**Biogeosciences
Discussions**

The importance of different spatial scales in determining structure and function of deep-sea infauna communities

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Abstract

The urge to understand spatial distributions of species and communities and their causative processes has continuously instigated the development and testing of conceptual models in spatial ecology. For the deep-sea, there is evidence that structure, diversity and function of benthic communities are regulated by a multitude of biotic and environmental processes that act in concert on different spatial scales, but the spatial patterns are poorly understood compared to those for other ecosystems. Deep-sea studies generally focus on very limited scale-ranges, thereby impairing our understanding of which spatial scales and associated processes are most important in driving diversity and ecosystem function of communities. Here, we used an extensive integrated dataset of free-living nematodes from deep-sea sediments to unravel which spatial scale is most important in determining benthic infauna communities. Multiple-factor multivariate permutational analyses were performed on different sets of community descriptors (structure, diversity, function, standing stock). The different spatial scales investigated cover two margins in the Northeast Atlantic, several submarine canyons/channel/slope areas, a bathymetrical range of 700–4300 m (represents different stations, 5–50 km apart), different sampling locations at each station (replication distances, 1–200 m), and vertical sediment profiles (cm layers). The results indicated that the most important spatial scale for diversity, functional and standing stock variability is the smallest one; infauna communities changed substantially more with differences between sediment depth layers than with differences associated to larger geographical or bathymetrical scales. Community structure differences were largest between stations at both margins. Important regulating ecosystem processes and the scale on which they occur are discussed. The results imply that, if we are to improve our understanding of ecosystem patterns of deep-sea infauna and the relevant processes driving their structure, diversity, function and standing stock, we must pay particular attention to the small-scale heterogeneity or patchiness and the causative mechanisms acting on that scale.

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1 Introduction

The great variability displayed by natural communities have continuously instigated ecologists to develop and test conceptual models that explain patterns at various temporal and spatial scales based on biological interactions and/or abiotic processes (e.g. Connell, 1978; Hubbell, 2001; Levin et al., 2001b; Volkov et al., 2003; Svensson et al., 2007). In applying these models to the deep-sea benthic environment, the evidence to date suggests that small-scale habitat variability and patchy disturbance, as well as global and regional variability, may play roles in maintaining deep-sea diversity (Snelgrove and Smith, 2002; Rex and Etter, 2010; Vanreusel et al., 2010; e.g. McClain et al., 2011). It is generally accepted that benthic distribution and diversity patterns can be related to local and regional-scale phenomena such as geographical barriers, productivity gradients, sediment grain size diversity, and current regimes, amongst others. In turn, environmental drivers, such as the changes in sedimentary trophic parameters and physical disturbances may regulate deterministic biotic processes including colonisation, competition for food resources, predation, etc., leading to the large and small-scale patterns in benthic fauna, but available data seem to suggest that particular attention should be paid to the scale relevant to the organism and their interactions when investigating such processes (Jumars, 1976). In marine biodiversity and ecosystem functioning studies, much attention is drawn to the processes themselves and the role played by single species or limited species groups (in an autecological approach), rather than applying a synecological approach whereby the community is investigated. Critical to gain insights in synecological dynamics is identifying the scale at which the important processes occur. The current lack of understanding the importance of scale impairs advancing our knowledge about biodiversity and ecosystem functioning as well as important underlying processes (Raffaelli and Friedlander, 2012), posing a limitation to further theoretical explorations (Paterson et al., 2012). An obvious step is to identify which spatial scale bears most importance in regulating community characteristics, an approach which has received relatively little attention in deep-sea scientific literature.

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Despite the generally accepted view that processes on various spatial scales are driving benthic communities, most of the evidence for the structure and dynamics of deep-sea communities and their causes originate from regional-scale sampling studies (Levin et al., 2001b), focusing on relatively large spatial scales (10–100 km), or typically on the scale of 0.1–10 km. Unfortunately, the importance of micro-scale (cm–m) habitat variability and patchiness in this context has been demonstrated for only a small subset of species or taxa and for a limited number of habitats (Snelgrove and Smith, 2002). Traditionally, deep-sea studies are performed along a single spatial scale, thereby renouncing the variable importance of different scales; from micro-scale (mm–cm) variability up to the larger geographic scale (100s km). Whilst it is critical to choose the appropriate scale in investigating diversity patterns (Huston, 1999) studies seeking to document the most important patterns and underlying processes for deep-sea benthic diversity and ecosystem functioning should consider the inherent scalability of patterns and processes and cover the whole spatial range.

For the benthic meiofauna (32–1000 µm, most abundant group of metazoans on Earth) in the deep sea, it has long been shown that smaller spatial scales (cm) are particularly important to detect diversity and distribution patterns (Thistle, 1978; Eckman and Thistle, 1988) and micro-scale variability of biogeochemical conditions and biotic interactions along the vertical sediment profile has been used to explain the structure of meiobenthic assemblages (Thiel, 1983; Jorissen et al., 1995; Soetaert et al., 2002; Braeckman et al., 2011; Ingels et al., 2011a,c). Knowledge on the importance of different spatial scales in shaping benthic patterns is essential in discerning the causative important processes. Without this knowledge, benthic faunal patterns may remain seemingly idiosyncratic without any understanding of the drivers of benthic diversity and functioning. In the absence of such understanding, conceptual models and their quantifications remain meaningless. Based on various interpretations of environmental variation and faunal interactions it is likely that there is a hierarchical complex of abiotic and biotic drivers which regulates different aspects of meiofauna communities on various spatial scales.

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Submarine canyons can perhaps be considered as the most heterogenic habitats in the marine realm, with great levels of within- and inter-canyon variability across a range of ecologically relevant processes (Tyler et al., 2009, Vetter et al., 2010). Submarine canyons are typified by great habitat heterogeneity, the result of extreme topography, diverse current regimes and substratum types, and detrital funnelling, together exerting a powerful influence on biotic diversity (Levin et al., 2010). At the same time, each canyon is considered unique in its environmental settings, implying great variability between canyon systems and adding to the heterogeneity observed on across-canyon scales. These canyon characteristics give support for their use in the present study to investigate the variable effects of scale in structuring deep-sea benthic assemblages.

The aim of this study was to address the question "what is the most determinant scale for processes that regulate structure, diversity and function of marine meiofauna in the deep sea?". A combination of four different datasets from deep-sea submarine canyon/slope ecosystems at six different geographic areas in the Northeast (NE) Atlantic were analysed in terms of community standing stocks, diversity, functional characteristics and structure on different spatial scales, using Nematoda as the most representative benthic component. The different spatial scales were: Irish Margin and Western Iberian Margin (ca. 1500 km apart), distance between adjacent canyon/slope areas (50–200 km), water depth (ca. 700, 1000, 3400 and 4300 m, representing different sampling locations within a canyon, 5–50 km apart), distance between cores from independent deployments (1–200 m), and vertical sediment depth differences (1–5 cm) (Fig. 1). Given the supposition that the size-scale of a group of organisms is important in identifying their communities' structure and function, we hypothesise that the sediment-dwelling meiofauna will be largely controlled by small-scale, local environmental conditions rather than large-scale differences between canyons, water depths and geographical areas or margins.

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2 Material and methods

2.1 Study areas

The samples used in this study stem from various canyon and slope systems from two geographical areas of the Northeast Atlantic, The Irish or Celtic Margin (IM) and the Western Iberian Margin (WIM).

The IM situated in the NE Atlantic is a highly productive system with significant primary production in the surface waters, which consequently supplies deep-sea sediments with high levels of organic matter and carbon (Lampitt et al., 1995; Longhurst et al., 1995) compared to other deep-sea areas. This is especially the case for mid-slope depths, which are influenced by additional export from the shelf or upper slope, where sediment organic loads are higher (Lampitt and Antia, 1997). At the Porcupine Seabight and further south along the Meriadzek Terrace, the margin is incised by numerous canyons and channels, which provide conduits for the transport of sediment from the shelf to the abyssal plain and over-bank turbidity currents, which deposit on the intervening terraces and spurs (Cunningham et al., 2005), but they also accumulate high amounts of sediments and organic matter. In addition, at the IM cascading of dense water masses down the slope is likely to occur (Ivanov et al., 2004) and may entrain fresh chlorophyll material rapidly down slope, as reported by Hill et al. (1998). Two different systems were investigated for this study, the Gollum Channel System and the Whittard Canyon. The Gollum Channel System is a tributary channel system incising the upper slope of the south-eastern Porcupine Seabight, and converging into one main channel that opens into the Porcupine Abyssal Plain. Samples were taken in the most northerly channel, the Bilbo channel, at ca. 700 m and 1000 m water depth (Ingels et al., 2011c). The upper 1000 m of the water column in this channel system is dominated by the Eastern North Atlantic Water and Mediterranean Outflow Water, resulting in relatively warm (8–10 °C) and saline water (ca. 35.5) between 700 and 1000 m water depth (White, 2006). The flow in the channel is dominated by the semi-diurnal tide, with a significant down-slope component and with currents strong enough to produce

significant turbidity. The Whittard Canyon comprises several deeply incised branches, extending from the shelf break south of the Goban Spur. Sampling locations at ca. 700 and 1000 m water depth were situated on the interfluvial area in between two upper NE branches (Ingels et al., 2006, 2011c). Down-slope sediment transport is dominated by turbidity currents in the head of the canyon, causing mud-flows to overspill the canyon walls and lead to deposition of mainly fine sediments in the adjacent areas.

The WIM comprises a narrow shelf and steep irregular slope, which is cut by various canyons. Hydrodynamic patterns in this area are mainly seasonal and are driven by seasonally varying winds which regulate the down- and upwelling regimes in winter and summer, respectively (Vitorino et al., 2002; Quaresma et al., 2007). The largest canyon, The Nazaré canyon, intersects the entire continental shelf and acts as a temporary sediment trap with intermittent transport of sediments and organic matter to the abyssal plain (de Stigter et al., 2007; Masson et al., 2011). Samples were taken at ca. 3400 and 4300 m water depth in the canyon (sediment-laden terrace, and canyon floor, respectively), and at similar depths along the adjacent slope to the north of the canyon (Ingels et al., 2009). The relatively short Cascais Canyon begins at the shelf edge southwest of the mouth of the Tagus Estuary and extends to the Tagus Abyssal Plain. The Setúbal Canyon cuts the continental shelf close to the Sado River Estuary, and also leads to the Tagus Abyssal Plain. Comparable sedimentation regimes have been observed for both the Cascais and Setúbal canyons, with accumulation of sediment in the upper parts and limited down-canyon transport (de Stigter et al., 2011). Current regimes seem variable in both canyons. Samples in both canyons were taken at ca. 3400 and 4300 m water depth, and more or less along the axes of the canyons (Ingels et al., 2011a)

2.2 Sampling design and sample processing

Data from four different deep-sea canyon studies (Ingels et al., 2009, 2011a–c) were merged (totalling 17 273 nematode individuals belonging to 248 different genera) to investigate the most important scale of variability in structure, diversity and function of

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small sediment-dwelling fauna in the deep sea. The samples cover two geographically distant margins (IM, WIM) which lie about 1500 km apart. For each margin, several canyon/slope areas were sampled by means of a coring device (for details on coring devices see Table 1) producing sediment cores with an intact sediment-water interface and similar cross-surface areas (Table 1). At each of the six canyon/slope areas, cores were taken at two different stations (ca. 700 and 1000 m for the IM, and ca. 3400 and 4300 m for the WIM). At each location, a minimum of three independently replicated (repeated deployments of the coring device) cores were taken. Each sediment core was subsequently split into 1-cm layers down to 5 cm vertical depth. An overview of the sampling design and meta-information on the samples is given in Fig. 1 and Table 1. A total of 162 samples were used for this study.

Nematoda, the most abundant metazoan phylum in the marine environment, was used as a model taxon for the small benthic fauna. Borax-buffered formalin (4 %) sediment samples were used to extract the meiofauna using standard procedures (Heip et al., 1985; 32–1000 µm sieves, LUDOX HS as centrifugation medium) to separate the organisms from the sediment particles. All nematodes were counted and between 100 and 150 individuals were picked out randomly from each 1-cm sample, transferred to glycerine (Seinhorst, 1959) and mounted on slides. All nematodes were identified under a compound microscope (100× magnification) to genus level using Platt and Warwick (1988), taxonomic literature of the Nematode Library at Ghent University, and the NeMys nematode database and identification keys (Deprez et al., 2005; http://nemys.ugent.be/). Specimens that could not be identified to the genus level were assigned to the appropriate higher taxon level. All individuals were grouped into four feeding types based on buccal morphology and teeth composition sensu Wieser (1953): selective deposit feeders (1A), non-selective deposit feeders (1B), epistratum feeders (2A), and predators/scavengers or omnivores (2B). This classification was amended with one extra group to account for "chemosynthetic" nematodes that lack a mouth and buccal cavity, have a degenerated alimentary canal and live in association with symbiotic micro-organisms (Ingels et al., 2011c). In addition, each nematode

individual was assigned a c–p score (score from 1 to 5 reflecting life history with 1 = colonizer and 5 = persister; in this context colonizers are regarded as r-strategists, and persisters are regarded to be k-strategists; cf. Bongers (1990) and Bongers et al., 1991). Length (excluding filiform tails) and maximum width were measured using a Leica DMR compound microscope and Leica LAS 3.3 imaging software.

2.3 Data treatment and analysis

Various descriptors for nematode structure, diversity and function were used to test the importance of different scales in determining community patterns (Table 2). Community structure was determined by using the relative abundances of genera in the sample assemblage. Diversity descriptors used were the four Hill numbers (Hill, 1973) and expected number of genera for a normalised sample size of 51 individuals (EG(51)), based on the formula by Sanders (1968) which was later corrected by Hurlbert (1971). Hill numbers were used because they give a measure of both richness, as well as equitability (evenness) of the communities studied (Heip et al., 1998). As functional descriptors, we used Trophic Diversity (TD) and the Maturity Index (MI). We used the reciprocal value of TD as defined by Heip et al. (1998), so that higher values correspond with higher trophic complexity, and it was modified for use with the four Wieser (1953) feeding groups and the extra "chemosynthetic" guild (Ingels et al., 2011c). The MI was originally defined by Bongers (1990) for soil nematodes, but has been applied to marine nematode communities (Bongers et al., 1991). The MI is a useful descriptor in that it characterises the community in terms of life-history and -strategies of its members and has been successfully used to infer various types of disturbance and subsequent recolonisation processes. Similarly to TD, MI is based on autecological information, but it is based on a broader character complex.

To distinguish the significance of different scale effects in determining deep-sea meiofauna communities four different sets of community descriptors were analysed (Table 2) by means of multivariate Permutational Analyses of Variance (PERMANOVA; Anderson, 2005) using PERMANOVA+ and Primer v6 (Clarke and Gorley, 2006;

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Anderson et al., 2008). Genera relative abundance data were standardised for sample size, square-root transformed, and Bray-Curtis was used as a similarity measure. The diversity descriptor data (Hill numbers, EG(51)) were normalised sensu Clarke and Gorley (2006) and Euclidean distance was used to construct the resemblance matrix. The same diversity data treatment was applied to the sets of standing stock (total abundance, total biomass) and functional descriptors (TD, MI).

For the PERMANOVA tests, we used a mixed-model hierarchical design (Table 3) with four factors: Area (Ar, fixed, with levels "Whittard", "Gollum", "Nazaré", "Setúbal", "Cascais", "Slope"), Water Depth (WD, fixed, with levels "700 m", "1000 m", "3400 m", "4300 m"), Core (Co, random, identifying each core in the dataset to account for replicate variability at the station level and adding an extra spatial scale to the model), and Sediment Depth (SD, fixed, with levels "0–1", "1–2", "2–3", "3–4", "4–5", identifying each sediment layer). Because the different levels of WD were not represented at each margin, the dataset was split into two groups, one for each margin.

The non-replicated nature of the vertical sediment layers within each core warranted a split plot design with Co nested in Ar and WD, leading to a repeated measures analysis, whereby the main-factor test was followed by a pairwise comparison test within each significant double or triple factor interaction term to investigate significant effects in the full-model test. The nesting of Co in Ar and WD had as a consequence that the variability contained in the term Co (Ar × WD) × SD, indicative of the variability of each layer within each core, is included in the residual term, leading to a more conservative test. Because of the unbalanced design (not all sediment layers are fully replicated for each Ar × WD combination) in the PERMANOVA model we used type III sums of squares (partial) leading to a conservative test while maintaining independence between terms. To assess the magnitude of the spatial variation at each spatial scale we used the estimated components of variation (ECV) as a percentage of the total variation. When negative variance components were encountered, these were set to zero in the assumption that they were sample underestimates of small or zero variances (Benedetti-Cecchi, 2001; Fletcher and Underwood, 2002). Several non-metrical

multidimensional scaling plots (MDS) were used to illustrate the variability contained within each descriptor set and visualise the main-factor and interaction effects.

3 Results

The community structure was significantly different for all factors and interaction terms (except for WD × SD at the WIM, Table 3), with greatest variability found at the station level (Ar × WD) for both IM and WIM margins as indicated by ECV values (Fig. 2a). Relative effect sizes were larger for the IM, except for the factor Ar. Community effects of WD, Core (Co) and three-way interaction terms were lower than those of Ar, SD and Ar × WD (station scale) at both margins (Fig. 2a). The effect size of sediment depth (SD) occupied third place at the WIM and was placed second at the IM, implying important variability occurring at the sediment micro-scale. The SD effect is clearly illustrated in Bray-Curtis space in Fig. 3a, showing the increasing variability contained within deeper SD layers. The 0–1 cm layers group tightly (smallest grey area), while with increasing SD the resemblance between samples gradually increases, with maximum variability exhibited for the 4–5 cm layer.

Figure 3c, d shows the different community variability contained within each area, and within each water depth, respectively as attested by the ECV values in Fig. 2a. Area differences, as evidenced by ECV values (Fig. 2a), are larger at the WIM than at the IM, which is also illustrated by the differential size of overlap between the grey-shaded areas in Fig. 3c for each margin. Water-depth differences are smaller at the WIM compared to the IM, as attested by the smaller overlap of grey-shaded areas in Fig. 3d and the WD ECV values (Fig. 2a) at the IM compared to those of the WIM.

Several double interaction terms were significant (Table 3; Fig. 2a) prompting us to investigate pairwise comparisons within each significant term (Supplement, Appendix A, Table A1). For the IM, these show that differences between the surface layers and the deepest sediment layers are more pronounced, and that these differences are variable between different areas and water depths. Similar patterns are observed for the WIM.

To investigate the significant three-way interaction factor (Ar × WD × SD), subsequent pairwise comparisons were performed within the three-way term for both margins (Table A1), and the reasons for the three-way interaction can be seen in Bray-Curtis space in Fig. 3b–d. For the IM, area differences are clear for nearly all WD × SD combinations (Table A1). WD differences on the other hand were only significant for each of the Whittard Canyon Ar × SD combinations. Pairwise SD comparisons for each station (Ar × WD) indicate that SD variability is a general phenomenon at the IM, with hardly any significant differences between stations. The SD gradient that can be seen for the IM in Fig. 3b is indeed similar for all stations, whilst the differences between WDs are more pronounced for the Whittard Canyon compared to the Gollum Channels.

At the WIM, there are three distinct groups of stations, visible in Fig. 3b. At each station (Ar × WD, exhibiting the largest effect scale), the variability contained along the vertical sediment depth differs considerably, with for instance smallest SD variation observed for the Nazaré 3400 m station and greatest SD variation at the Nazaré 4300 m station (Fig. 3b).

Core effects were significant for both margins (PERMANOVA; $p < 0.01$), but were small compared to Ar, SD and station (Ar × WD) effects (Fig. 2a). Sediment depth variability within each core was high as illustrated by the spatial coverage in the MDS plots (Fig. 3e, f), but was variable depending on the Ar, WD or Ar × WD considered.

The PERMANOVA results for the diversity descriptors (Table 3) at the IM indicate that SD is the main factor causing most variability (SD differences are greater when comparing surface layers with the deepest layers, cf. pairwise comparisons), and Ar × SD the most important interaction term. Area, WD and Ar × WD, although significant, constitute only minor sources of variability. The reason behind the significant Ar × SD interaction lies in the fact that SD diversity differences are differently expressed in the Gollum and Whittard areas (Figs. 2b, 4a), and this is confirmed by pairwise comparison tests (Supplement, Appendix A, Table A2). Together with the significant double interaction terms, the significant three-way interaction term Ar × WD × SD suggests that SD variability is also differently expressed within each level of WD and Ar × WD at the IM (Table 2b;

Fig. 4b). The case for the WIM is different; SD and Ar are the most important in terms of effect size (Fig. 2b). Similar to the IM, however, SD diversity differences vary according to which level of Ar × WD is considered. These interactions are visible in the MDS plot of Fig. 4b. The factor Co was not significant, indicating no differences between

5 cores from different deployments at each station. Overall, diversity patterns between margins differed with a partial separation of samples from different margins based on Euclidean distance values (Fig. 5a), but this may have been caused by the WD differences between margins inherent to our sampling design since a very similar separation is visible for the factor WD (Fig. 5b).

10 The PERMANOVA results for the functional descriptors can be interpreted in the same way as the diversity results. For the IM, SD is the main factor with the highest effect size (Fig. 2d). The IM Ar × SD significant interaction term signifies the differential SD diversity in different areas (Fig. 4c). The main factors Ar and WD only cause minor variability based on function descriptors. For the WIM, SD is again the most important

15 main factor for which variability is significant (Fig. 2d), with differences between different areas and stations (Fig. 4d) and see pairwise comparisons in Table A3 (Supplement, Appendix A), causing the interaction terms Ar × WD, Ar × SD, and Ar × WD × SD to be significant as well. The factor Co was not significant, indicating no differences between different deployments at each station. No clear margin or water depth separation was

20 observed based on Euclidean distance measures of sample diversity (Fig. 5c, d), but variability between samples was greater at the WIM than at the IM as illustrated by the spatial coverage of the sample clouds in Fig. 5c, d.

The variability observed for standing stocks is mainly caused by differences at the scale of sediment layers. This is particularly the case at the IM, where ECV for the

25 factor SD explains 55 % of the total variation; at the WIM, this is only 21.3 %. At the IM, the SD differences are variable between different levels of Ar and WD effects, resulting in significant interactions (Ar × SD, WD × SD, Ar × WD × SD; Fig. 2c, Supplement, Appendix A, Table A4), which are clearly discernible in Bray-Curtis space as illustrated in Fig. 4e. Overall, no clear standing stock patterns arose in the MDS plot of Fig. 5e, f

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due to margin or WD differences, but the WD × SD effect at the IM is visible in that the 1000 m sample points are more dispersed compared to the 700 m sample points.

4   Discussion

The aim of this study was to analyse and assess the importance of different spatial scales in structuring deep-sea meiofaunal communities. To achieve this, a large set of sediment samples from different submarine canyons along the European margins in the northeast Atlantic, encompassing spatial scales ranging centimetres to 100s of kilometres, were analysed for nematode community patterns, using different sets of descriptors to describe community structure, diversity, function and standing stocks. This study is the first to include functional parameters as descriptors of meiofauna communities to reveal the importance of different spatial scales and discuss associated processes on deep-sea benthic communities. In support of using nematodes as representative taxon, we note here that they comprise 90 % or more of the metazoan organisms in the deep sea, they exhibit very high species and genus richness, are sensitive to environmental perturbations and have well established functional traits which have been used successfully in biodiversity and ecosystem functioning studies (Danovaro, 2012).

By using submarine canyons – assumed to be the most heterogeneous environments in the deep marine realm – to test the importance of different spatial scales, we perhaps reduce the possibility that larger scale gradients, such as latitudinal and bathymetrical, attain an important status in driving benthic assemblages because local-scale heterogeneity can be the paramount effect in structuring the resident fauna (Rex et al., 1993, 2006; Rex and Etter, 2010). Yet, considering the pervasiveness of canyons along the world's continental margins (De Leo et al., 2010; Harris and Whiteway, 2011), an important source of heterogeneity may be omitted in studies that exclude canyon ecosystems in assessing spatial-scale importance.

4.1 Margins, water depth and inter-canyon comparisons: the large spatial patterns and processes

Latitudinal and bathymetrical gradients in benthic assemblages have been widely recognised in the deep sea (Rex et al., 1993, 2006; Rex and Etter, 2010), including for meiofaunal organisms (Rex et al., 2001; Lambshead et al., 2002; Mokievsky and Azovsky, 2002; Mokievsky et al., 2007). These large geographical gradients may represent environmental gradients or contrasts that drive the faunal assemblages. We noticed clear differences in community structure – and to some extent diversity – between the IM and WIM, but we cannot rule out that these are the result of bathymetric variability since water-depth comparisons were not the same at each investigated margin. Water depth and latitude (or margin differences) may be inextricably linked because of ocean basin topography, water-mass characteristics, oceanographic currents and fronts, and sampling design, and the role of depth needs to be accounted for when analysing latitudinal patterns to avoid confounding the role of the most important scale (Lambshead et al., 2001; Rex et al., 2001). In doing so, Rex et al. (2001) suggested that nematode patterns are predominantly shaped by bathymetrical changes rather than latitudinal differences when comparing only those two variables. Within each margin, our analyses showed that WD affected community structure and diversity, but not biomass, whilst nematode function only differed with WD at the Irish Margin. The benthic environment at different margins can be typified by different euphotic productivity regimes, and consequently variable phytodetrital influx and quality. Water depth differences may add to the gradient created by variable surface production through the degradation processes that ensue; deeper stations may receive more degraded organic matter compared to shallower locations, resulting in benthic structure and diversity differences. The contrast between 700 m and 1000 m stations at the IM in terms of phytodetrital influx and presence of organic matter may be greater than is the case when comparing 3400 and 4300 m depth stations (WIM), because of the higher down-canyon transport, more rugged topography, and greater accumulation rates in the upper regions

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of the canyon/channel systems compared to the deeper parts. The nematode functional differences between water depths at the IM, and the lack of them at the WIM, may be representative for such contrasts – nematode trophic diversity (function) may have complied with the differences in food arrival. Exacerbating the effect of the here observed WD-contrast between margins could be the underlying regional differences in euphotic production. The North Atlantic is a particularly productive area with high deep-sea fluxes because of inadequate zooplankton grazing in the upper water column (Longhurst et al., 1995; Longhurst, 2007). This is particularly the case for the Porcupine Abyssal Plain and adjacent margin where the Gollum Channels are situated and further south along the Goban Spur, below which the Whittard Canyon is located (Levin et al., 2001a, and references therein). Phytodetrital fluxes to the deep seafloor are much less common at the WIM than at the IM (Levin and Gooday, 2003, and references therein). Water mass characteristics at each margin may have added to the benthic contrasts. The IM locations were characterised by higher temperatures and salinity than the deeper stations at the WIM due to their position within the Mediterranean Outflow Water (Ingels et al., 2011c). Enhanced phytodetrital input and higher temperatures at and above the seabed can stimulate bacterial growth and densities, consequently adding to the total pool of meiobenthic food resources (Moeseneder et al., 2012; Lochte and Turley, 1988; Boetius et al., 2000) with subsequent nematode structural and diversity changes. Reduced oxygen availability in areas associated with high production levels and carbon burial, such as reported for Oxygen Minimum Zones worldwide (including canyons, e.g. De Leo et al. (2012)), should also be considered at the WD scale. Reduced oxygen levels may stimulate meiofauna such environments because their high tolerance to hypoxia, the abundant food supply and release from predation by the reduced macro- and megafauna (Levin, 2003). Sedimentary organic enrichment as observed in the Whittard Canyon (Duineveld et al., 2001; Ingels et al., 2011c) may even lead to chemotrophic species benefiting from the resulting reduced conditions (Ingels et al., 2011c). For the Whittard Canyon and Gollum Channels (IM), the abundance of chemotrophic species (*Astomonema southwardorum* and *Parabostrichus bathyalis*)

varied substantially with water depth (Ingels et al., 2011c, Tchesunov et al., 2012), possibly explaining the WD differences observed for community structure, diversity and function. These community differences may also contribute to the higher WD effect-sizes observed for the IM compared to the WIM, since chemotrophic nematode genera are absent from the WIM in the here analysed dataset. Water depth differences may also bear a relation to grain size differences, particularly in canyons where hydrodynamic flow is able to sort sediment particles efficiently along a WD gradient. Grain size is known to regulate benthic diversity (Etter and Grassle, 1992) beyond the effects of water depth and food input (Leduc et al., 2012), and a WD effect on community structure and diversity is evident here. Significant community descriptor differences between WD levels hence suggest the existence of regulating mechanisms on the associated spatial scale, but differences were not clear for standing stock descriptors, suggesting biomass and abundance patterns are likely driven by patchiness and processes on smaller spatial scales within each investigated canyon system.

Turning to the regional spatial scales within each margin separately, we have to appreciate the contrasts posed between different areas, represented by the different canyon systems. It was clearly shown that the canyon communities differed between different margins, but variability is also high within each margin. Area differences were significant for the community structure and the diversity and functional descriptors (Table 2a–c), albeit with several significant interactions with WD and SD, implying levels of variability being expressed differently within different factor combinations. Submarine canyons are arguably the most heterogeneous habitats in the deep sea, displaying high diversity in terms of morphology, topography, sediment transport processes, hydrodynamic activity, geological structure, size, sinuosity, substratum types, position and distance from land and river systems; all characteristics that may be determinative for the type of fauna that resides in canyons. Inter-canyon community and diversity differences were more pronounced for the WIM than for the IM, even though the Gollum Channels and Whittard Canyon (IM) appear more different in terms of geomorphological structure compared to the canyons and slope area at the WIM. The integration of

slope samples in the canyon dataset at the WIM, and the fact that not all WIM canyons are connected to river systems may be the reason for the higher Ar effect size at the WIM. This highlights the importance of inter-canyon differences (i.e. Ar differences) and processes that act on this scale and their role in regulating benthic communities, which seems superimposed on the effects associated with continental margin and WD differences.

4.2 Stations, replicates and sediment depth comparisons: the small spatial scales and processes

The heterogeneity observed between canyons extends to the within-canyon comparison between subhabitats or stations (Ar × WD, 5–50 km apart), and between the locations of replicated samples at each station (Co (Ar × WD), 1–200 m). Highest effect sizes on community descriptors occurred at the level of stations (Ar × WD) and vertical sediment depth, implying that processes that act on these spatial scales are determinative for structure, diversity, function and standing stocks of the resident communities. Differences between replicate locations (Co(Ar × WD)) were minor compared to SD and station differences, suggesting the distances between replicate samples hosted no great faunal variability. Only for the community structure, significant differences were observed between replicates, with similar effect sizes as Ar and WD differences. Community structure differences between adjacent patches of seafloor indicate that small-scale heterogeneity may be at the basis of niche separation for different genera in this case, with different genera benefiting from different environmental conditions over small (1–200 m) distances. Diversity, function and standing stocks, on the other hand are more uniform over these distances, and seem more susceptible to differences over cm scales.

Submarine canyons offer a highly heterogeneous habitat relative to similar depths on slopes (Levin and Gooday, 2003), which translates into numerous available subhabitats within these systems (flanks, walls, overhangs, thalweg, sedimented terraces and slopes, etc.). Although this study only investigated sedimented areas within the

canyon systems, increased heterogeneity also applies for these subhabitats as indicated by the high Ar × WD (station) interaction effect sizes. Processes acting on the station scale, such as hydrodynamic activity and frequency and intensity of sediment disturbance events may be superimposed on the patterns caused by larger spatial scale processes such as regional or water depth-dependent phytodetrital input, and this seems particularly the case for submarine canyon systems. Environmental variables such as oxygen, temperature, resource availability, and grain size may vary with within-canyon morphology and associated flow dynamics, including enhanced currents and detrital flows, exerting control on the faunal communities present (Vetter and Dayton, 1999). Topographical effects on the within-canyon scale have also been observed to drive the quantity and availability of food resourcesleading to different faunal communities at short distances from each other (McClain and Barry, 2010). The aggregation of organisms at locations with enhanced food availability within a canyon may augment the effects of biotic interactions between different faunal groups and species, leading to further fluctuations of community characteristics over small to medium distances (Gallucci et al., 2008a; McClain and Barry, 2010). The within-canyon processes relevant for the km-scale mentioned here are likely more important than the larger-scale processes in this study judging by the high Ar × WD variance components, particularly for community structure (Fig. 2a).

Community structure differs between stations, and hence the processes associated with that scale, but the sediment depth effect is here considered as the most important factor affecting community diversity, function and standing stocks and may be related to numerous processes, environmental and biological, acting on the cm scale. The implications of this are not limited to the vertical gradients per se, but may be seen as representative for small horizontal variations along the deep-sea floor. Environmental gradients on the cm scale are imperative in driving benthic assemblages because they define the suitability of the niches that are exploited by different small-sized benthic taxa, and are influenced by the activities of the taxa themselves (e.g. bioturbation and nutrient flux generation). Previous studies suggest that the spatial dynamics of

meiofauna communities are highly localized (e.g. Gallucci et al., 2008b; Fonseca et al., 2010; Guilini et al., 2011), but small-scale patterns of deep-sea meiofauna are still poorly understood (Snelgrove and Smith, 2002). It is believed that like macrofauna organisms, meiofauna species are patchily distributed with patch sizes ranging a few centimetres to meters (Gallucci et al., 2009) which accords with our results. Nematodes, for instance, are attracted to patches with high levels of food, but the scale on which food input drives nematode communities varies from local scale patches to regional scale phytodetrital input. Fonseca et al. (2010) reported that chloroplastic pigments, as an indicator of food availability, may vary most on very small scales (cm), implying that these are the results of local variability. In the same study, however, sediment depth was not the most important scale of variability and hence stands in contrast with our results. The distances between cores was one of the moret important scales in the Arctic deep-sea study, possibly related to the distribution patterns of chloroplastic pigment content of the sediments, but the authors also suggested that other (unmeasured) environmental variables are likely the main cause of small-scale fauna variability. The contrast between Arctic deep-sea sediments (Fonseca et al., 2010) and the canyon sediments in the present study may explain the difference in importance of vertical scale in driving communities; whilst Arctic deep-sea sediments are characterised by a surficial layer of phytodetrital food over larger areas, regulated by strong seasonality, canyon sediments are characterised by different levels of disturbance and temporal dynamics allowing the burial of organic matter in deeper sediment layers and enhancement of microhabitat variability. The strong heterogeneity on small spatial and short temporal (disturbance-related) scales in canyon sediments may hence add to the contrasting observations.

It is on the small cm scale that also the sediment grain size should be considered as a direct regulating factor for benthic communities. Particle-size diversity is known to positively influence meiofaunal diversity through increased partitioning of food resources based on particle size, and/or greater habitat heterogeneity (Leduc et al., 2012 and references therein), which would also result in higher functional complexity of the

community (Ingels et al., 2009, 2011c). In the case of canyons, grain size composition can vary greatly between locations because of variable sediment deposition and hydrodynamic sorting. Disturbance events such as gravity flows and slumps, add to this variability by redistributing the sediments, as does the feeding and burrowing activity of benthic organisms. These processes cause granulometric differences predominantly on very small scales, supporting their importance in regulating benthic patterns along the vertical sediment depth and horizontal cm scale.

Both food availability and strength and frequency of disturbance events can be considered in the patch mosaic model, whereby the spatio-temporal mosaic of sediment-dwelling communities is driven by highly localised processes, such as colonisation following disturbance events. This supposition is not limited to the meiofauna, macrofauna also exhibits spatial dispersion patterns driven by the presence of a mosaic of micro-habitats in canyon sediments (Lamont et al., 1995). Further evidence for this can be found in the association of meiofauna with biogenic structures, such as foraminifera and sponges (Levin et al., 1986; Hasemann and Soltwedel, 2011) which may provide protection against small disturbance events and may indirectly increase food-availability thereby attracting a suite of prokaryotic and metazoan organisms (Levin and Gooday, 1992) or providing a more complex habitat structure (Hasemann and Soltwedel, 2011). In addition, the physically controlled sedimentary environment is modified at the mm to cm scale by bioturbation, a common feature in many canyons.

Considering the biochemistry of sediments, we have to appreciate the role of oxygen and other chemical gradients along the vertical scale, since it has been shown that such variables affect the meiobenthic communities greatly (Vanreusel et al., 1995; Soetaert et al., 1997, 2009; Cook et al., 2000; Gooday et al., 2000; Moodley et al., 2000; Braeckman et al., 2011). Moreover, the interaction between oxygen and food has been found to affect meiofauna assemblages via mechanics explained by the TROX model (Jorissen et al., 1995). In organically enriched canyon sediment patches, the ecosystem is no longer food-controlled, but instead oxygen takes over and drives the structure and diversity of benthic fauna (Jorissen et al., 1995). This is exemplified here at the IM, with

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higher structural and functional diversity compared to the WIM, partly because of the presence of chemotrophic nematode genera in response to reduced micro-patches, and a redox layer appearing closer to the sediment surface (Ingels et al., 2011c). Hence, the role of sediment depth is more important at the IM for different commu-
5 nity descriptors (Fig. 2a–d). In recent years, evidence has emerged that oxygen could be a particularly powerful mediator in creating patches (anoxic micro-environments) and/or small-scale reduced environments, in areas that are not truly chemosynthetic (e.g. Van Gaever et al., 2004; Ingels et al., 2011c) with effects on meiobenthic diversity and function as a result.

10   The results of the present study suggest that differences on small spatial scales are more important than larger spatial scales in identifying benthic patterns. If we are to improve our understanding of these patterns and underlying processes that drive sediment-dwelling faunal communities, their structure, diversity and functioning, we need to focus on the small scales in deep-sea environments, particularly for canyons.
15 Patchy input and local reworking of phytodetritus and sediments, seafloor microtopography, sediment biogeochemistry as well as benthic biogenic processes in the sediment (e.g. bioturbation, biogeochemical processes mediated by fauna and chemical interactions), and disturbance events, are likely the cause of the high variability observed along the vertical sediment scale in the present study and further investigations into
20 the causal mechanisms are warranted.

Supplementary material related to this article is available online at:
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Anderson, M.: PERMANOVA: Permutational Multivariate Analysis of Variance, Department of Statistics, Auckland, 2005.

Anderson, M. J., Gorley, R. N., and Clarke, K. R.: PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods, PRIMER-E Ltd, Plymouth, 2008.

Andrassy, I.: The determination of volume and weight of nematodes, Acta Zool. Hung., 2, 1–15, 1956.

Benedetti-Cecchi, L.: Variability in abundance of algae and invertebrates at different spatial scales on rocky sea shores, Mar. Ecol.-Prog. Ser., 215, 79–92, 2001.

Boetius, A., Ferdelman, T., and Lochte, K.: Bacterial activity in sediments of the deep Arabian Sea in relation to vertical flux, Deep-Sea Res. Pt. II, 47, 2835–2875, 2000.

Bongers, T.: The maturity index: an ecological measure of environmental disturbance based on nematode species composition, Oecologia, 83, 14–19, 1990.

Bongers, T., Alkemade, R., and Yeates, G. W.: Interpretation of disturbance-induced maturity decrease in marine nematode assemblages by means of the maturity index, Mar. Ecol.-Prog. Ser., 76, 135–142, 1991.

Braeckman, U., Provoost, P., Moens, T., Soetaert, K., Middelburg, J. J., Vincx, M., and Vanaverbeke, J.: Biological vs. physical mixing effects on benthic food web dynamics, Plos One, 6, e18078, doi:10.1371/journal.pone.0018078, 2011.

Clarke, K. R. and Gorley, R. N.: PRIMER v6: User Manual/Tutorial, PRIMER-E, Plymouth, UK, 2006.

Connell, J. H.: Diversity in tropical rain forests and coral reefs – high diversity of trees and corals is maintained only in a non-equilibrium state, Science, 199, 1302–1310, 1978.

Cook, A. A., Lambshead, P. J. D., Hawkins, L. E., Mitchell, N., and Levin, L. A.: Nematode abundance at the oxygen minimum zone in the Arabian Sea, Deep-Sea Res. Pt. II, 47, 75–85, 2000.

Cunningham, M. J., Hodgson, S., Masson, D. G., and Parson, L. M.: An evaluation of along- and down-slope sediment transport processes between Goban Spur and Brenot Spur on the Celtic Margin of the Bay of Biscay, Sediment. Geol., 179, 99–116, 2005.

Danovaro, R.: Extending the approaches of biodiversity and ecosystem functioning to the deep ocean, in: Marine Biodiversity and Ecosystem Functioning: Frameworks, Methodologies, and

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Integration, edited by: Solan, M., Aspden, R. J., and Paterson, D. M., Oxford University Press, Oxford, 115–126, 2012.

De Leo, F. C., Smith, C. R., Rowden, A. A., Bowden, D. A., and Clark, M. R.: Submarine canyons: hotspots of benthic biomass and productivity in the deep sea, P. Roy. Soc. B-Biol. Sci., 227, 2783–2792, 2010.

De Leo, F. C., Drazen, J. C., Vetter, E. W., Rowden, A. A., and Smith, C. R.: The effects of submarine canyons and the oxygen minimum zone on deep-sea fish assemblages off Hawai'i, Deep-Sea Res. Pt. I, 64, 54–70, 2012.

de Stigter, H. C., Boer, W., Mendes, P., Jesus, C. C., Thomsen, L., van den Bergh, G. D., and van Weering, T. C. E.: Recent sediment transport and deposition in the Nazare Canyon, Portuguese continental margin, Mar. Geol., 246, 144–164, 2007.

de Stigter, H. C., Jesus, C. C. S., Boer, W., Richter, T. O., Costa, A., and van Weering, T. C. E.: Recent sediment transport and deposition in the Lisbon-Setúbal and Cascais submarine canyons, Portuguese continental margin, Deep-Sea Res. Pt. II, 58, 2321–2344, 2011.

Deprez, T., Steyaert, M., Vanaverbeke, J., Speybroeck, J., Raes, M., Derycke, S., De Smet, G., Ingels, J., Vanreusel, A., Van Gaever, S., and Vincx, M.: NeMys, World Wide Web electronic publication, nemys.ugent.be, Department of Marine Biology, Ghent University, 2005.

Duineveld, G., Lavaleye, M., Berghuis, E., and de Wilde, P.: Activity and composition of the benthic fauna in the Whittard Canyon and the adjacent continental slope (NE Atlantic), Oceanol. Acta, 24, 69–83, 2001.

Eckman, J. E. and Thistle, D.: Small-scale spatial pattern in meiobenthos in the San-Diego Trough, Deep-Sea Res., 35, 1565–1578, 1988.

Etter, R. J. and Grassle, J. F.: Patterns of species diversity in the deep sea as a function of sediment particle size diversity, Nature, 360, 576–578, 1992.

Fletcher, D. J. and Underwood, A. J.: How to cope with negative estimates of components of variance in ecological field studies, J. Exp. Mar. Biol. Ecol., 273, 89–95, 2002.

Fonseca, G., Soltwedel, T., Vanreusel, A., and Lindegarth, M.: Variation in nematode assemblages over multiple spatial scales and environmental conditions in Arctic deep seas, Prog. Oceanogr., 84, 174–184, 2010.

Gallucci, F., Fonseca, G., and Soltwedel, T.: Effects of megafauna exclusion on nematode assemblages at a deep-sea site, Deep-Sea Res. Pt. I, 55, 332–349, 2008a.

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Gallucci, F., Moens, T., Vanreusel, A., and Fonseca, G.: Active colonisation of disturbed sediments by deep-sea nematodes: evidence for the patch mosaic model, Mar. Ecol.-Prog. Ser., 367, 173–183, 2008b.

Gooday, A. J., Bernhard, J. M., Levin, L. A., and Suhr, S. B.: Foraminifera in the Arabian Sea oxygen minimum zone and other oxygen-deficient settings: taxonomic composition, diversity, and relation to metazoan faunas, Deep-Sea Res. Pt. II, 47, 25–54, 2000.

Guilini, K., Soltwedel, T., van Oevelen, D., and Vanreusel, A.: Deep-sea nematodes actively colonise sediments, irrespective of the presence of a pulse of organic matter: results from an in-situ experiment, Plos One, 6, e18912, doi:10.1371/journal.pone.0018912, 2011.

Harris, P. T. and Whiteway, T.: Global distribution of large submarine canyons: geomorphic differences between active and passive continental margins, Mar. Geol., 285, 69–86, 2011.

Hasemann, C. and Soltwedel, T.: Small-scale heterogeneity in deep-sea nematode communities around biogenic structures, Plos One, 6, e29152, doi:10.1371/journal.pone.0029152, 2011.

Heip, C., Vincx, M., and Vranken, G.: The ecology of marine nematodes, Oceanogr. Mar. Biol., 23, 399–489, 1985.

Heip, C., Herman, P., and Soetaert, K.: Indices of diversity and evenness, Oceanis, 24, 61–87, 1998.

Hill, A. E., Souza, A. J., Jones, K., Simpson, J. H., Shapiro, G. I., McCandliss, R., Wilson, H., and Leftley, J.: The Malin cascade in winter 1996, J. Mar. Res., 56, 87–106, 1998.

Hill, M. O.: Diversity and evenness: a unifying notation and its consequences, Ecology, 54, 427–432, 1973.

Hubbell, S. P.: The Unified Neutral Theory of Biodiversity and Biogeography, Princeton University Press, Princeton, New Jersey, USA, 2001.

Hurlbert, S. H.: The nonconcept of species diversity: a critique and alternative parameters, Ecology, 52, 577–586, 1971.

Huston, M. A.: Local processes and regional patterns: appropriate scales for understanding variation in the diversity of plants and animals, Oikos, 86, 393–401, 1999.

Ingels, J.: Structural and functional biodiversity of metazoan meiobenthic communities in submarine canyon and slope sediments, Ph. D. thesis, Ghent University, Ghent, 2009.

Ingels, J., Van Rooij, D., and Vanreusel, A.: HERMES RV Belgica 2006/13 biology cruise report (23–29 June 2006): Gollum Channels and Whittard Canyon, Internal publication, RCMG, Ghent University, 2006.

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

Ingels, J., Billett, D. S. M., Kiriakoulakis, K., Wolff, G. A., and Vanreusel, A.: Structural and functional diversity of Nematoda in relation with environmental variables in the Setúbal and Cascais canyons, Western Iberian Margin, Deep-Sea Res. Pt. II, 58, 2354–2368, 2011a.

Ingels, J., Billett, D. S. M., and Vanreusel, A.: An insight into the feeding ecology of deep-sea canyon nematodes – results from field observations and the first in-situ ^{13}C feeding experiment in the Nazaré Canyon, J. Exp. Mar. Biol. Ecol., 396, 185–193, 2011b.

Ingels, J., Tchesunov, A., and Vanreusel, A.: Meiofauna in the Gollum Channels and the Whittard Canyon, Celtic Margin – how local environmental conditions shape nematode structure and function, Plos One, 6, e20094, doi:10.1371/journal.pone.0020094, 2011c.

Ivanov, V. V., Shapiro, G. I., Huthnance, J. M., Aleynik, D. L., and Golovin, P. N.: Cascades of dense water around the world ocean, Prog. Oceanogr., 60, 47–98, 2004.

Jorissen, F. J., de Stigter, H. C., and Widmark, J. G. V.: A conceptual model explaining benthic foraminiferal microhabitats, Mar. Micropaleontol., 26, 3–15, 1995.

Jumars, P. A.: Deep-sea species diversity – does it have a characteristic scale, J. Mar. Res., 34, 217–246, 1976.

Kiriakoulakis, K., Blackbird, S., Ingels, J., Vanreusel, A., and Wolff, G. A.: Organic geochemistry of submarine canyons: the Portuguese margin, Deep-Sea Res. Pt. II, 58, 2477–2488, 2011.

Lambshead, P. J. D., Tietjen, J., Moncrieff, C. B., and Ferrero, T. J.: North Atlantic latitudinal diversity patterns in deep-sea marine nematode data: a reply to Rex et al., Mar. Ecol.-Prog. Ser., 210, 299–301, 2001.

Lambshead, P. J. D., Brown, C. J., Ferrero, T. J., Mitchell, N. J., Smith, C. R., Hawkins, L. E., and Tietjen, J.: Latitudinal diversity patterns of deep-sea marine nematodes and organic fluxes: a test from the central equatorial Pacific, Mar. Ecol.-Prog. Ser., 236, 129–135, 2002.

Lamont, P. A., Gage, J. D., and Tyler, P. A.: Deep-sea macrobenthic communities at contrasting sites off Portugal, preliminary results: II spatial dispersion, Int. Rev. ges. Hydrobio., 80, 251–265, 1995.

Lampitt, R. S. and Antia, A. N.: Particle flux in deep seas: regional characteristics and temporal variability, Deep-Sea Res. Pt. I, 44, 1377–1403, 1997.

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Leduc, D., Rowden, A. A., Probert, P. K., Pilditch, C. A., Nodder, S. D., Vanreusel, A., Duineveld, G. C. A., and Witbaard, R.: Further evidence for the effect of particle-size diversity on deep-sea benthic biodiversity, Deep-Sea Res. Pt. I, 63, 164–169, 2012.

Levin, L. A.: Oxygen minimum zone benthos: adaptation and community response to hypoxia, Oceanogr. Mar. Biol., 41, 1–45, 2003.

Levin, L. A. and Gooday, A. J.: Possible roles for xenophyophores in deep-sea carbon cycling, in: Deep-Sea Food Chains and the Global Carbon Cycle, edited by: G. T. Rowe and Pariente, V., Kluwer Academic Publishers, The Netherlands, 93–104, 1992.

Levin, L. A. and Gooday, A. J.: The deep Atlantic Ocean, in: Ecosystems of the Deep Oceans. Ecosystems of the World, edited by: Tyler, P. A., Elsevier, Amsterdam, Netherlands, 111–178, 2003.

Levin, L. A., Demaster, D. J., McCann, L. D., and Thomas, C. L.: Effects of giant protozoans (class *Xenophyophorea*) on deep-seamount benthos, Mar. Ecol.-Prog. Ser., 29, 99–104, 1986.

Levin, L. A., Boesch, D. F., Covich, A., Dahm, C., Erseus, C., Ewel, K. C., Kneib, R. T., Moldenke, A., Palmer, M. A., Snelgrove, P., Strayer, D., and Weslawski, J. M.: The function of marine critical transition zones and the importance of sediment biodiversity, Ecosystems, 4, 430–451, 2001a.

Levin, L. A., Etter, R. J., Rex, M. A., Gooday, A. J., Smith, C. R., Pineda, J., Stuart, C. T., Hessler, R. R., and Pawson, D.: Environmental influences on regional deep-sea species diversity, Annu. Rev. Ecol. Syst., 32, 51–93, 2001b.

Levin, L. A., Sibuet, M., Gooday, A. J., Smith, C. R., and Vanreusel, A.: The roles of habitat heterogeneity in generating and maintaining biodiversity on continental margins: an introduction, Mar. Ecol., 31, 1–5, 2010.

Lochte, K. and Turley, C. M.: Bacteria and cyanobacteria associated with phytodetritus in the deep sea, Nature, 333, 67–69, 1988.

Longhurst, A. R.: Ecological Geography of the Sea, Academic Press, San Diego, 2007.

Longhurst, A., Sathyendranath, S., Platt, T., and Caverhill, C.: An estimate of global primary production in the ocean from satellite radiometer data, J. Plankton Res., 17, 1245–1271, 1995.

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Masson, D. G., Huvenne, V. A. I., de Stigter, H. C., Arzola, R. G., and LeBas, T. P.: Sedimentary processes in the middle Nazaré Canyon, Deep-Sea Res. Pt. II, 58, 2369–2387, 2011.

McClain, C. R. and Barry, J. P.: Habitat heterogeneity, disturbance, and productivity work in concert to regulate biodiversity in deep submarine canyons, Ecology, 91, 964–976, 2010.

McClain, C. R., Stegen, J. C., and Hurlbert, A. H.: Dispersal, environmental niches and oceanic-scale turnover in deep-sea bivalves, P. Roy. Soc. B-Biol. Sci., 279, 1993–2002, doi:10.1098/rspb.2011.2166, 2011.

Moeseneder, M. M., Smith Jr., K. L., Ruhl, H. A., Jones, D. O. B., Witte, U., and Prosser, J. I.: Temporal and depth-related differences in prokaryotic communities in abyssal sediments associated with particulate organic carbon flux, Deep-Sea Res. Pt. I, 70, 26–35, 2012.

Mokievsky, V. and Azovsky, A.: Re-evaluation of species diversity patterns of free-living marine nematodes, Mar. Ecol.-Prog. Ser., 238, 101–108, 2002.

Mokievsky, V. O., Udalov, A. A., and Azovskii, A. I.: Quantitative distribution of meiobenthos in deep-water zones of the World Ocean, Oceanology, 47, 797–813, 2007.

Moodley, L., Chen, G. T., Heip, C., and Vincx, M.: Vertical distribution of meiofauna in sediments from contrasting sites in the Adriatic Sea: clues to the role of abiotic versus biotic control, Ophelia, 53, 203–212, 2000.

Paterson, D. M., Defew, E. C., and Jabour, J.: Ecosystem function and co-evolution of terminology in marine science and management, in: Marine Biodiversity and Ecosystem Functioning: Frameworks, Methodologies, and Integration, edited by: Solan, M., Aspden, R. J., and Paterson, D. M., Oxford Univeristy Press, Oxford, 24–33, 2012.

Platt, H. M. and Warwick, R. M.: Freeliving marine nematodes: part II, British chromadorids: pictorial key to world genera and notes for the identification of British species, 1988.

Quaresma, L. S., Vitorino, J., Oliveira, A., and da Silva, J.: Evidence of sediment resuspension by nonlinear internal waves on the western Portuguese mid-shelf, Mar. Geol., 246, 123–143, 2007.

Raffaelli, D. and Friedlander, A. M.: Biodiversity and ecosystem functioning: an ecosystem-level approach, in: Marine Biodiversity and Ecosystem Functioning: Frameworks, Methodologies, and Integration, edited by: Solan, M., Aspden, R. J., and Paterson, D. M., Oxford University Press, Oxford, 149–163, 2012.

Rex, M. A. and Etter, R. J.: Deep-Sea Biodiversity: Pattern and Scale, Harvard Univ. Pr., 2010.

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Rex, M. A., Stuart, C. T., Hessler, R. R., Allen, J. A., Sanders, H. L., and Wilson, G. D. F.: Global-scale latitudinal patterns of species-diversity in the deep-sea benthos, Nature, 365, 636–639, 1993.

Rex, M. A., Stuart, C. T., and Etter, R. J.: Do deep-sea nematodes show a positive latitudinal gradient of species diversity? The potential role of depth, Mar. Ecol.-Prog. Ser., 210, 297–298, 2001.

Rex, M. A., Etter, R. J., Morris, J. S., Crouse, J., McClain, C. R., Johnson, N. A., Stuart, C. T., Deming, J. W., Thies, R., and Avery, R.: Global bathymetric patterns of standing stock and body size in the deep-sea benthos, Mar. Ecol.-Prog. Ser., 317, 1–8, 2006.

Sanders, H. L.: Marine benthic diversity: a comparative study, Am. Nat., 102, 243–282, 1968.

Seinhorst, J. W.: A rapid method for the transfer of nematodes from fixative to unhydrous glycerine, Nematologica, 4, 67–69, 1959.

Snelgrove, P. V. R. and Smith, C. R.: A riot of species in an environmental calm: the paradox of the species-rich deep-sea floor, in: Oceanography and Marine Biology, vol. 40, edited by: Gibson, R. N., Barnes, M., and Atkinson, R. J. A., Taylor & Francis Ltd, London, 311–342, 2002.

Soetaert, K., Vanaverbeke, J., Heip, C., Herman, P. M. J., Middelburg, J. J., Sandee, A., and Duineveld, G.: Nematode distribution in ocean margin sediments of the Goban Spur (northeast Atlantic) in relation to sediment geochemistry, Deep-Sea Res. Pt. I, 44, 1671–1683, 1997.

Soetaert, K., Muthumbi, A., and Heip, C.: Size and shape of ocean margin nematodes: morphological diversity and depth-related patterns, Mar. Ecol.-Prog. Ser., 242, 179–1793, 2002.

Soetaert, K., Franco, M., Lampadariou, N., Muthumbi, A., Steyaert, M., Vandepitte, L., vanden Berghe, E., and Vanaverbeke, J.: Factors affecting nematode biomass, length and width from the shelf to the deep sea, Mar. Ecol.-Prog. Ser., 392, 123–132, 2009.

Svensson, J. R., Lindegarth, M., Siccha, M., Lenz, M., Molis, M., Wahl, M., and Pavia, H.: Maximum species richness at intermediate frequencies of disturbance: consistency among levels of productivity, Ecology, 88, 830–838, 2007.

Tchesunov, A. V., Ingels, J., and Popova, E. V.: Marine free-living nematodes associated with symbiotic bacteria in deep-sea canyons of north-east Atlantic Ocean, J. Mar. Biol. Assoc. UK, 1, 1–15, 2012.

Thiel, H.: Meiobenthos and nanobenthos of the deep sea, in: Deep-Sea Biology, edited by: Rowe, G. T., Wiley, New York, 167–230, 1983.

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Thistle, D.: Harpacticoid dispersion patterns – implications for deep-sea diverity maintenance, J. Mar. Res., 36, 377–397, 1978.

Tyler, P., Amaro, T., Arzola, R., Cunha, M. R., de Stigter, H., Gooday, A., Huvenne, V., Ingels, J., Kiriakoulakis, K., Lastras, G., Masson, D., Oliveira, A., Pattenden, A., Vanreusel, A., Van Weering, T., Vitorino, J., Witte, U., and Wolff, G.: Europe's Grand Canyon Nazare Submarine Canyon, Oceanography, 22, 46–57, 2009.

Van Gaever, S., Vanreusel, A., Hughes, J. A., Bett, B., and Kiriakoulakis, K.: The macro- and micro-scale patchiness of meiobenthos associated with the Darwin Mounds (north-east Atlantic), J. Mar. Biol. Assoc. UK, 84, 547–556, 2004.

Vanreusel, A., Vincx, M., Schram, D., and Vangansbeke, D.: On the vertical-distribution of the metazoan meiofauna in shelf break and upper slope habitats of the NE Atlantic, Int. Rev. ges. Hydrobio., 80, 313–326, 1995.

Vanreusel, A., Fonseca, G., Danovaro, R., da Silva, M., Esteves, A., Ferrero, T., Gad, G., Galtsova, V., Gambi, C., Genevois, V., Ingels, J., Ingole, B., Lampadariou, N., Merckx, B., Miljutin, D., Miljutina, M., Muthumbi, A., Netto, S., Portnova, D., Radziejewska, T., Raes, M., Tchesunov, A., Vanaverbeke, J., Van Gaever, S., Venekey, V., Bezerra, T., Flint, H., Copley, J., Pape, E., Zeppilli, D., Martinez, P., and Galeron, J.: The contribution of deep-sea macrohabitat heterogeneity to global nematode diversity, Mar. Ecol.-Evol. Persp., 31, 6–20, 2010.

Vetter, E. W. and Dayton, P. K.: Organic enrichment by macrophyte detritus, and abundance patterns of megafaunal populations in submarine canyons, Mar. Ecol.-Prog. Ser., 186, 137–148, 1999.

Vetter, E. W., Smith, C. R., and De Leo, F. C.: Hawaiian hotspots: enhanced megafaunal abundance and diversity in submarine canyons on the oceanic islands of Hawaii, Mar. Ecol., 31, 183–199, 2010.

Vitorino, J., Oliveira, A., Jouanneau, J. M., and Drago, T.: Winter dynamics on the northern Portuguese shelf. Part 1: Physical processes, Prog. Oceanogr., 52, 129–153, 2002.

Volkov, I., Banavar, J. R., Hubbell, S. P., and Maritan, A.: Neutral theory and relative species abundance in ecology, Nature, 424, 1035–1037, 2003.

White, M.: HERMES Deliverable 44: Preliminary Report on the Hydrography of the Porcupine Seabight (WP5 – Canyon Systems), 2006.

Wieser, W.: Beziehungen zwischen Mundhöhlengestalt, Ernährungsweise und Vorkommen bei freilebenden marinen Nematoden, Ark. Zool., 2, 439–484, 1953.

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Table 1. Information on the samples used for this study.

Cruise	Margin	Area	Station	Cast/dive	core	Lat	Long	WD (m)	WD class	Surface	Gear	Sampling date	SD (cm)
D297	WIM	Nazaré	D15735	1	a	39.58330	−10.31940	4340	4300	25.518	MegaCorer	2 Aug 2005	0–1
D297	WIM	Nazaré	D15737	1	a	39.50000	−9.93710	3453	3400	25.518	MegaCorer	2 Aug 2005	0–1
D297	WIM	Nazaré	D15753	1	a	39.50040	−9.93650	3528	3400	25.518	MUC	8 Aug 2005	0–5
D297	WIM	Nazaré	D15753	2	a	39.49980	−9.93700	3425	3400	25.518	MUC	8 Aug 2005	0–1
D297	WIM	Nazaré	D15758	3	a	39.58300	−10.31740	4435	4300	25.518	MUC	9 Aug 2005	0–5
D297	WIM	Nazaré	D15758	4	a	39.58350	−10.31670	4335	4300	25.518	MUC	9 Aug 2005	0–1
D297	WIM	Slope	D15770	1	a	40.07327	−10.36530	4277	4300	25.518	MUC	14 Aug 2005	0–5
D297	WIM	Slope	D15770	2	a	40.07317	−10.36500	4275	4300	25.518	MUC	14 Aug 2005	0–1
D297	WIM	Slope	D15770	3	a	40.07333	−10.36570	4275	4300	25.518	MUC	15 Aug 2005	0–1
D297	WIM	Slope	D15771	1	a	40.59500	−10.36730	3400	3400	25.518	MUC	15 Aug 2005	0–5
D297	WIM	Slope	D15771	1	b	40.59550	−10.36800	3401	3400	25.518	MUC	15 Aug 2005	0–1
D297	WIM	Slope	D15771	3	a	40.59567	−10.36820	3403	3400	25.518	MUC	15 Aug 2005	0–1
CD179	WIM	Cascais	CD56838	3	11	38.10820	−9.99900	4482	4300	28.274	MegaCorer*	4 May 2006	0–5
CD179	WIM	Cascais	CD56838	4	8	38.10870	−9.99980	4485	4300	28.274	MegaCorer*	4 May 2006	0–5
CD179	WIM	Cascais	CD56842	1	7	38.10750	−9.99900	4482	4300	28.274	MegaCorer	5 May 2006	0–5
CD179	WIM	Cascais	CD56836	1	1	38.29980	−9.83270	3209	3400	28.274	MegaCorer*	1 May 2006	0–5
CD179	WIM	Cascais	CD56823	2	11	38.30020	−9.78370	3218	3400	28.274	MegaCorer*	27/04/2006	0–5
CD179	WIM	Cascais	CD56821	2	2	38.29950	−9.78150	3214	3400	28.274	MegaCorer*	27/04/2006	0–5
CD179	WIM	Setùbal	CD56837	7	2	38.37480	−9.89200	4243	4300	28.274	MegaCorer	3 May 2006	0–5
CD179	WIM	Setùbal	CD56837	8	5	38.37480	−9.89200	4244	4300	28.274	MegaCorer*	3 May 2006	0–5
CD179	WIM	Setùbal	CD56837	5	8	38.37500	−9.89130	4241	4300	28.274	MegaCorer*	2 May 2006	0–5
CD179	WIM	Setùbal	CD56810	1	2	38.15370	−9.61700	3224	3400	28.274	MegaCorer*	23 Apr 2006	0–5
CD179	WIM	Setùbal	CD56804	6	8	38.15430	−9.61570	3275	3400	28.274	MegaCorer*	21 Apr 2006	0–5
CD179	WIM	Setùbal	CD56806	1	6	38.15480	−9.61600	3275	3400	28.274	MegaCorer*	21 Apr 2006	0–5
JC10	WIM	Nazaré	95-PUC02	48	2	39.49923	−9.93675	3512	3400	25.518	PC (ISIS)	12 Jun 2007	0–5
JC10	WIM	Nazaré	95-PUC03	48	3	54.86667	−9.93663	3512	3400	25.518	PC (ISIS)	12 Jun 2007	0–5
JC10	WIM	Nazaré	95-PUC09	48	9	54.91667	−9.93665	3512	3400	25.518	PC (ISIS)	12 Jun 2007	0–5
Belgica 2006/13	IM	Gollum	GOL700	1	4	50.72563	−11.16289	740	700	25.518	MidiCorer*	24 Jun 2006	0–5
Belgica 2006/13	IM	Gollum	GOL700	10	4	50.72622	−11.16174	770	700	25.518	MidiCorer*	25 Jun 2006	0–5
Belgica 2006/13	IM	Gollum	GOL700	10bis	2	50.72622	−11.16174	770	700	25.518	MidiCorer*	25 Jun 2006	0–5
Belgica 2006/13	IM	Gollum	GOL1000	2	3	50.72970	−11.25814	1085	1000	25.518	MidiCorer*	24 Jun 2006	0–5
Belgica 2006/13	IM	Gollum	GOL1000	4	3	50.73013	−11.26183	1094	1000	25.518	MidiCorer*	25 Jun 2006	0–5
Belgica 2006/13	IM	Gollum	GOL1000	5	3	50.73028	−11.26186	1075	1000	25.518	MidiCorer*	25 Jun 2006	0–5
Belgica 2006/13	IM	Whittard	WHS700	2	1	48.77410	−10.65248	708	700	25.518	MidiCorer*	26 Jun 2006	0–5
Belgica 2006/13	IM	Whittard	WHS700	3	1	48.77488	−10.64867	815	700	25.518	MidiCorer*	26 Jun 2006	0–5
Belgica 2006/13	IM	Whittard	WHS700	4	1	48.77460	−10.64961	764	700	25.518	MidiCorer*	26 Jun 2006	0–5
Belgica 2006/13	IM	Whittard	WHS1000	1	4	48.68402	−10.84876	1155	1000	25.518	MidiCorer*	26 Jun 2006	0–5
Belgica 2006/13	IM	Whittard	WHS1000	2	4	48.68370	−10.84855	1155	1000	25.518	MidiCorer*	26 Jun 2006	0–5
Belgica 2006/13	IM	Whittard	WHS1000	3	4	48.68347	−10.84836	1175	1000	25.518	MidiCorer*	26 Jun 2006	0–5

WD: water depth.
Surface: sediment surface of the sample.
SD: sediment depth.
* indicates a subcore was taken from a 100 mm-diameter core.

Table 2. Descriptors used to characterise the community, including the formulas used, explanations of the formula components, and references.

Community characteristic	Descriptor	Formula	Formula components	References
Assemblage structure	Genera relative abundances	–	–	–
Diversity	H_0 (genus richness) H_1 (genus richness and evenness) H_2 (genus richness and evenness) H_{inf} (genus evenness)	$H_a = \left(\sum_i p_i^a \right)^{1/(1-a)}$	• p_i = relative proportion of genus i in sample • a defines the order of the Hill number	(Hill, 1973; Heip et al., 1998)
	EG(51) (genus richness)	$\sum_{i=1}^{g} \left(1 - \dfrac{\left[\begin{smallmatrix} N - N_i \\ n \end{smallmatrix} \right]}{\left[\begin{smallmatrix} N \\ n \end{smallmatrix} \right]} \right)$	• N_i = the number of individuals belonging to genus i in the full sample • n = number of individuals in normalized sample size • g = number of genera • square bracket notation $\left[\begin{smallmatrix} A \\ B \end{smallmatrix} \right]$ indicates number of permutations of A elements in groups of size B	(Hurlbert, 1971; Heip et al., 1998) Adapted for normalized sample size of 51 individuals
Function	TD (trophic diversity)	$\left(\sum_{i=1}^{n} q_i^2 \right)^{-1}$	• q_i = proportion of feeding type i in the assemblage • n = number of feeding types (5)	Reciprocal of index defined by Heip et al. (1998)
	MI (maturity index)	$\sum_{i=1}^{n} v_i * p_i$	• p_i = relative proportion of genus i in sample • v_i = c-p score	(Bongers, 1990; Bongers et al., 1991)
Standing stock	Total nematode abundance (ind./10 cm^2)	–	–	–
	Biomass (µg dry weight/10 cm^2)	$\sum_i \left[\dfrac{\sum_{x_i} \left[\frac{L \cdot W^2}{1.6 \times 10^6} \right]_{x}}{x_i} * p_i \right] \cdot A$	• p_i = relative proportion of genus i in sample • L = length, W = maximum width • x_i = number of individuals belonging to genus i • A = total nematode abundance (ind./10 cm^2)	Based on Andrassy (1956) As used in Ingels et al. (2011c)

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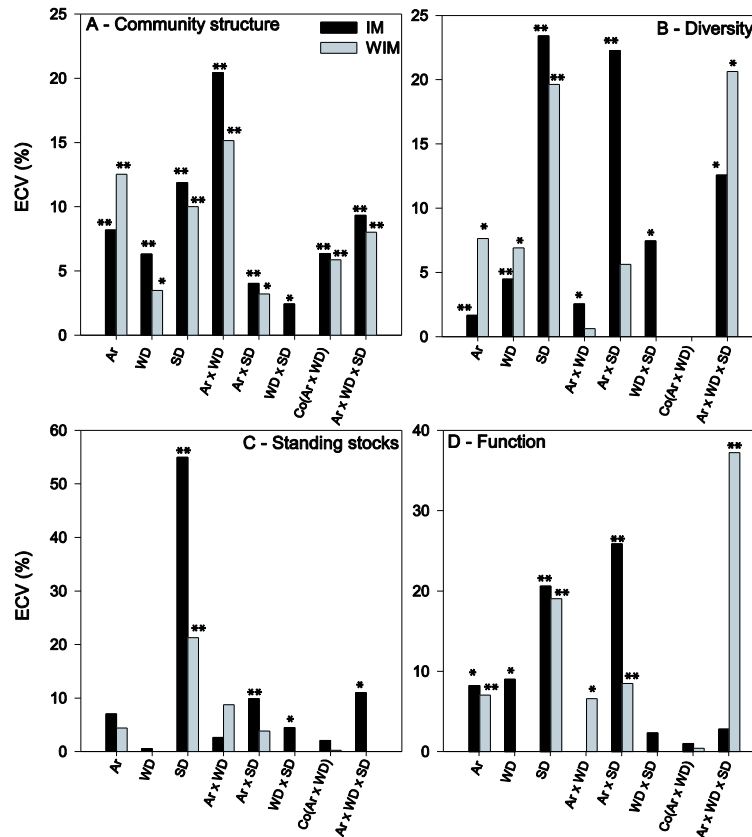Full Screen / Esc

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Table 3. 4-factor PERMANOVA results for the different descriptor sets and 1000 permutations. IM: Irish Margin; WIM: Western Iberian Margin; df: degrees of freedom; MS: means of squares; $\sqrt{ECV}$: square root of estimated components of variance; ECV%: percentage of ECV to total variation; Ar: area; WD: water depth; SD: sediment depth; Co: core; Res: residual. Bold values: $p < 0.05$; bold, italic values: $p < 0.01$.

Margin	Term	Community structure						Diversity						Standing stocks						Function					
		df	MS	Pseudo-F	p	√ECV	ECV%	df	MS	Pseudo-F	p	√ECV	ECV%	df	MS	Pseudo-F	p	√ECV	ECV%	df	MS	Pseudo-F	p	√ECV	ECV%
IM	Ar	1	10515	4.85	***0.002***	16.9	8.2	1	4.91	5.47	**0.010**	0.37	1.7	1	4.5	8.75	0.058	0.46	7.0	1	8.0	7.94	**0.018**	0.49	8.3
	WD	1	8606	3.97	***0.005***	14.9	6.3	1	11.6	12.99	***0.005***	0.61	4.5	1	0.8	1.60	0.228	0.13	0.5	1	8.7	8.60	**0.014**	0.51	9.1
	SD	4	5939	5.47	***0.001***	20.4	11.9	4	24.6	11.72	***0.001***	1.39	23.4	4	12.7	58.27	***0.001***	1.28	55.0	4	7.9	9.17	***0.001***	0.77	20.7
	Ar × WD	1	12590	5.81	***0.003***	26.8	20.5	1	4.0	4.43	**0.026**	0.46	2.6	1	1.3	2.46	0.168	0.28	2.7	1	0.9	0.92	0.392	0.00	0.0
	Ar × SD	4	1910	1.76	***0.002***	11.9	4.0	4	12.8	6.10	***0.001***	1.36	22.3	4	1.3	6.15	***0.002***	0.54	9.9	4	5.2	6.12	***0.001***	0.87	26.0
	WD × SD	4	1583	1.46	**0.014**	9.2	2.4	4	5.7	2.71	**0.025**	0.79	7.5	4	0.7	3.35	**0.020**	0.37	4.5	4	1.3	1.48	0.213	0.26	2.4
	Co(WD × Ar)	8	2174	2.00	***0.001***	14.9	6.4	8	0.9	0.42	0.961	0.00	0.0	4	0.5	2.36	0.057	0.25	2.1	8	1.0	1.18	0.309	0.18	1.1
	Ar × WD × SD	4	2039	1.88	***0.001***	18.1	9.3	4	5.1	2.44	**0.044**	1.02	12.6	4	0.8	3.87	**0.014**	0.57	11.0	4	1.1	1.28	0.25	0.29	2.9
	Res	3	1086			33.0	31.0	31	2.1			1.45	25.5	15	0.2			0.47	7.3	31	0.9			0.93	29.6
	Total	58					100.0	58					100.0	38					100.0	58					100.0
WIM	Ar	3	5160	4.21	***0.001***	16.7	12.5	3	13.4	4.20	**0.022**	0.74	7.6	3	2.38	2.04	0.12	0.29	4.4	3	4.4	5.60	***0.005***	0.51	7.1
	WD	1	2229	2.06	**0.012**	8.8	3.5	1	0.5	3.82	**0.038**	0.71	6.9	1	0.47	0.41	0.634	0.00	0.0	1	0.4	0.57	0.556	0.00	0.0
	SD	4	4038	4.35	***0.001***	14.9	10.0	4	16.0	8.06	***0.001***	1.19	19.6	4	6.73	5.83	***0.002***	0.63	21.3	4	10.4	13.84	***0.001***	0.83	19.1
	Ar × WD	3	3605	2.94	***0.001***	18.4	15.1	3	3.5	1.13	0.360	0.21	0.6	3	2.37	2.04	0.161	0.41	8.8	3	2.5	3.15	**0.037**	0.49	6.7
	Ar × SD	12	1220	1.31	**0.014**	8.5	3.2	8	4.9	1.59	0.068	0.64	5.6	8	1.51	1.31	0.243	0.27	3.8	12	2.0	2.67	***0.001***	0.56	8.5
	WD × SD	4	929	1.00	0.476	0.1	0.0	4	7.4	0.78	0.580	0.00	0.0	4	0.54	0.47	0.772	0.00	0.0	4	0.5	0.70	0.686	0.00	0.0
	Co(WD × Ar)	19	1362	1.47	***0.002***	11.4	5.9	19	2.2	0.81	0.753	0.00	0.0	19	1.17	1.01	0.462	0.07	0.2	19	0.8	1.08	0.389	0.13	0.5
	Ar × WD × SD	12	1291	1.39	***0.003***	13.4	8.0	8	5.4	2.08	**0.015**	1.22	20.7	8	0.10	0.09	1	0.00	0.0	12	3.5	4.65	***0.001***	1.16	37.3
	Res	44	929			30.5	41.7	44	2.8			1.67	38.9	44	1.15			1.07	61.5	44	0.8			0.87	20.8
	Total	102					100.0	94					100.0	94					100.0	102					100.0
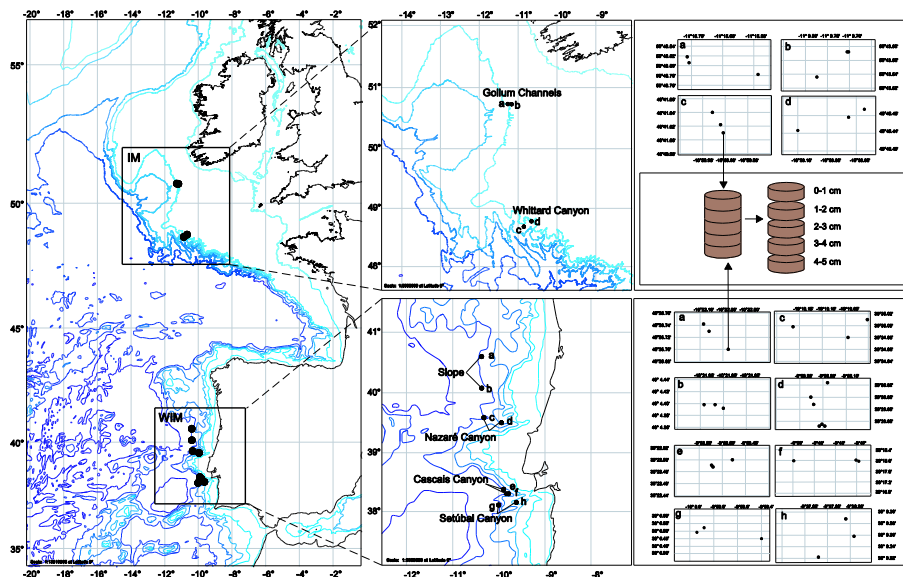
Fig. 1. Maps and diagram illustrating the different spatial scales of the sampling design. Left panel shows the geographic scale of the samples taken at two different margin systems in the Northeast Atlantic; IM: Irish Margin, WIM: Western Iberian Margin. Middle panels show distribution of stations at each margin; letters correspond to panels on the right hand side. Right upper panels show the distribution of the cores taken at IM; a: Gollum Channels 1000 m; b: Gollum Channels 700 m; c: Whittard Canyon 1000 m; d: Whittard Canyon 700 m. Right lower panels show the distribtution of the cores taken at the WIM; a: Slope 3400 m; b: Slope 4300 m; c: Nazaré Canyon 4300 m; d: Nazaré Canyon 3400 m; e: Cascais Canyon 4300 m; f: Cascais Cayon 3400 m; g: Setúbal Canyon 4300 m; h: Setúbal Canyon 3400 m. (Maps created with PanMap; Diepenbroek et al. (2000) PanMap; http://www.pangaea.de/Software/PanMap.)

Fig. 2. Percentages of estimated components of variation from the PERMANOVA tests for different descriptor sets. IM: Irish Margin; WIM: Western Iberian Margin; Ar: area; WD: water depth; SD: sediment depth; Co: core. * indicates significance of the PERMANOVA tests at $p < 0.05$; ** indicates significance at $p < 0.01$.

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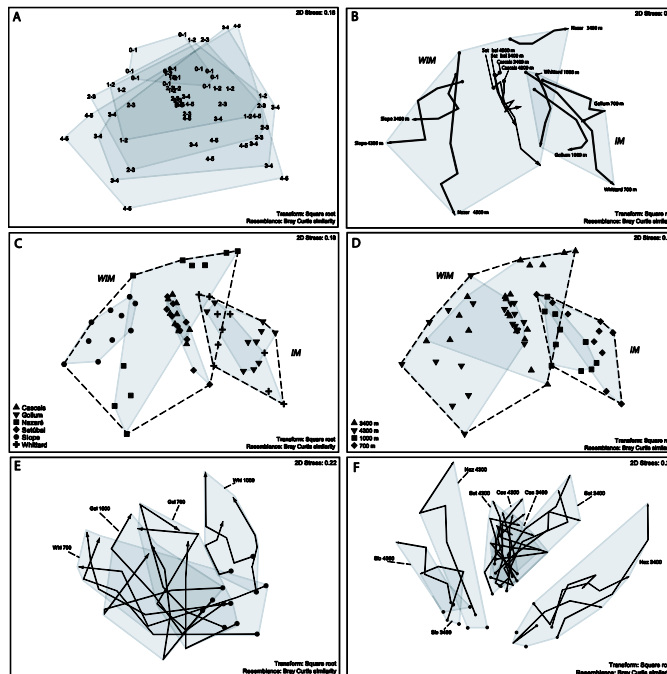
Fig. 3. Multidimensional scaling plots of Bray–Curtis similarity matrices based on standardised, square root-transformed genera abundance data. **(A–D)**: based on averaged data per station (averaged over replicates or cores per station for each station; Ar × WD combination). **(A)** Labels denote sediment depth in cm; grey planes encompass variability for each sediment layer by connecting the outer data points. **(B)** same plot as **(A)**, but lines connect consecutive sediment layers within each core (● = 0–1 cm, ►= 4–5 cm); grey planes represent different margins; IM: Irish Margin; WIM: Western Iberian Margin. **(C)** same as **(A)**, but symbols and grey planes denote the different areas; outer points belonging to the same margin are connected with dashed lines. **(D)** same as **(C)**, but symbols and grey planes denote different water depths. **(E–F)** based on unaveraged data whereby each core is represented seperately. **(E)** Irish Margin; lines connect consecutive sediment layers within each core (● = 0–1 cm, ►= 4–5 cm); grey planes represent stations. **(F)** Western Iberian Margin; lines connect consecutive sediment layers within each core (● = 0–1 cm, ►= 4–5 cm); grey planes represent stations.
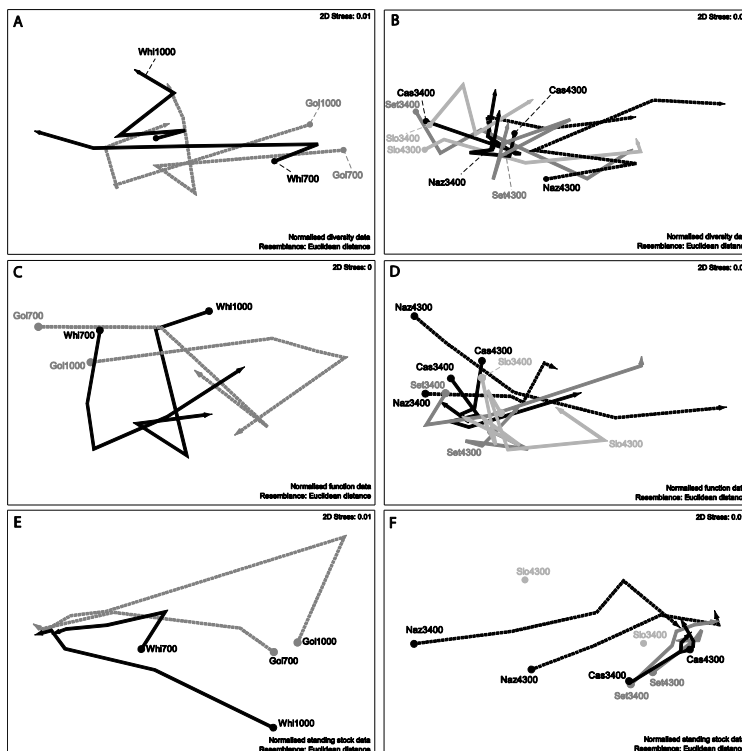
Fig. 4. Multidimensional scaling plots of Euclidean distance similarity matrices based on diversity data for the IM **(A)**, WIM **(B)**; functional data for IM **(C)**, WIM **(D)**; standing stock data for IM **(E)**, WIM **(F)**. Data was averaged per Ar × WD level (station) and normalized. Lines connect consecutive sediment layers for each station (● = 0–1 cm, ▶ = 4–5 cm).
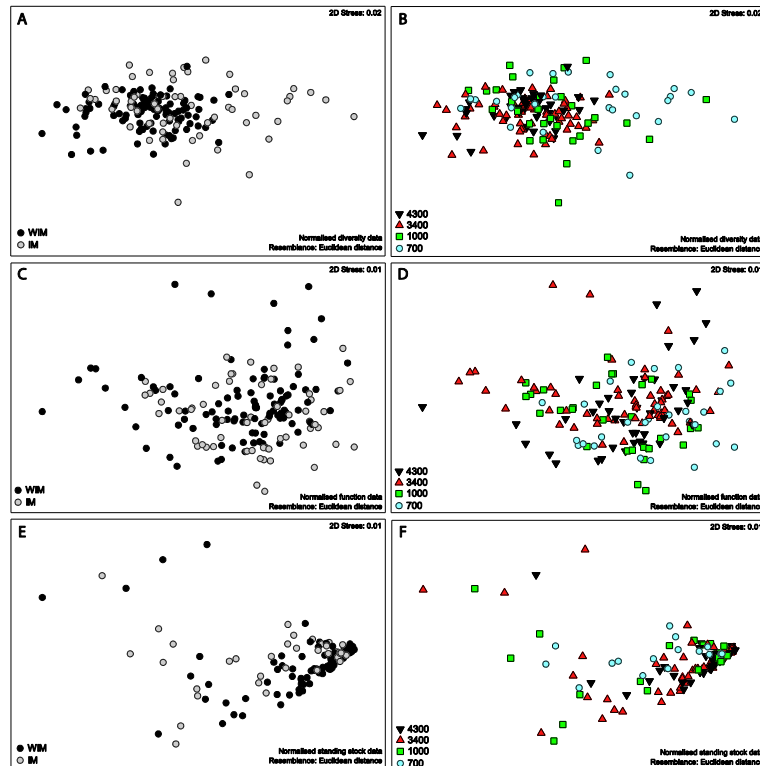
Fig. 5. Multidimensional scaling plots of Euclidean distance similarity matrices of samples based on diversity, function and standing stock for both margins. **(A)** diversity data showing margin variability; **(B)** diversity data showing water depth variability; **(C)** functional data showing margin variability; **(D)** functional data showing water depth variability; **(E)** standing stock data showing margin variability; **(F)** standing stock data showing water depth variability.

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