodora*, *Richtersia*, *Ceramonema* and *Desmoscolex*. In contrast to the slope samples Monhysteridae (mainly *Thalassomonhystera*), *Sabatieria*, *Acantholaimus* and *Daptonema* were low in abundance. However the seamount assemblages were not representative of general patterns because of the low number of samples (3) and the restricted geographical coverage (2 seamounts in the NE Atlantic). The same was true for the trench habitat, which was only represented by 3 samples from the Atacama Trench.

Shelf and slope also differed in terms of proportions of taxa, since Monhysteridae (mainly *Thalassomonhystera*), *Acantholaimus*, *Halalaimus* and *Daptonema* showed higher abundances along the slope, whereas they were only occasionally found on the shelf. *Sabatieria* was a dominant genus on the shelf and slope but showed, on average, lower abundance along the slope compared with the shelf. Vent samples differed from slope samples by the increased dominance of the Monhysteridae (*Thalassomonhystera* and *Halomonhystera*), and the presence in greater abundance of *Anticoma* and *Desmodora*, two genera that were rather rare on the slope. Seep samples differed from slope samples by the high dominance of *Halomonhystera* and *Sabatieria*, whereas other typical slope genera such as *Acantholaimus*, *Thalassomonhystera* and *Halalaimus* were still present but reduced in abundance. Corals also showed much reduced abundance of *Thalassomonhystera* and *Sabatieria* compared with soft sediments from similar depths but were characterized by typical genera such as *Desmoscolex* and *Epsilonema*. Some typical genera such as *Theristus* and

*Marisalbinema* appeared in the nodule samples while these genera were either not important or absent on slopes or in other abyssal samples.

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

Figure 7 illustrates to what extent each of the habitats contributed to the overall slope diversity by calculating the total diversity of pooled samples combining each habitat respectively with the slope. Since the number of genera (Fig 7b) will be dependent on the number of samples analysed within a habitat, diversity is also expressed as EG(100) (Fig 7a). Particularly the abyssal plains and nodules increased the total genus richness of the slope (Fig. 7b). Except for the under-sampled seamounts and trenches, all habitats added to the total genus pool but to a lesser extent (see also table 2). In terms of expected number of genera (Fig 7a) the contribution of the abyssal plain and the nodules became less pronounced due to the higher dominance in both habitats. Based on EG(100) it was shown that, except for the shelf samples, mainly the corals increased the diversity due to the higher evenness, combined with the high number of genera present.

In order to differentiate between the importance of habitat heterogeneity and regional (ocean basin) differences in structuring genus composition, turnover was calculated and illustrated by a ternary plot (Fig. 8). Turnover (1) between communities from different habitats within the same region on the one hand and (2) between communities from the same (or comparable) habitats but found in different regions on the other, was compared. The ternary plot revealed no differences in turnover rates between habitats and between regions, and a high variation in  $\beta$ -diversity ( $\beta_{sim}$ ) in both cases. This implies that regional differences contribute significantly to global biodiversity, as much as habitat heterogeneity within each region. The absence of a (statistically significant) difference was confirmed by a Kruskal-Wallis ANOVA by ranks, based on  $\beta_{sim}$ -values ( $df = 1$ ;  $p = 0.56$ ). A two-way crossed ANOSIM analysis, based on relative abundances of genera, combined both an ocean basin and a habitat comparison. The analysis confirmed ( $p > 0.01$ ) the importance of regional differences in addition to habitat differences, although R-values were low ( $R = 0.42$  and  $0.5$ , respectively). Pairwise comparisons revealed the absence of significant differences between the North Atlantic on the one hand and the South Atlantic and Arctic Ocean on the other. However, for some regions, too few samples were available for a statistically robust comparison. Between habitats, the slope was found not to be

different from the trench and the abyssal plain. The R-value was also relatively low when comparing slopes with canyons, although the significance level still indicated potential differences.

## **Discussion**

### **Methodological problems**

Investigating ecological patterns on large scales is associated with the compilation of large databases, thereby increasing the heterogeneity of the data involved, and interpretation of the analyses is not without risk (Soetaert & Heip 1995). Data compiled for this study were obtained by a number of different sampling gears, from small box corer (e.g. Muthumbi *et al.* 2004) to larger box-corer (e.g. Netto *et al.* 2005), multiple corer (e.g. Fonseca & Soltwedel 2007), ROV push cores (Van Gaever *et al.* accepted) or even mussel pots (Flint *et al.* 2006...), for which sampling efficiency is known to vary occasionally especially for 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 did occur as several genera are differentiated by relatively small differences, possibly subject to personal interpretation but this was taken into account by pooling difficult genera at a higher taxon level (e.g. Monhysteridae) (Fonseca & Decraemer 2008). The patterns observed in our analyses were robust across the data set and the different habitats were represented by a multitude of characteristic genera. As such we are confident that the approach used in this study is the only way to overcome impediments of conducting large sampling campaigns and detect large-scale patterns in deep-sea nematodes.

### **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 in the different habitats 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 due to the presence of coral rubble, sponge skeletons or manganese nodules on top of the soft sediments. These observations suggest that increased substrate heterogeneity play 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 may provide more diverse ways of 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 lead to reduced diversity, despite the high food availability. Some opportunistic genera take advantage of the increased organic load associated with the seeps or vents and dominate these communities, while 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 (micro-) habitats in a seep. 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 always associated with oligotrophic areas where low densities lead to low diversity.

At the large scale, i.e. considering all samples from a given habitat as one (fig 7), it was the abyssal habitats that increased the total diversity, contradicting the source sink hypothesis that the abyss only acts as a sink for typical bathyal species (Rex et al, 2005 ). Corals increased the total slope diversity through increased evenness, whereas the nodules, as an exclusively abyssal habitat, also increase total abyssal diversity. These results suggest that habitat heterogeneity plays an important role in maintaining regional diversity of deep-sea environments by preserving taxa that are usually rare in soft sediments.

### **Habitat specific nematode assemblages**

The most striking result after combining all these independent data sets is 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. Actually, it seems that there is only a minority of genera (about 25% of the total genera) that are restricted to one particular habitat, including the slope habitat. The majority (15% of the total) of unique genera were encountered at the soft slope, while all other habitats together only contributed 10% of the genus richness. Since most of these habitat-specific genera occurred at low abundance, this suggests that their absences from other habitats may also have been due to (1) under-sampling, (2) possible misidentifications or (3) accidental colonisation of the specific habitat. Most genera have the potential to colonize a variety of deep-sea substrates, although some genera which are dominant in one habitat disappear in others (eg *Sabatieria* in the abyss, *Acantholaimus* and *Halalaimus* in vents) or become rather rare. The cosmopolitan character of most genera, does not necessarily apply for species, since the few studies done at species level have already shown that while there are occasionally some widespread nematode species, many are restricted in their distribution (Vermeeren et al. 2006, Ingels et al. 2007; and Fonseca et al. 2007a,b).

This analysis also shows that each different habitat facilitates the presence of certain nematode genera that are usually rare in the most common soft sediments of bathyal or abyssal depths. This is mainly because such habitats have completely different sedimentary and biochemical conditions from the adjacent sediments. For instance, the 3-dimensional structure of deep-sea corals enhances the abundance of non-burrowing, rather interstitial or epifaunal forms such as desmocoelocids and epsilonematids, while the gravel sediments of the seamounts facilitates nematodes with coarser cuticle like *Ceramonema*, *Richtersia* and *Desmodora*. Habitats rich in sulphide and hydrothermal vents had higher abundances of *Terschellingia*, *Sabatieria* and *Halomonhystera* which are better known from organically enriched shallow water environments than from other deep-sea habitats. Also *Marisalbinema* is a typical genus from a nodule area in the Pacific Ocean.

### **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 which

support cold-water coral banks and their degradation zones, since dead coral thickets are progressively degraded 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 forms such as members Epsilonematidae and Draconematidae (for details see Raes & Vanreusel 2006 and Raes et al. 2008), which are unusual for ocean margins (Decraemer et al., 2001). Both large biogenic substrata lie relatively unprotected on the ocean margin seabed and their associated fauna is therefore subject to stronger current activity typical for 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 here. Epsilonematidae and Draconematidae are characterised by the presence of unique locomotory structures: 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 most comparable to that of a geometrid caterpillar (Stauffer, 1924; Lorenzen, 1973). A comparable mode of locomotion was also observed in *Desmoscolex* (Stauffer, 1924), the second most abundant genus on coral fragments and the dominant genus on sponge skeletons.

### **Seamounts**

Interestingly, higher abundances of *Epsilonema* and *Desmoscolex*, together with *Desmodora*, *Richtersia* and *Ceramonema*, were also observed on the Great Meteor Seamount studied here. This seamount is characterized by coarse biogenic sediments composed of corals and mollusc shells, and 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 next 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 might be additional morphological advantages for survival in such physically harsh environments. This comparison suggests that the intricate physical micro-structure of the substrate might be one of the most important driving factor structuring nematode assemblages. Detailed information on the genera *Desmodora*, *Richtersia* and *Ceramonema* is absent, as we know little about their biology on the deep-sea floor.

### **Nodules**

Polymetallic nodule deposits on the abyssal seafloor, for example, are also considered a unique habitat type in which assemblages inhabit both the hard substratum offered by each nodule (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 underlying the nodules and in which the nodules are partly submerged. Data from two nodule areas from the Clarion-Clipperton Fracture Zone (CCFZ) were analysed (east and west) (Radziejewska, 2002) at depths of about 4300-4400 m and the central area (CCFZ-C) at depths of about 4950-5050 m (Miljutina et al., submitted). Samples in the two areas were collected, using a multiple corer, from both the nodule-bearing and nodule-free patches of the bottom. At the eastern area of the Clarion-Clipperton Fracture Zone (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, at the western side of the CCFZ, the dominant genera were thread-like interstitial forms such as Monhysteridae, *Acantholaimus*, and *Theristus*. These genera were also commonly found in soft sediments all around the world. Nevertheless, the analysis showed that 22 genera were unique for the nodulised seafloor and of these genera, not one was common between the two areas. The differences between the two CCFZ areas were further accentuated by different dominant genera. Especially the genus *Marisalbinema* was one of the characteristic dominant genera in the CCFZ-Z, and atypical for any other deep-sea habitat. In Remarkable was also the fact that the composition of the nematode fauna in CCFZ-E differed significantly from all the other deep-sea samples included in this analysis. Due to the dominance of *Terschellingia* these samples showed the highest similarity with seep habitats (Nordic margin) or shelf samples. Based on this observation it was assumed that other environmental conditions are prevailing except for the presence of nodules and that this area was maybe not a typical nodule area. Therefore these samples were not included in the MDS analysis. It was even suggested 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*) was somehow related to a possible presence of hydrothermal venting the signature of which, in the form of elevated metal contents in the water column, were reported from the area (Tkatchenko et al., 1997). Dominance of *Terschellingia* was indeed also common in cold seeps (Nordic margin) (Van Gaever et al. 2006; Van Gaever et al. in press), while this genus is previously also recorded as abundant in sulphidic, shallow-water habitats (Heip et al. 1985; Vranken et al. 1988). Apparently this nematode species is tolerant of harsh biochemical conditions which are often lethal to other meiofaunal organisms. In addition, nematode assemblages in the eastern part showed a distinct temporal shift in the suite of dominants, from *Terschellingia* in samples from the first (1995) campaign to desmoscolecids in the subsequent (1997) sampling programme, most probably in response to phytodetritus sedimentation event, the signature of which was detected in the sediment (Radziejewska, 2002).

### **Seeps and hydrothermal vents**

The presence of thriving nematode genera at relatively high abundance was occasionally observed at hydrothermal vents and more commonly at seeps. The Nordic cold seep was especially characterized by higher densities of *Halomonhystera* and also *Terschellingia* although with lower densities, while the cold seep in the Gulf of Guinea was characterized by the dominance of *Sabatieria*. Hydrothermal vents were particularly characterized by high densities of *Thalassomonhystera*, *Halomonhystera* and *Anticoma*. With the

exception of *Thalassomonhystera*, which is a typical soft bottom deep-sea genus, the other genera are mostly rare in deep-sea sediments and are known to attain high abundance/dominance in shallow waters (Heip et al 1985). Particularly, *Sabatieria* occurs at higher abundance along the shelf and upper slope but gradually disappears almost completely in well oxygenated soft sediments deeper than 2000 m (Soetaert & Heip 1995; Vanaverbeke *et al.* 1997). There are different possible alternatives to explain their presence in such reduced conditions such as the relatively larger body size which might be an advantage to tolerate low oxygen availability (Jensen, 1987). As already observed for other marine nematode genera (Ott et al 2004), symbioses with sulphur-oxidizing chemoautotrophic bacteria might be also an alternative to survive in seeps and hydrothermal vents. However there is so far little evidence of symbiosis in deep-sea nematodes associated with reduced environments.

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

### **Canyons**

Another source of spatial heterogeneity in the deep-sea is the presence of canyons, known as large-scale geomorphological formations, disrupting the monotony of the seafloor. Canyon samples included in this analysis covered the Western Iberian Margin (Nazaré Canyon) (Ingels et al submitted), 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 particular for each site and time scale (de Stigter *et al.*, 2007). Highly active axes and the relatively undisturbed areas, such as terraces aside the active channels, result in very contrasting environmental conditions (see also Ingels et al, submitted). Consequently we may expect that nematode assemblages might also be very variable and respond accordingly to each sub-habitat. From the present study, it was indeed clear that heterogeneity in canyons, as illustrated by the low similarity value of 27.91 %, is high and caused by extraordinary topographic and hydrodynamic complexity, driving variability on various spatial and temporal scales (Canals *et al.*, 2006; de Stigter *et al.*, 2007). Especially the contrast between highly active canyon axes and the more undisturbed areas, such as terraces beside the active channels, result in very different observations of abundance, composition and diversity of the nematode communities (Ingels *et al.*, submitted; Garcia et al, 2007). This is in concordance with the ANOSIM tests which indicated that canyon assemblages differed significantly from those of the other habitats except for the slope. There was, indeed, a strong overlap between canyons and slope communities, however, 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%) due to the generally harsh canyon conditions, resulting in 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-sediments. In the same way, it was found that the chemistry of the sediments from seeps and hydrothermal vents was similar in the same analysis.

### **Trenches**

Only data from the Atacama trench (Gambi et al. 2003) was used in this analysis. The Atacama Trench is a particular hadal system, characterized by close proximity to the continent (ca 80 km). In addition the Atacama trench is right beneath one of the largest upwelling regions (Peru-Chile upwelling system). The specific geographic setting confers to this hadal system the characteristics of eutrophic systems, 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 only two other hadal systems (the Puerto Rico and the South Sandwich trenches) have been analysed for nematode assemblage composition (not included here). While in the three systems genus richness decreased significantly from the slope to the hadal depths (Tietjen 1989; Gambi *et al.* 2003; Vanhove *et al.* 2004), genus composition varied significantly and each hadal system was characterized by different dominant genera (Gambi et al. 2003). Studies carried out in Venezuela basin and Puerto Rico Trench suggest that the decrease of nematode biodiversity at hadal depths reflected, as well as the reduced food availability, the 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 this might result in an increase of nematode diversity (Tietjen 1984). The role of habitat heterogeneity is potentially important also in the Atacama Trench, where the rather homogeneous sediments at hadal depths hosted a number of genera approximately 40% lower than at bathyal depths, where sediments were more heterogeneous (Gambi et al., 2003). The inaccessibility of hadal sediments makes fine spatial scale studies and a detailed analysis of habitat heterogeneity difficult, and further studies are needed to clarify the role of habitat heterogeneity on nematode biodiversity at hadal depths.

### **Abyssal**

In comparison with the slope environment, the vast abyss is also considered a peculiar habitat for the fauna (Rex et al. 2005; Smith et al. 2008). The abyss mainly differs from the other habitats reported here by the low current velocity, sediments formed mainly by fine sand and clay and habitat structures mostly being biogenic, comprising the tests of giants protozoans and the burrows, mounds and tracks of megabenthos (for review see Smith et al. 2008). For different macro- and megafaunal taxa, the abyss is normally characterized by a distinct 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 abyssal assemblages differed significantly from slope assemblages. However the abyss 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), assemblages are dominated by Monhysteridae (including *Thalassomonhystera*, *Monhystrella*), *Halalaimus* and *Acantholaimus*. Apart from the constant dominance of

Monhysterids, the sub-dominance of abyssal nematode assemblages seems to be related to the surface primary production. It has also been already observed that higher flux of particulate-organic carbon promoted changes in polychaetes and nematode assemblages in the equatorial Pacific (Smith et al. 1997, Brown et al. 2002). However, primary productivity is not rule, since we also observed that areas characterized by similar primary production levels (Northeast tropical Atlantic and Northwest tropical Atlantic) showed different sets of dominants and subdominants. In this case other environmental factors may be involved.

### **Regional differences versus habitat heterogeneity**

The absence of any (significant) differences in turnover (based on presence/absence data) between habitats and regions indicates that neither of both factors has a distinctly higher structuring effect on the nematode communities. Turnover levels are extremely variable, indicating that nematode assemblages from different regions or habitats can be composed of a rather different set of genera, but is also very similar in many cases. This agrees well with our finding that many nematode genera are cosmopolitan, inhabiting a variety of deep-sea habitats and oceans, but that many nematode genera are also rare present in low abundances in only a few samples. Studies dealing with larger scale patterns of deep-sea nematodes are mostly recent and still limited to a within regional scale. Some of these studies have addressed depth gradients (Soetaert and Heip 1995, Vincx et al, 1994) whereas studies on latitudinal gradients are restricted to the North Atlantic and North Pacific (Lamshead et al. 2000, 2002), and longitudinal patterns are restricted to the Mediterranean (Danovaro et al. 2008, see also Gambi and Danovaro 2006). Vanreusel et al (2000) also investigated large scale patterns of deep-sea nematodes in the Central Arctic Ocean. Comparative studies of nematode assemblages combining more than one region are virtually inexistent. Nevertheless, in a recent attempt, by merging different published studies, Fonseca and Soltwedel (2007) showed that distinct Arctic deep-sea regions harboured distinct nematode assemblages which in turn were also different from the northern North Atlantic.

The present study expands our knowledge on regional patterns of deep-sea nematodes since we observed that for particular habitats there are differences between oceans, mainly caused by the balance of the dominant and subdominant species, but also by the presence of particular dominant genera that are absent in other regions. For instance the cold seeps of the Nordic margin are dominated by *Halomonhystera* or *Terschellingia*, while in the guinea basin the dominant genera are *Sabatieria* and to a lesser extent *Desmodora* (Van Gaever et al, accepted a and b) The fact that regional changes in deep-sea nematodes can be as important as changes caused by habitat heterogeneity may be due to the fact that within each region habitats favoured the presence of genera from the local pool of species (like in the case of cold seeps), instead of presenting a typical habitat assemblage across the different regions. It should be noted however that the above observations were based on particular habitats and that the samples included here were not necessarily representative of the whole possible range of habitat variability and geographical coverage. We are aware that three samples of the Meteor Great seamount are not representative of the habitat seamount, nor that the Atacama trench represents a typical trench. More samples from each ocean are needed in order to generalize

our findings. Further large-scale studies will definitely contribute for the understanding of deep-sea biodiversity.

### **Conclusions**

It is clear that from this study that habitat heterogeneity in the deep-sea is important for global nematode diversity. However the question to what extent habitat heterogeneity contributes has no single answer. It was confirmed by this analysis that many nematode deep-sea genera are cosmopolitan inhabiting a variety of deep-sea habitats and oceans, while only 25 % of all deep-sea genera recorded are restricted to a single habitat. Furthermore these unique genera are never dominant or general present in all samples within a habitat suggesting their possible accidental presence or absence rather than a selective colonization of particular habitats. On the other hand different habitats like 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 regular soft sediments. Furthermore clear shifts in relative proportions in the dominant genera are observed between soft sediment habitats from the shelf to hadal depths. In this sense we can conclude that different deep-sea habitats harbour specific nematode assemblages, but that few genera are unique for a habitat. The soft sediments of the slope can be clearly identified as hot spots of biodiversity being responsible for more than 60 % of all the unique genera, but it is clear that many habitats such as nodule areas, corals, seamounts, canyons and trenches remain under-sampled. However in terms of local diversity it are especially the nodule areas and coral rubble samples that are identified as habitats where most genera co-exist in equal proportions. The added complexity of the substrate facilitates both sediment-dwelling as well as epifaunal taxa in the same environment. However on top of the importance of habitat heterogeneity to total nematode diversity, also regional differences in nematode assemblages are significant.

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

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

Fig 3 Average relative abundances of genera present in 9 or more habitats being dominant (> 5 %) in at least one of the habitats

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

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

Fig 6: Expected number of genera (EG(51)) per sampling station (black dots). Averages and standard deviations shown by the vertical bars with error bars.

Fig. 7 (A): Expected number of genera (EG(100)) and (B): Total genus diversity of the slope habitat and the slope combined with each of the other habitats.

Fig. 8. Ternary plots based on genus presence/absence data in which the right scale towards the top (a') represents the fraction of shared genera for each couple of samples, the left scale increasing towards c', and the bottom scale towards b' represent respectively the fraction of unique genera for each of the samples. The colour gradient represents turnover in genera between pairs of samples with the lower dark red area representing maximum turnover in genera composition and the top dark green area representing a maximum overlap.



## References

- Bazzaz FA (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., Lamshead P.J.D., Gooday A.J., Ferrero T., Dinert A. (1994) Sampler bias in the quantitative study of deep-sea meiobenthos. *Marine Ecology Progress Series*, **104**, 197–203.
- Brandt A., A.J. Gooday, S.N. Brandão, S Brix, W Brökeland, T Cedhagen, M. Choudhury, N. Cornelius, B. Danis, I. De Mesel, R. J. Diaz, D.C. Gillan, B. Ebbe, J.A. Howe, D. Janussen, S. Kaiser, K. Linse, M. Malyutina, J. Pawlowski, M. Raupach & A Vanreusel (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. (2007a) Species richness of the genus *Molgolaimus* (Nematoda) from local to ocean scale along continental slopes. *Marine Ecology – An Evolutionary Perspective*, **28**, 446–459.
- Fonseca G., Decraemer W. (2008) State of the art of the free-living marine Monhysteridae (Nematoda). *Journal of the Marine Biological Association of the United Kingdom*, **88**, 1371–1390.
- 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 University 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 Series* 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 evenness: 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., submitted. Nematode diversity in relation to quantity and quality of sedimentary organic matter in the Nazaré Canyon, Western Iberian Margin. *Deep Sea Research Part I: Oceanographic Research Papers*.
- Jensen P (1987) Differences in microhabitat, abundance, biomass and body size between oxybiotic and thiobiotic free-living marine nematodes. *Oecologia* **71**: 1432-1939
- Koleff, P., K. J. Gaston & J. J. Lennon (2003) Measuring Beta Diversity for Presence-Absence Data. *The Journal of Animal Ecology*, **72**, 367-382
- Levin, L.A. RJ Etter, MA Rex, AJ Gooday, CR Smith, J. Pineda, CT Stuart, RR Hessler, D. Pawson. (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.
- Miljutina M.A., Miljutin D.M., Mahatma R., Galeron J. (submitted) Deep-sea nematode communities from the nodule-bearing area and the adjacent area free of nodules (Clarion-Clipperton Fracture Zone, the North-Eastern Pacific). *Marine Biodiversity*.
- 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 et al 2005
- Sebastian S., Raes M., De Mesel I., Vanreusel A. (2007) Comparison of the nematode fauna from the Weddel Sea Abyssal Plain with two North Atlantic abyssal sites. *Deep-Sea Research II*, **54**, 1727–1736.
- Smith C R., , F C. De Leo<sup>1</sup>, A. F. Bernardino<sup>1</sup>, A. K. Sweetman<sup>1</sup>, & P. Martinez Arbizu (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.
- Thistle D., Sherman K. (1985) The nematode fauna of a deep-sea site exposed to strong near bottom currents. *Deep-Sea Research A*, **31**, 1077–1088.
- 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. (in press) 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*.
- Van Gaever S., Galéron J., Sibuet M., Vanreusel A. (submitted) Deep-sea habitat heterogeneity influence on meiofaunal communities in the Gulf of Guinea. *Deep-Sea Research II*.
- 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.

- 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.
- 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.
- Wefer, G, D. Billett, D. Hebbeln, BB Jorgensen, M. Schlüter, TCE van Weering (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     |
|--------------------|---|----------------------------|------------------------|-----------|
| Shelf              | Soft sediments                                      | Flat                       | Oxic                   | < 200m    |
| Slope              | Soft sediments                                      | Regular                    | Oxic                   | 200–4100m |
| Abyssal            | Soft sediments                                      | Flat                       | Oxic                   | > 4100m   |
| Nodules            | Mn nodules on sediments                             | Flat                       |                        | > 4100m   |
| Corals             | Coral and other biogenic rubble or coarse sediments | Mounds                     |                        |           |
| Canyons            | Sediments   | Channel                    |                        |           |
| Seeps              | Soft sediments                                      | Pockmarks or mud volcanoes | Sulphidic and methanic |           |
| Hydrothermal vents | Sediments, Musselbeds                               | Ridge or Rise              | Sulphidic              |           |
| Seamounts          | sediments   | Mounds                     |                        |           |
| Trenches           | Soft sediments                                      |                            |                        | > 6000 m  |

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

| Habitat   | EG<br>(51) | Total nr of<br>genera | Nr of unique<br>genera | Nr of samples<br>analysed |
|-----------|------------|-----------------------|------------------------|---------------------------|
| Shelf     | 35.3       | 210                   | 2                      | 43                        |
| Slope     | 31.2       | 325                   | 48                     | 355                       |
| Abyssal   | 19.4       | 143                   | 11                     | 25                        |
| Nodules   | 21.3       | 90                    | 9                      | 14                        |
| Corals    | 27.9       | 112                   | 2                      | 22                        |
| Canyons   | 26.4       | 130                   | 2                      | 15                        |
| Seeps     | 13.8       | 120                   | 1                      | 26                        |
| Vents     | 10.5       | 31                    | 2                      | 36                        |
| Seamounts | 1          | 33                    | 0                      | 3                         |
| Trenches  | 15.9       | 27                    | 0                      | 3                         |
| Total     |            | 362                   |                        |                           |

Table 2 : Genus diversity indices , number of unique genera recorded, and number of samples analysed for the each of the 10 habitats

|                              | <b>slope</b> | <b>shelf</b> | <b>abyss</b> | <b>nodules</b> | <b>corals</b> | <b>canyons</b> | <b>seeps</b> | <b>vents</b> | <b>seamounts</b> | <b>trenches</b> |
|------------------------------|--------------|--------------|--------------|----------------|---------------|----------------|--------------|--------------|------------------|-----------------|
| <i>Acantholaimus</i>         | 6,67         | 0,65         | 14,49        | 17,44          | 5,62          | 11,57          | 4,32         | 0,54         | 0,53             | 11,57           |
| <i>Halalaimus</i>            | 7,20         | 3,22         | 5,72         | 3,43           | 6,37          | 10,06          | 3,08         | 0,08         | 2,15             | 7,77            |
| <i>Desmodora</i>             | 0,55         | 2,27         | 0,50         | 1,28           | 2,03          | 0,18           | 7,95         | 5,66         | 18,19            | 0,36            |
| <i>Desmoscolex</i>           | 2,59         | 3,51         | 3,30         | 3,54           | 8,14          | 2,36           | 2,00         | 0,24         | 8,87             | 3,30            |
| <i>Thalassomonhystera</i>    | 9,65         | 2,21         | 23,80        | 19,47          | 2,52          | 10,38          | 5,80         | 52,39        |                  | 24,85           |
| <i>Theristus</i>             | 1,99         | 1,10         | 4,91         | 10,67          | 3,07          | 3,27           | 0,98         | 0,05         | 0,97             |                 |
| <i>Microlaimus</i>           | 2,48         | 4,13         | 7,91         | 1,79           | 1,30          | 7,87           | 4,46         |              |                  | 8,84            |
| <i>Daptonema</i>             | 5,51         | 4,67         | 2,69         | 1,23           | 0,51          | 3,13           | 2,29         |              |                  | 6,24            |
| <i>Paralongicyatholaimus</i> | 0,51         | 0,53         | 0,19         | 0,28           | 0,13          | 1,65           | 0,33         |              |                  | 5,62            |
| <i>Ceramonema</i>            | 0,13         | 0,16         | 0,10         | 0,32           | 3,55          | 0,02           |              |              | 9,49             |                 |
| <i>Sabatieria</i>            | 8,71         | 11,32        |              |                | 1,91          | 2,40           | 12,97        | 2,37         |                  |                 |
| <i>Anticoma</i>              | 0,22         |              |              | 0,67           | 4,44          |                | 0,23         | 9,05         |                  |                 |
| <i>Richtersia</i>            | 0,27         | 0,88         |              |                | 0,23          | 0,40           |              |              | 10,88            |                 |
| <i>Epsilonema</i>            | 0,04         | 0,00         |              |                | 4,70          | 0,89           | 0,55         |              | 0,85             |                 |
| <i>Halomonhystera</i>        |              |              | 0,06         |                |               |                | 24,08        | 13,67        |                  |                 |
| <i>Marisalbinema</i>         |              |              | 0,01         | 4,83           |               |                | 0,02         |              |                  |                 |

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





