Local and regional variation in deep-sea polychaete diversity: canyon influence (Whittard Canyon system, NE Atlantic)

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Abstract

We examined deep-sea macrofaunal polychaete species assemblage composition, diversity and turnover in the Whittard Canyon system (NE Atlantic; 3500 m water depth). Replicate Megacore samples were collected from three of the canyon branches and one site on the continental slope to the west of the canyon, all at c. 3500 m water depth. A total of 110 polychaete species were recorded. *Paramphinome jeffreysii* was the most abundant species (2326 ind m^{-2}) followed by *Aurospio* sp. B (646 ind m^{-2}), Opheliidae sp. A (393 ind m^{-2}), *Prionospio* sp. I (380 ind m^{-2}), and *Ophelina abranchiata* (227 ind m^{-2}). Species composition varied significantly across all sites. From west to east, the dominance of *Paramphinome jeffreysii* increased from 12.9 % on the slope to 39.6 % in the Eastern branch. Ordination of species composition revealed that the Central and Eastern branches were most similar, whereas the Western branch and slope sites were more distinct. High abundances of *P. jeffreysii* and Opheliidae sp. A characterised the Eastern branch of the canyon and may indicate an opportunistic response to a possible recent input of organic matter inside the canyon. Species diversity indices were higher on the slope than inside the canyon, and the slope site had higher species evenness. Within the canyon, species diversity between branches was broadly similar. Our data does not suggest that the Whittard Canyon makes a substantial contribution to the regional diversity of soft-bottom benthic polychaetes.

Keywords: Biodiversity, Polychaeta, Whittard Canyon, Deep sea, Northeast Atlantic, Biogeography

1. Introduction

Describing and understanding patterns of biodiversity on our planet is a fundamental aim in biology (Gaston 2000). The deep-sea floor may harbour some of the highest levels of local (alpha) species diversity on earth (Hessler & Sanders 1967, Sanders 1968, Sanders & Hessler 1969, Grassle & Maciolek 1992). Local diversity is thought to generally exhibit a parabolic distribution with depth. This pattern is particularly pronounced in the North Atlantic, with peaks at intermediate (i.e. bathyal) depths and reduced levels of diversity at upper bathyal and abyssal depths (Rex 1981, Rex 1983). Submarine canyons, major deep-sea topographic features incising the continental shelf and slope, are potential exceptions to this general pattern. They may show either increased species richness in their deeper parts (Cunha et al. 2011) or depressed diversity throughout (Vetter & Dayton 1998). Faunal diversity is also reported to vary down the canyon axis and over the adjacent canyon fan (Tyler et al. 2009); e.g. foraminifera (Duros et al. 2011) and polychaetes (Paterson et al. 2011). There is also no general agreement on whether alpha diversity is typically higher inside canyons (Vetter & Dayton 1998, 1999, Vetter et al. 2010, De Leo et al. 2012) or higher on the adjacent slope outside canyons (Gage et al. 1995, Curdia et al. 2004, Garcia et al. 2007, Koho et al. 2007).

The drivers that influence marine diversity at regional and local scales are not well understood (Levin et al. 2001, Snelgrove & Smith 2002). In the case of submarine canyons, a complex interplay of numerous factors is likely to regulate the diversity of biological communities (McClain & Barry 2010). These topographic features are typically associated with high surface water productivity, high levels of physical disturbance and a considerable degree of habitat heterogeneity, all of which could influence species diversity. Canyons have also been described as benthic biomass ‘hotspots’ (De Leo et al. 2010), reflecting an enhanced food supply compared with the surrounding continental slope and abyssal plain. They can act as conduits for the delivery of sediment and organic matter to the abyssal plains (Vetter & Dayton 1998). This enhanced supply of organic matter could increase diversity. Conversely, if enrichment is excessive, it may favour opportunistic species (Paterson et al. 2011) and act to depress species diversity (Stuart et al. 2003, Whittaker 1965) as reported, for example, from the Nazare Canyon (Curdia et al. 2004). Diversity may also be influenced by physical disturbance, for example, steep topography may focus internal tides in the upper reaches of canyons (Gardner 1989), while tidal currents, episodic slumps, turbidity flows and dense shelf water cascading may periodically transport sediments into the deeper parts (Canals et al. 2006).

Factors such as extreme topography, diverse current regimes, varying substratum types, and detrital funnelling from the continental shelf serve to increase habitat heterogeneity within canyons (Levin et al. 2010). For example, currents may distribute organic matter and sediment in a patchy manner (McClain & Barry 2010). Similarly, sediment granulometry can be expected to vary throughout a canyon, with potential impact on macrofaunal (Etter & Grassle 1992) and meiofaunal (Leduc et al. 2012) diversity. Sessile megafauna add to the habitat complexity inside canyons; for example, deep-water corals can be found throughout canyon systems, providing refuge for diverse associated faunal communities (Mortensen & Buhl-Mortensen 2005, Buhl-Mortensen et al. 2010, Huvenne et al. 2011). All of these factors may increase small and medium-scale environmental heterogeneity, particularly within active canyons, and thereby enhance diversity compared with the adjacent slope (Tews et al. 2004). Indeed, increased macrohabitat heterogeneity inside canyons has been linked to the high beta diversity of nematode assemblages within canyons (Vanreusel et al. 2010).

On a larger scale, it is unclear whether canyons act to enhance regional diversity across continental margins. Species turnover (beta diversity) links local and regional scales of diversity and has been understudied in the deep sea (Paterson et al. 1998, Glover et al. 2002, Ellingsen et al. 2007a). In deep-sea, soft-sediment habitats, variation in beta diversity is expected to be gradual except when interrupted by topography, hard substratum, intense bottom currents, nutrient depo-centres, abrupt shifts in water masses, or other extreme environmental circumstances (Rex & Etter 2010). Many of these factors operate inside canyons. Thus, as in continental shelf settings (Ellingsen & Gray 2002), it seems likely that changes in environmental variables within canyons will have a stronger effect on beta diversity than spatial distance between sites. The bathymetric and geographical ranges of species, and hence beta diversity, are influenced by the interplay between adaptive traits and environmental drivers. Adaptive traits include feeding type, metabolic and locomotory capacity, morphological specialisation, larval dispersal, adult mobility, body size and shape, and enzymatic pressure sensitivity (reviewed by Rex and Etter 2010). Those traits typical of canyon settings will depend on the species present, which in turn will reflect the environmental conditions. Thus the interaction of species traits and environmental influences that determine the bathymetric and geographical ranges of species will be complex (Rex & Etter 2010). Since the environmental conditions inside canyons are often very different from those on the open slope, the faunal assemblages may differ correspondingly. This would act to increase faunal turnover across the continental margin and lead to enhanced regional diversity.

Much less quantitative data on species richness is available from deep-sea soft sediments than from comparable shallow-water settings (Gray 2002). As a result of their rugged terrain and inaccessibility, submarine canyons are particularly hard to sample. Thus, relatively little is known about the patterns and drivers of canyon diversity. This study will investigate diversity at different spatial scales inside the Whittard Canyon system (NE Atlantic), focussing on sites at a common water depth (3500 m). A previous study, on the same samples from the Whittard Canyon, reported macrofaunal abundance and community composition at the higher taxon level (Gunton et al. 2015).

In the present study, a species-level assessment of polychaete assemblages, the dominant deep-sea macrofauna taxon, will be used to address the following hypotheses: 1) Species composition and diversity are consistent between Whittard Canyon branches 2) Species composition is distinct and species diversity is depressed inside the Whittard Canyon compared with the adjacent open slope. 3) Regional diversity is impacted by the Whittard Canyon system.

2. Methods

2.1. Sample collection and processing

Sediment samples were collected using a Megacorer (Gage and Bett, 2005) at three sites inside the Whittard Canyon system (NE Atlantic) and one on the adjacent continental slope to the west of the canyon during RRS *James Cook* cruise 036 in June and July 2009 (Table 1; Fig. 1). All sites were located at c. 3500 m depth. The Megacorer was fitted with eight large (100 mm internal diameter) core tubes. Five deployments were conducted in the Western branch, six in the Central and Eastern branches and five on the slope site. One extra deployment was made in the Central and Eastern branches to compensate for the failure to recover sufficient cores. Full details of macrofaunal sample processing are given in Gunton et al. (2015). In the present study, the top three sediment horizons (i.e. 0-1, 1-3 and 3-5 cm) were analysed *in toto*.

2.2 Faunal analyses

In the laboratory, polychaetes were transferred from the formalin onto a 300 µm mesh sieve, rinsed with fresh water and sorted in 70 % ethanol. A Leica MZ9.5 stereomicroscope and a DM5000 compound microscope were used to identify polychaete specimens to species level. Polychaetes were assigned a Latin binomial name where possible using published identification keys. Where specimens could not be assigned to a described species they were recorded as an informal morphospecies in a genus (e.g. *Prionospio* sp. A) or family (e.g. Spionidae sp. A). Fragmented specimens were only counted if they included a head. The full species list, including abundance counts, is given in supplementary data (Table S1).

2.3 Data Analysis

2.3.1 Diversity measures

Simple polychaete species dominance was calculated as the Berger-Parker index (i.e. Rank 1 Dominance; Magurran 2004) via Microsoft Excel. K-dominance plots (Lambshead et al. 1983) were drawn in SigmaPlot V12.5. The software package PRIMER V6 (Clarke & Gorley 2006) was used to calculate conventional diversity indices from the polychaete count data: Shannon index (Pielou 1966), Simpson's index (Simpson 1949) and Pielou's evenness (Pielou 1975). Polychaete species richness was also estimated using individual based rarefaction curve (Gotelli & Colwell 2001, 2011). Rarefaction curves based on polychaete count data were constructed using the EstimateS software package (Colwell 2009). This approach was also applied to comparative polychaete species level data available from canyons on the Iberian margin (Paterson et al., 2011).

In order to assess beta diversity across the canyon system, Whittaker's measure $\beta_W = \gamma / \overline{\alpha}$ (Whittaker 1960, 1972) was calculated, where γ is the diversity of the complete system, and $\overline{\alpha}$ is average sample diversity, where each sample is a standard (rarefied) size. Beta diversity was calculated using the number equivalents (Hill numbers) of species richness, ${}^0D = S$, Shannon index, ${}^1D = \exp (- \Sigma p_i \log p_i)$ and Simpson index, ${}^2D = 1 / \Sigma p_i^2$ (See Chao et al, 2012; Jost 2007), derived from the output of EstimateS, after individual samples had been rarefied to 47 individuals, and pooled samples (the γ value) rarefied to 235 individuals (i.e. 5 replicate samples of 47 individuals). Details of rarefaction with Hill numbers are given by Chao et al. (2014).

2.3.2 Composition assessment

Polychaete species density data were transformed to square root, and the Bray-Curtis similarity calculated between samples. The resultant similarity matrix was visualised using non-metric multidimensional scaling plots (MDS plots), and further assessed using the Analysis of Similarity (ANOSIM) and Similarity Percentage (SIMPER) methods given in PRIMER V6.

A canonical correspondence analysis (CCA) on untransformed polychaete density was performed to examine the potential relationships between assemblages and environmental variables. The CCA was performed using R statistical software (RCoreTeam 2014) with the Vegan: Community Ecology package (Oksanen et al. 2013). Details of the available environmental factors are given in Gunton et al. (2015).

3. Results

3.1 The polychaete assemblage

A total of 2225 polychaetes was examined; 1959 (88%) of these were assigned to species-level taxa. Across all sites, we recognised 110 species, of which 35 were described, and 75 could not be assigned to a known species and were possibly new to science. The Eastern branch yielded the highest number of species (68), followed by Central branch (65), the slope (64) and the Western branch (53) sites. Overall, 46 species were found only in the canyon branches, and 11 were found only at the slope site. Between site variation in species composition is illustrated in Fig. 2. By far the most abundant species was the amphinomid *Paramphinome jeffreysii* with a total of 2326 ind m^{-2}. *Aurospio* sp. B was ranked second (646 ind m^{-2}), Opheliidae sp. A third (393 ind m^{-2}, represented by juvenile individuals), *Prionospio* sp. I fourth (380 ind m^{-2}) and *Ophelina abranchiata* fifth (277 ind m^{-2}). *Paramphinome jeffreysii* increased in relative abundance from 21 % in the Western branch to 34 % and 40 % in the Central and Eastern branches, respectively (Table 2). It was less common at the slope site, where the most abundant species was *Aurospio* sp. B (Table 2). In contrast to *P. jeffreysii, Aurospio.* sp. B decreased in relative abundance from west to east (slope 14 %, Eastern branch 6 %).

There were notable differences in species composition with depth in the sediment profile. The percentage abundance of *Paramphinome jeffreysii* increased into the sediment across all of the sites (Fig. 3). At the Eastern branch, where it was most abundant, *P. jeffreysii* constituted 50 % of the polychaete species in the 1-3 and 3-5 cm sediment layers. Juvenile opheliids (Opheliidae sp. A) were particularly abundant (c. 20%) in the 0-1 cm layer of the Eastern branch.

3.2 Species diversity

Rank 1 dominance differed between sites (Table 1). The Eastern branch had the highest rank 1 dominance (39 %) and the slope the lowest (14 %). The *k*-dominance plot (Fig. 4) revealed a similar trend in dominance, highest at the Eastern branch site and lowest at the slope site, with the Western and Central branches having intermediate values.

Simple alpha diversity measures indicated that diversity varied between sites. The average Simpson index ($1-\lambda'$) was highest at the slope site (0.92), intermediate in the Western and Central branches (0.88 and 0.86 respectively) and lowest in the Eastern branch (0.80)(Table 1). The average Shannon index (H' (log2)) was likewise highest at the slope site (4.10) and lowest in the Eastern branch (3.66). Species evenness decreased from west to east across the sites. The average evenness index (*J'*) was highest on the slope and lowest in the canyon branches (Table 1).

Rarefied polychaete species richness was highest on the slope, intermediate in the Western and Central branches and lowest in the Eastern branch (Fig. 5a). None of the rarefaction curves reached an asymptote, suggesting that the local diversity was undersampled even when the results were pooled. The higher richness at the slope site was evident from the individual based (Fig. 5a) rarefaction curves, although confidence intervals overlapped, indicating that the differences were not statistically significant. When all sites were rarefied to 47 individuals, the slope site had the highest species richness (21 species). All three canyon sites had similar predicted numbers of species with $E[S_{47}]$ values decreasing only very slightly (from 20 to 18) from west to east (Table 4).

3.3 Beta diversity

There is little if any variation in beta diversity within or among the sites studies, whether assessed as Hill number 0, 1 or 2 (Table 4). However, rarefied average α

diversity, and rarefied γ diversity are uniformly maximal at the slope site. Similarly, rarefied average α diversity, and rarefied γ diversity are uniformly enhanced from canyon-level to regional-level assessments. The degree of enhancement appears to be related to the Hill number, with a lesser enhancement of richness, and greater enhancement of inverse Simpson. Taken together these results suggest both increased richness and reduced dominance at the slope site relative to the canyon sites.

3.4 Species composition

A multidimensional scaling ordination of polychaete species data (Fig. 6) illustrated appreciable differences in community composition between all four study sites. The Eastern and Central branch sites were most similar to each other. Western branch samples formed a looser grouping, nonetheless distinct from those of the other canyon sites. The slope samples grouped together and were distinct from the canyon sites. Global ANOSIM indicated significant variation ($p < 0.001$), with all pair-wise site comparisons significant at $p < 0.01$, except slope and Western branch, which was significant at $p < 0.02$. SIMPER analysis indicated that *P. jeffreysii* abundance was responsible for most of the observed similarity within sites. *Aurospio* sp. B abundance was second or third most important at all sites. Between site dissimilarity was mostly driven by the abundance of *P. jeffreysii,* Opheliidae sp. A and *Ancistrosyllis sp.* A.

A CCA (Fig. 7) showed the potential interactions between environmental factors and the distribution of polychaete species. Axis 1 was positively correlated with water depth and negatively correlated with macrofaunal density (a potential proxy of organic matter supply, Gunton et al. 2015). Axis 2 was correlated with sediment characteristics, including grain size and slope angle. Species such as *Leanira hystricis, Ancistrosyllis* sp. A, *Sternaspis* sp. A and *Chaetozone* sp. C were characteristic of the deeper and lower density macrofaunal sites in the Western branch (supplementary Fig. S1). Opheliidae sp. B, *Anguillosyllis capensis* and Scalibregmatidae sp. B were characteristic of the coarser-grained sediment with a higher clay percentage on the slope. Opheliidae sp. A (juveniles), *Paramphinome jeffreysii* and *Leitoscoloplos* sp. B were characteristic of the Eastern and Central branches, which shared similar environmental characteristics.

4. Discussion

4.1 Polychaete assemblage

The species composition of the polychaete assemblages differed between branches of the Whittard Canyon. This is consistent with previous family-level studies of polychaetes in the same canyon system (Hunter et al., 2013; Gunton et al., 2015). Multidimensional scaling and a CCA revealed that the Eastern and Central branch species assemblages were closely related (Figs. 6 & 7); again, this pattern was also observed at the family level (Gunton et al. 2015). This faunal similarity may reflect a combination of similar environmental conditions and geographical proximity (Gunton et al. 2015). The Western branch samples yielded a more distinct assemblage, characterised by *Ancistrosyllis* sp. A (a member of the family Pilargidae), which made up 10% of the polychaete species in the Western branch but was not present in other canyon branches. There is very little information regarding the ecology of the Pilargidae (Fauchald & Jumars 1979), making it difficult to speculate why this species was abundant in the Western branch.

In addition to these intra-canyon patterns, polychaete assemblage composition differed between the canyon branches and the adjacent open slope. The CCA suggested that these species-level differences might be linked to the different sediment characteristics (e.g. coarser-grained sediments on the slope than in the canyon) and increased organic matter input into the canyon branches (Fig. 7). Duros et al. (2011) attributed differences in the benthic foraminiferal species composition between the branches and the slope, at depths comparable to those of the present study, to the preferential deposition of organic detritus in canyon branches.

Paramphinome jeffreysii was the top-ranked species at all sites (Table 2). A SIMPER analysis suggests it was also responsible for much of the similarity between stations inside the canyon and between the canyon and the slope (Table 3). The relative abundance of *P. jeffreysii* increased from west to east, reaching almost 40 % of the assemblage in the Eastern branch. It was also more common in the deeper sediment layers (1-3, 3-5 cm) than in the upper 1 cm horizon (Fig. 3). The abundance of this small, omnivorous polychaete (Fauchald & Jumars 1979) throughout the canyon may indicate an opportunistic response to organic matter being transported down the canyon. Significant increases in the abundance of the same species in the North Sea have been linked to an increase in food availability (Kroncke et al. 2011). High abundances of *P. jeffreysii* were also associated with organically-enriched sediments near fish farms along the Norwegian coastline (Bannister et al. 2014) and a trough (100 m depth) off the Swedish west coast (Rosenberg 1995).

Juvenile polychaetes in the family Opheliidae (Opheliidae sp. A) were common in the top sediment layer (0-1 cm) of samples from the Eastern branch, where they accounted for 11% of the assemblage and were ranked second after *P. jeffreysii*. This too may indicate a recent input of organic matter onto the top sediment layer. During a time-series study at a deeper site (~ 4850 m), located 464 km to the west of our study area on the Porcupine Abyssal Plain (PAP), morphologically very similar juvenile opheliids were found in high densities in the upper 2 cm layer of multicore samples (Vanreusel et al. 2001). Over the two year study period, a stable population of juvenile Opheliidae displayed a slow increase in the body size (Vanreusel et al. 2001). These opheliids were interpreted as opportunists that had recently been recruited following the deposition of a pulsed input of phytodetritus. A separate contribution to the same time-series study (Soto et al. 2010) also recorded a large increase in the abundance of opheliid juveniles at PAP. Again, this was interpreted as a recruitment event linked to phytodetritus deposition. Studies of shallow-water opheliids suggest that they have an opportunistic life history (Hermans 1978). Experiments on the continental shelf off North Carolina showed opheliid and capitellid abundance increasing by 2 - 90 times in enriched sediment trays compared with unenriched trays (Renaud et al. 1999). Population densities of the opheliid *Armandia brevis* from waters off San Juan Island, Washington, fluctuate markedly throughout the year as a result of reproductive events (Woodin 1974). The opheliids may be opportunists waiting for optimal conditions before converting their energy resources into a reproductive effort (Vanreusel et al. 2001).

It is interesting to note the large depth range (3500 – 4850 m) of Opheliidae sp. A, which spans both the lower bathyal and abyssal zones in the NE Atlantic. It has been suggested that depth zonation amongst macrofauna is closely related to their dispersal abilities during their early development (Grassle et al. 1979). Assuming they all represent the same species, larvae of the opheliid recognised in the present study may be well adapted to dispersal, allowing them to span a large depth range. All juvenile opheliids in Vanreusel et al. (2001) were presumed to belong to the same species. This species could not be determined as adult opheliids found at the PAP site in previous studies were new to science and not formally identified. The most abundant identified opheliid in our material was *Ophelina abranchiata.* It is not clear whether the juveniles represent this species or a complex of several species. Further work using genetic methods may elucidate this problem.

4.2 Polychaete diversity

4.2.1 Alpha diversity

Polychaete species diversity was similar in the Western, Central and Eastern branches of the Whittard Canyon, with the Western branch samples yielding slightly higher values of H' than the other two branches (Table 1). Total species numbers (species richness) were highest in the Eastern branch, followed by the Central, and Western branches, consistent with the higher abundances in the Eastern branch.

Compared with the canyon, polychaete diversity was higher at the slope site and dominance also lower, while species richness values lay between those of the Western and Central branches. Depressed species diversity inside canyons has been noted in the case of macrobenthos in the Nazaré Canyon (Curdia et al. 2004) and polychaetes in the Portuguese canyons (Patterson et al 2011).

A number of ecological studies have suggested a unimodal relationship between diversity and productivity (Rosenzweig 1995). In oligotrophic settings, diversity increases with increasing food availability to reach maximal values at intermediate levels of productivity. Where levels of food availability are excessive, diversity may be depressed (Levin et al., 2001). In coastal marine systems, increased organic enrichment resulting from pollution can lead to higher infaunal standing stocks. However, it can also lead to oxygen depletion and hence dominance by a few hypoxia-tolerant species leading to low evenness (Pearson & Rosenberg 1978). This has also been observed in upper bathyal oxygen minimum zones where dense, high-dominance, low-diversity benthic assemblages are associated with natural organic enrichment (Levin et al. 1994; Levin 2003; Gooday et al. 2010). However, there is no evidence for comparably high levels of organic enrichment and associated oxygen depletion at our study sites.

High levels of physical disturbance inside the canyon may also suppress polychaete diversity, in accordance with the Intermediate Disturbance Hypothesis (Connell 1978, Huston 1979), which predicts maximal levels of local species diversity when disturbance is neither too rare nor too frequent. At the High Energy Benthic Boundary Layer Experiment (HEBBLE) site in the North Atlantic, disturbance generated by episodic strong currents ('benthic storms') was linked to high species dominance in polychaetes and bivalves (Thistle et al. 1985). Disturbance in the form of high-energy currents was considered important in the structuring of polychaete diversity on the Hebridean Slope in the Rockall Trough (Paterson & Lambshead 1995). It has been suggested that community disturbance resulting from strong currents, high sedimentation rates and re-suspension explains the depressed diversity and increased dominance of certain species in the Nazaré (Gage et al. 1995, Curdia et al. 2004, Koho et al. 2007, Ingels et al. 2009) and Setubal (Gage et al. 1995) canyons. Paterson et al. (2011) attributed the dominance of a *Prionospio* species in the Nazaré Canyon to an opportunistic response to a disturbance event. The disturbance could have been caused by the periodic deposition of organically enriched sediment, but a spring-tide mediated turbidite event or increased bioturbation of larger macro/megafauna were also thought possible (Patterson et al. 2011). The lower diversity of sessile and sedentary megafauna in Hawaiian canyons was believed to have been caused by periodic disturbances, such as sediment slumps and turbidity currents (Vetter et al. 2010).

Polychaete diversity in the Whittard Canyon system is relatively high compared with that in Iberian Margin canyons (Fig. 5b). Paterson et al. (2011) analysed polychaete diversity in the Nazaré, Setubal and Cascais canyons on the Iberian Margin, in each case at depths of 1000, 3400, and 4300 m. Considering only the data from their 3400 m sites, i.e. closest in depth to our samples, rarefied species richness in the Whittard Canyon is generally higher than that in the Iberian canyons (Fig. 5b). Among the latter, rarefied species richness was lower in the Nazaré and Setubal Canyons than that in the Cascais Canyon. Paterson et al. (2011) attributed differences in polychaete rarefied species richness between Iberian Margin canyons to different environmental characteristics (Patterson et al., 2011). The Nazaré Canyon is active with periodic disturbances and relatively high current speeds (de Stigter et al. 2007, Garcia et al. 2007). Lower productivity characterised the mid-Setubal Canyon leading to reduced diversity. The higher diversity in the Cascais Canyon suggested that it is a more quiescent canyon, where disturbance and productivity effects are balanced (Patterson et al., 2011). If correct, these inferences suggest that the Whittard Canyon may be less disturbed/ more quiescent than the Iberian canyons, at least around 3400 m in the middle section.

4.2.2 Beta diversity

Levels of beta diversity on the ocean floor are poorly understood and appear to vary between taxa (Ellingsen et al 2007a). Paterson et al. (1998) reported a difference in the species composition of polychaete assemblages at sites on NE Atlantic and equatorial Pacific abyssal plains separated by 500 -1000 km. They suggested that faunal turnover occurred across scales of 1000 + km on abyssal plains. Similarly, Glover et al. (2001) report differences in polychaete species assemblages at four sites in the NE Atlantic (Porcupine, Tagus and Cape Verde Abyssal Plains) that were separated by distances of up to 3300 km. However, our data suggest there is a change in polychaete species composition across the 60 km spanned by our four study sites. It seems likely, therefore, that rates of beta diversity are considerably higher on continental margins dissected by canyons than they are on abyssal plains, which are topographically much less complex and offer fewer barriers to dispersal than the ocean margins.

Another way to assess the change in species composition across the study sites is provided by Whittaker's beta diversity (β_{W}). There was no clear variation in beta diversity in the present study, though we should note that the sample size limitations (minimum number of specimens per sample) may have restricted our ability to detect a change. Our beta diversity assessment (Table 4) nevertheless makes clear the enhanced α and γ diversity levels of the slope site over the canyon sites. This consequently meant that all aspects of diversity (^{0}D, ^{1}D, ^{2}D) were reduced when canyon data were added to the slope data.

There was surprisingly little difference in the species composition of assemblages between the slope and the Western canyon branch (Fig. 8). Our canyon samples are all from soft-bottom areas that are not too dissimilar in terms of sediment characteristics from the open slope. However, the Whittard Canyon as a whole encompasses a wide range of different habitats. The head of the canyon is characterised by turbidity currents and oxygen-limited, possibly sulphidic conditions (Ingels et al. 2011). Vertical cliffs (Huvenne et al. 2011) and cold-water corals (Morris et al. 2013, Huvenne et al. 2011, Robert et al. 2014) are present in the upper to mid reaches, flat areas of soft sediment in the thalweg (Robert et al. 2014) and deeper parts of the canyon. Analysis of polychaete assemblages from these different areas inside the canyon would almost certainly increase species-level differences in the assemblages both between canyon and slope and within the canyon and thereby enhance species turnover. McClain and Barry (2010) observed that the highest rate of faunal turnover in the Monterey Canyon off the central Californian coast, USA, was closest to the canyon wall. The authors concluded that the canyon walls enhanced the input of organic debris, which significantly altered the benthic assemblages. Our canyon samples were all collected from or next to the thalweg, so the effect of the canyon wall would be negligible.

4.2.3 Regional species diversity?

Continental margins are characterised by high species diversity (Hessler & Sanders 1967, Levin et al. 2010), related in part to the considerable habitat heterogeneity that characterises these regions of the deep sea (Levin & Dayton 2009, Levin et al. 2010). By virtue of their extreme topography, complex current regimes, and tendency to concentrate organic matter and sediment, submarine canyons make a substantial contribution to this heterogeneity (Vetter & Dayton 1999, McClain & Barry 2010). Canyons in the Hawaiian Archipelago were thought to enhance the regional diversity of megafauna, with 41 species being only found inside the canyon and not on the slope (Vetter et al. 2010). In the present study, 46 polychaete species were only recorded from the canyon branches, which might suggest that the canyon harbours species that are not found on the adjacent slope. However, our sampling effort was not equal at the canyon and slope sites (i.e. 15 and 5 samples respectively). When sites are compared with rarefaction (Fig. 5c; Table 4), all sites combined have a lower expected number of species than the slope site alone. This would seem to suggest that the Whittard Canyon does not substantially increase the regional diversity of polychaetes. Our conclusions must, however, be limited to the soft-sediment environment at c. 3500 m water depth.

4.3 Polychaete Biogeography

The 25 species that were found at all four study sites accounted for 72.3 % of polychaete specimens. The two most abundant species (*Paramphinome jeffreysii* and *Aurospio* sp. B), which were among those found at all sites, made up 39.4 % of the total number of identified polychaetes in our samples. The 43 species that occurred at a single site accounted for only 2.9 % of specimens. This pattern is consistent with the observations of Glover et al. (2001), who recognised a core group of polychaete species that were widely distributed at their four NE Atlantic abyssal plain sites. These species represented about 70 % of the fauna at the Madeira Abyssal Plain but around 50 % or less at three other sites. However, a large majority (81 %) of the species they recognised were unique to one of their sites. They attributed the large number of unique species to a vast regional species pool and inadequate sampling effort. Wide spatial distributions of the most abundant species and the apparent compressed range of the least common species were also noted in the case of polychaetes from the Southern Ocean (Ellingsen et al. 2007b). Indeed, this pattern is suggested for many groups of species, habitat types and spatial scales (Brown 1984).

Some species found in the Whittard Canyon apparently have cosmopolitan distributions on a global scale. For example, there are records of *Aurospio dibranchiata*, which was found at all four of our sites and from the Atlantic, Pacific and Southern Oceans (Glover, Paterson and Smith in Smith et al. 2006). With fewer barriers to dispersal in the deep sea, compared with shallow-water habitats, wide dispersal of species might be expected (Grassle and Morse-Porteous, 1987). However, barriers do exist and these are probably more common on continental margins than abyssal plains (McClain and Mincks Hardy, 2010). Despite these restrictions to dispersal, some species do appear to have cosmopolitan distributions in the deep sea, particularly at abyssal depths (Wilson and Hessler, 1987; McClain and Mincks Hardy, 2010). In the case of certain foraminifera, this is supported by molecular evidence (Pawlwoski et al., 2007; Lecroq et al., 2009). Conversely, some species identified morphologically as 'cosmopolitan' have proved to comprise a complex of cryptic species with smaller ranges when investigated with molecular methods (e.g.,Vrijenhoek et al. 1994; France and Kocher, 1966; Quattro et al. 2001).

Paterson et al. (2011) suggest that canyons may harbour endemic polychaete species. Forty-six polychaete species were found inside the Whittard Canyon branches but not on the adjacent slope. Of these 46 species, 34 could not be assigned a binomial Latin name. This prevalence of undescribed species is typical of the generally poor state of knowledge of deep-sea polychaete taxonomy (Paterson et al. 2011), which makes it difficult to determine whether there are any polychaete species endemic to the Whittard Canyon. Two species found in this study, Aurospio sp. B and *Prionospio* sp I., were also recorded in the Iberian margin canyons and are currently under description (Paterson et al. in prep). To date these new species have only been recorded in canyons (Lenka Neal pers. comm.). Whether these species are true canyon endemics or are easier to detect inside canyons, owing to the presence of larger populations remains open to question. Endemics are found in canyons, but these are generally species endemic to a particular region (e.g. the Mediterranean) and not a specific canyon (Danovaro et al. 2010). A more likely scenario, suggested by Patterson et al. (2011), is that species are adapted to the disturbed conditions typical of some canyons rather than being restricted to one particular canyon. Indeed, 90 % of species richness in the deep sea is attributed to species that have not been formally described (Smith et al 2006), consequently, species distributions are very poorly understood (Glover et al., 2001; McClain and Mincks Hardy 2010). Further research on the taxonomy of deep-sea canyon polychaetes using both morphological characteristics and genetic methods is required to understand endemics in canyons and connectively between different canyons.

Conclusions

Within the Whittard Canyon, significant variation in species composition was noted between branches but diversity appeared to be broadly similar. There was appreciable variation in diversity and species composition between the slope and canyon sites, which had an impact on regional diversity. Diversity (as ${}^0D$, ${}^1D$ and ${}^2D$) is depressed within the canyon when compared with the slope. Consequently, in this case the Whittard Canyon acts to depress regional diversity through both reduced species richness and increased species dominance.

Acknowledgements

We thank the captain, crew and shipboard scientific party of RRS *James Cook* cruise 036 for the collection of the Megacore samples. This research was supported by a PhD studentship grant from the Natural Environmental Research Council (NE/J500227/1) with CASE studentship from the Natural History Museum, London. This work contributes to the NERC Marine Environmental Mapping Programme (MAREMAP).

Table 1. Sites and diversity summary. Average = mean of five stations. J′, Pielou’s evenness; H′ (log2), Shannon index; 1-λ′, Simpson index.

Deploy.	Lat.(N)	Long.(W)	Depth(m)	Area sampled (m^{-2})	Poly. dens. (ind. m^{-2})	Total species	J′	H′ (log2)	1-λ′	Rank 1 dom. (%)
W002	48°09.18′	10°33.70′	3670	0.063	1226	22	0.800	3.567	0.870	26.66
W003	48°09.17′	10°33.70′	3661	0.055	1328	22	0.818	3.646	0.875	27.94
W011	48°09.22′	10°32.36′	3582	0.047	1422	24	0.861	3.949	0.905	20.31
W026	48°09.18′	10°33.73′	3670	0.039	1223	19	0.891	3.784	0.904	19.14
W043	48°09.15′	10°33.76′	3657	0.047	1443	23	0.792	3.582	0.848	34.37
Ave. W						**22.0**	**0.832**	**3.706**	**0.880**	**25.68**
Sl016	47°56.79′	10°46.85′	3511	0.063	939	21	0.876	3.848	0.902	22.64
Sl017	47°56.78′	10°46.85′	3512	0.055	982	23	0.923	4.175	0.932	13.72
Sl018	47°56.81′	10°46.91′	3514	0.047	1358	28	0.885	4.253	0.927	15.87
Sl019	47°56.74′	10°46.94′	3505	0.063	1337	30	0.857	4.207	0.920	18.51
Sl020	47°56.78′	10°46.85′	3514	0.055	1364	25	0.870	4.039	0.910	22.97
Ave. Sl						**25.4**	**0.882**	**4.104**	**0.918**	**18.74**
C063	48°16.89′	10°18.74′	3375	0.047	1995	25	0.748	3.474	0.799	42.69
C064	48°16.97′	10°18.65′	3382	0.063	2388	34	0.762	3.877	0.850	35.61
C065	48°17.04′	10°18.89′	3373	0.055	2165	36	0.810	4.187	0.887	29.82
C067	48°16.98′	10°18.72′	3376	0.055	1528	27	0.791	3.761	0.854	34.17
C066	48°16.83′	10°18.72′	3381	0.063	2308	37	0.798	4.155	0.891	27.14
C068	48°17.01′	10°18.83′	3375							
Ave. C						**31.8**	**0.782**	**3.891**	**0.856**	**33.89**
E093	48°15.89′	10°09.56′	3424	0.063	1942	35	0.723	3.709	0.797	43.58
E094	48°15.78′	10°09.57′	3429	0.053	2583	33	0.762	3.842	0.845	36.23
E095	48°15.78′	10°09.58′	3429	0.063	3184	43	0.712	3.866	0.821	40.10
E096	48°15.76′	10°09.60′	3424							
E097	48°15.89′	10°09.54′	3425	0.039	4304	29	0.662	3.214	0.764	45.23
E098	48°15.76′	10°09.60′	3432	0.031	4330	32	0.730	3.652	0.843	33.58
Ave. E						**34.4**	**0.718**	**3.656**	**0.814**	**39.74**

Table 2. Top ten most abundant species at each site. Relative abundance shown in brackets.

Slope	**Western branch**	**Central branch**	**Eastern branch**
Aurospio sp. B (14.3%)	*Paramphinome jeffreysii* (21.2%)	*Paramphinome jeffreysii* (33.6%)	*Paramphinome jeffreysii* (39.6%)
Paramphinome jeffreysii (12.9%)	*Aurospio* sp. B (11.2%)	*Aurospio* sp. B (8.3%)	Opheliidae sp. A (11.0%)
Anguillosyllis capensis (9.3%)	*Ancistrosyllis* sp. A (10.2%)	*Ophelina abranchiata* (4.9%)	*Prionospio* sp. I (5.5%)
Prionospio sp. I (7.1%)	*Levinsenia gracilis* (6.5%)	*Levinsenia gracili*s (3.8%)	*Aurospio* sp. B (5.5%)
Aurospio dibranchiata (6.3%)	*Prionospio* sp. I (6.0%)	*Chaetozone* sp. F (3.4%)	*Leitoscoloplos* sp. B (2.2%)
Flabelligella cf. biscayensis (5.4%)	*Leanira hystricis* (3.9%)	*Ophelina cylindricaudata* (3.3%)	*Ophelina abranchiata* (2.1%)
Ampharetidae new genus sp. A (4.7%)	*Ophelina abranchiata* (3.8%)	Polychaetae larva sp. A (3.0%)	*Glycera capitata* (2.0%)
Glycera capitata (3.4%)	*Chaetozone* sp. F (3.1%)	*Aurospio dibranchiata* (2.8%)	*Aricidea simplex* (1.8%)
Chaetozone sp. F (3.4%)	*Chaetozone* sp. C (1.8%)	*Chaetozone* sp. A (2.5%)	*Prionospio* sp. B (1.7%)
Levinsenia gracilis (2.8%)	*Chaetozone* sp. A (1.7%)	*Leitoscoloplo*s sp. B (2.5%)	*Ophelina cylindricaudata* (1.4%)

Table 3. SIMPER analysis of the Whittard Canyon and adjacent slope sites.

Slope (%)	**Western branch (%)**	**Central branch (%)**	**Eastern Branch (%)**
Similarity between samples within sites			
Paramphinome jeffreysii - 6.7 %	*Paramphinome jeffreysii* - 9.2%	*Paramphinome jeffreysii* - 11.4 %	*Paramphinome jeffreysii* - 12.0 %
Aurospio sp. B - 6.7 %	*Aurospio* sp. B - 6.8 %	*Aurospio* sp. B - 4.9%	Opheliidae sp. A - 4.4 %
Anguillosyllis capensis - 5.8%	*Ancistrosyllis* sp. A - 4.1 %	*Levinsenia gracilis* - 3.5 %	*Aurospio* sp. B - 4.1%
Aurospio dibranchiata - 4.6 %	*Chaetozone* sp. F - 3.9 %	*Ophelina cylindricaudata* - 3.5 %	*Prionospio* sp. I - 3.7 %
Flabelligella cf. biscayensis - 4.4 %	*Prionospio* sp. I - 3.1 %	*Chaetozone* sp. F - 3.0 %	*Leitoscoloplos* sp. B - 2.9 %
Dissimilarity between sites			
C&E (%)	**C&S (%)**	**C&W (%)**	**S&W (%)**
Opheliidae sp. A - 2.6 %	*Paramphinome jefreysii* - 3.8%	*Paramphinome jeffreysii* - 2.7%	*Ancistrosyllis* sp. A - 3.31%
Paramphinome jeffreysii - 2.0 %	*Anguillosyllos capensis* - 2.8%	*Ancistrosyllis* sp. A - 2.5%	*Anguillosyllis capensis* - 2.42%
Prionospio sp. I - 1.4 %	*Ophelina cylindricaudata* - 2.0%	*Ophelina cylindricaudata* - 2.2%	Ampharetidae new genus sp. A - 2.1%
S&E (%)	**E&W (%)**		
Paramphinome jefreysii - 5.5%	*Paramphinome jefreysii* - 4.6%		
Opheliidae sp. A - 3.6%	Opheliidae sp. A - 4.1%		
Leitoscoloplos sp. B - 2.0%	*Ancistrosyllis* sp. A - 2.5%		

Table 4. Assessment of beta diversity via rarefaction with Hills numbers (^{0}D, richness; ^{1}D, exponential Shannon; ^{2}D, inverse Simpson), α rarefied to 47 individuals, and γ rarefied to 235 individuals. Canyon = all canyon sites. Region = all canyon sites + slope site.

Site	^{0}D			^{1}D			^{2}D		
	$\overline{\alpha}$	β	γ	$\overline{\alpha}$	β	γ	$\overline{\alpha}$	β	γ
West	18.5	2.5	46.1	12.2	1.7	20.2	8.4	1.4	11.5
Centre	19.9	2.3	45.7	11.8	1.5	18.1	7.0	1.1	7.6
East	18.4	2.5	45.9	8.8	1.5	14.5	5.4	1.0	5.6
Slope	21.2	2.6	54.0	15.7	1.6	24.8	11.9	1.3	15.0
Canyon	18.9	2.6	49.0	11.3	1.7	18.7	6.9	1.1	7.5
Region	19.5	2.7	51.8	12.4	1.7	21.1	8.2	1.1	8.7

Figure Captions

Fig. 1. Locality map of Whittard Canyon in NE Atlantic, based on GEBCO data (www.gebco.net) and bathymetric chart of Whittard Canyon, based on data provided by the Geological Survey of Ireland (www.gsiseabed.ie). The four study sites are indicated: Western Branch (W), Central Branch (C) and Eastern Branch (E) of the canyon and one site on the adjacent slope (Sl).

Fig. 2. Composition of the most abundant polychaete species at each of the four study sites. 1, Others; 2, *Paramphinome jeffreysii*; 3, *Aurospio* sp. B; 4, Opheliidae sp. A; 5, *Anguillosyllis capensis*; 6, *Prionospio* sp. I; 7, *Aurospio dibranchiata* 8, *Flabelligella* cf. *biscayensis*; 9, Ampharetidae Genus A; 10, *Glycera capitata*; 11, *Chaetozone* sp. F; 12, *Levinsenia gracilis*; 13, *Ancistrosyllis* sp. A;14, *Leanira hystricis*;15, *Ophelina abranchiata*;16, *Chaetozone* sp. C;17, *Chaetozone* sp. A; 18, *Ophelina cylindricaudata*; 19, Polychaete larva sp. A; 20, *Leitoscoloplos* sp. B; 21, *Aricidea simplex*; 22, *Prionospio* sp. B

Fig. 3. Vertical distribution of polychaetes in sediments (0-1, 1-3 and 3-5 cm) at each site represented as percentage abundance.

Fig. 4. k-dominance plot for Whittard Canyon and slope sites, using pooled data from five samples at each of the four sites.

Fig. 5. Polychaete diversity estimated using rarefaction, 95% confidence intervals shown as grey shading. (A) Slope site, Western, Central and Eastern branches. (B) Combined Whittard Canyon branches (Western, Central and Eastern branches) and

Iberian Margin canyons (Nazare, Setubal and Cascais Canyons) at 3400 m. (C) Combined Whittard Canyon branches, slope site and Whittard Canyon region (Slope site, Western, Central and Eastern branches).

Fig. 6. nMDS ordination plot of polychaete species composition at four study sites (grey symbols represent centroids)

Fig. 7. Canonical correspondence analysis of polychaete species composition at four study sites. Depth, water depth; fine BPI, fine-scale bathymetry position index; clay, percentage clay; Density.om macrofaunal density as a proxy for organic matter input; slope.angle, slope angle ; Ruggosity; silt, silt percentage; Sediment, sediment grain size.

Fig. 8. Plot of nMDS ordination x-value against sampling identity for polychaete species composition at four study sites.

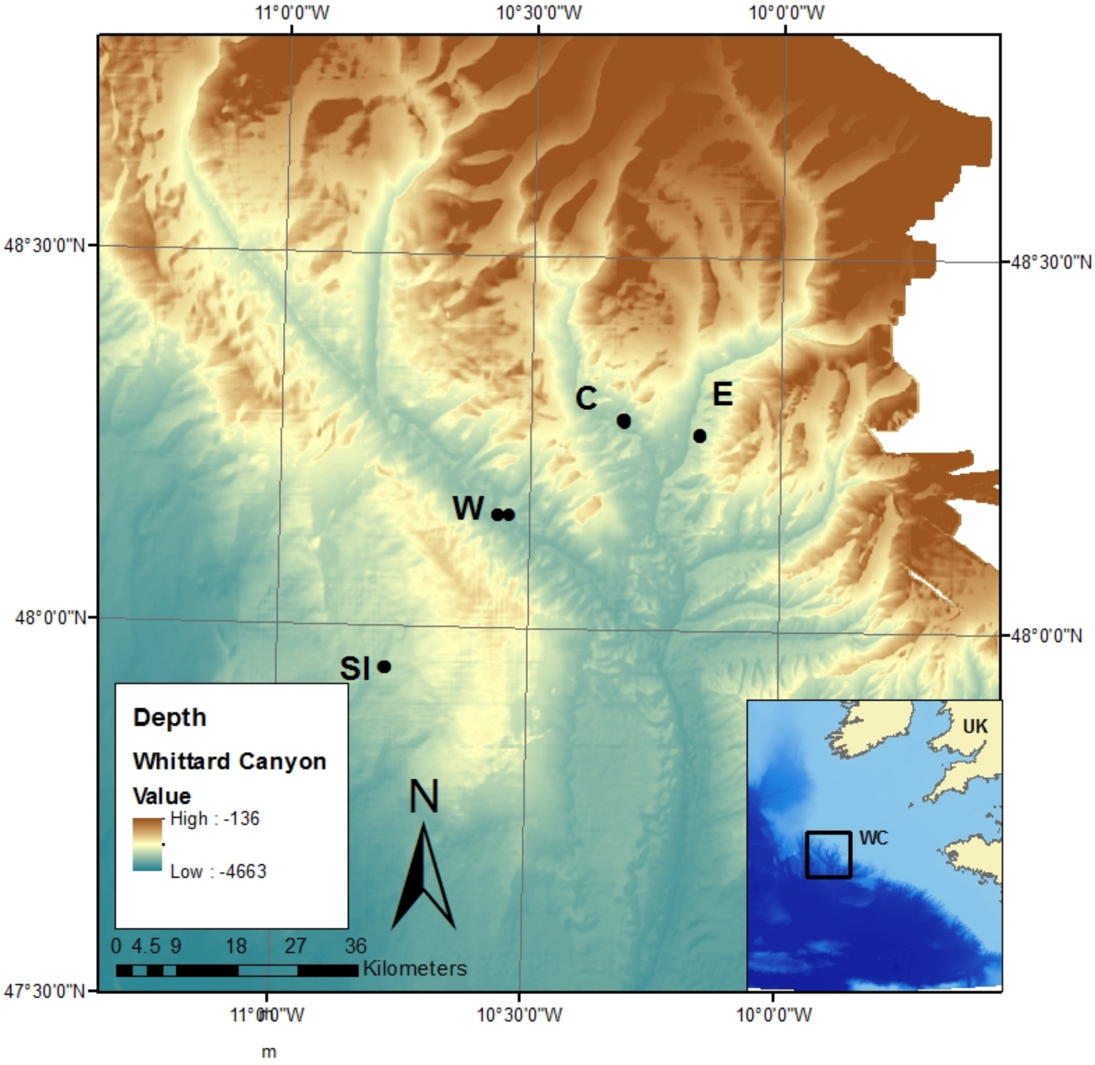
11°0'0"W
10°30'0"W
10°0'0"W
48°30'0"N
48°0'0"N
47°30'0"N
C
E
W
SI
Depth
Whittard Canyon
Value
High : -136
Low : -4663
N
0 4.5 9 18 27 36
Kilometers
UK
WC
m

Fig. 1

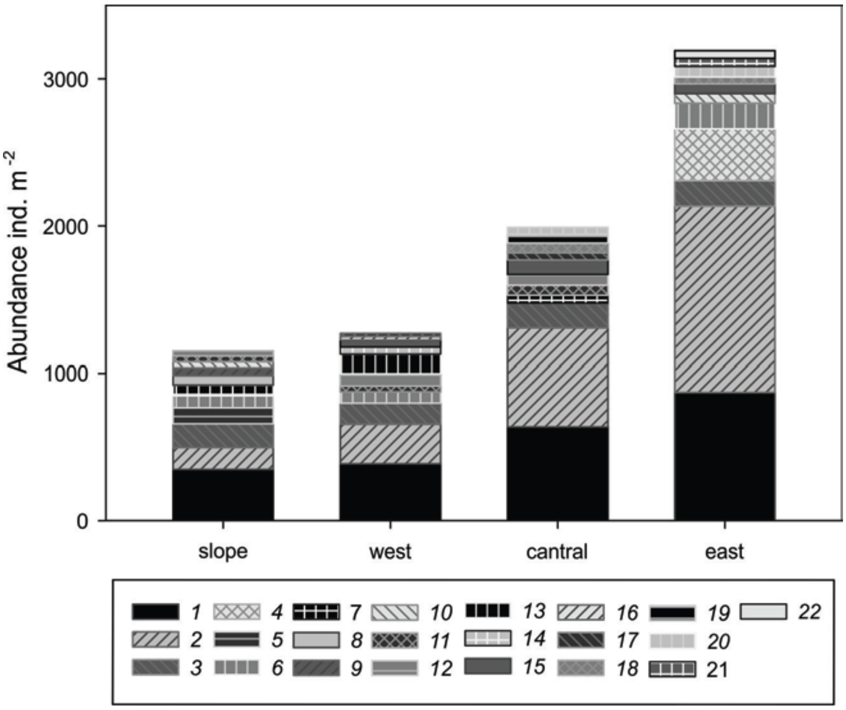
Abundance ind. m-2
0
1000
2000
3000
slope
west
cantral
east
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22

Fig. 2

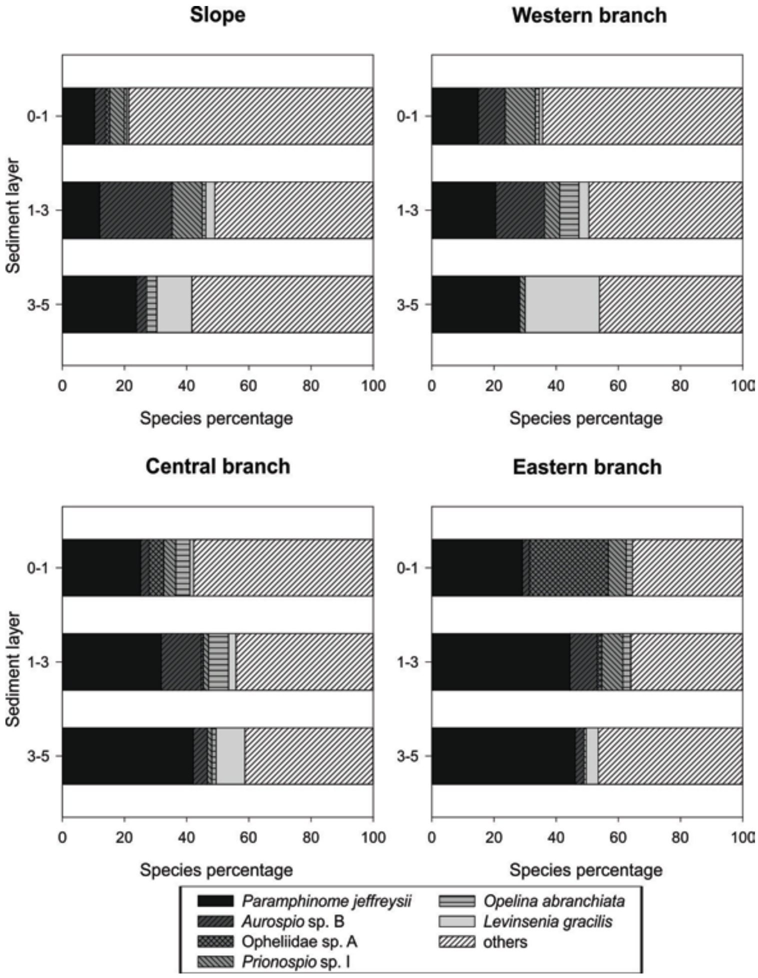
Slope
Western branch
Central branch
Eastern branch
Sediment layer
0-1
1-3
3-5
0
20
40
60
80
100
Species percentage
Paramphinome jeffreysii
Aurospio sp. B
Opheliidae sp. A
Prionospio sp. I
Opelina abranchiata
Levinsenia gracilis
others

Fig. 3

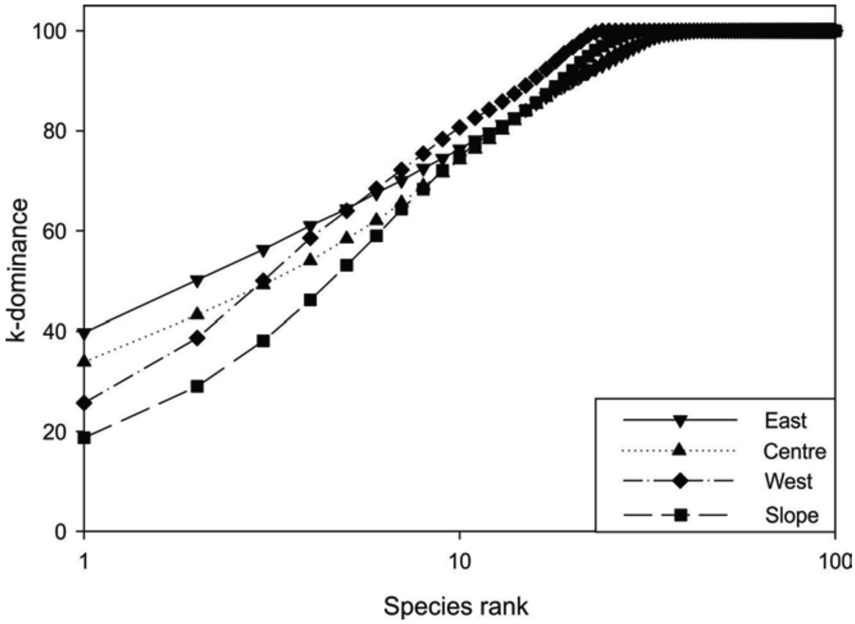
k-dominance
0
20
40
60
80
100
1
10
100
Species rank
East
Centre
West
Slope

Fig. 4

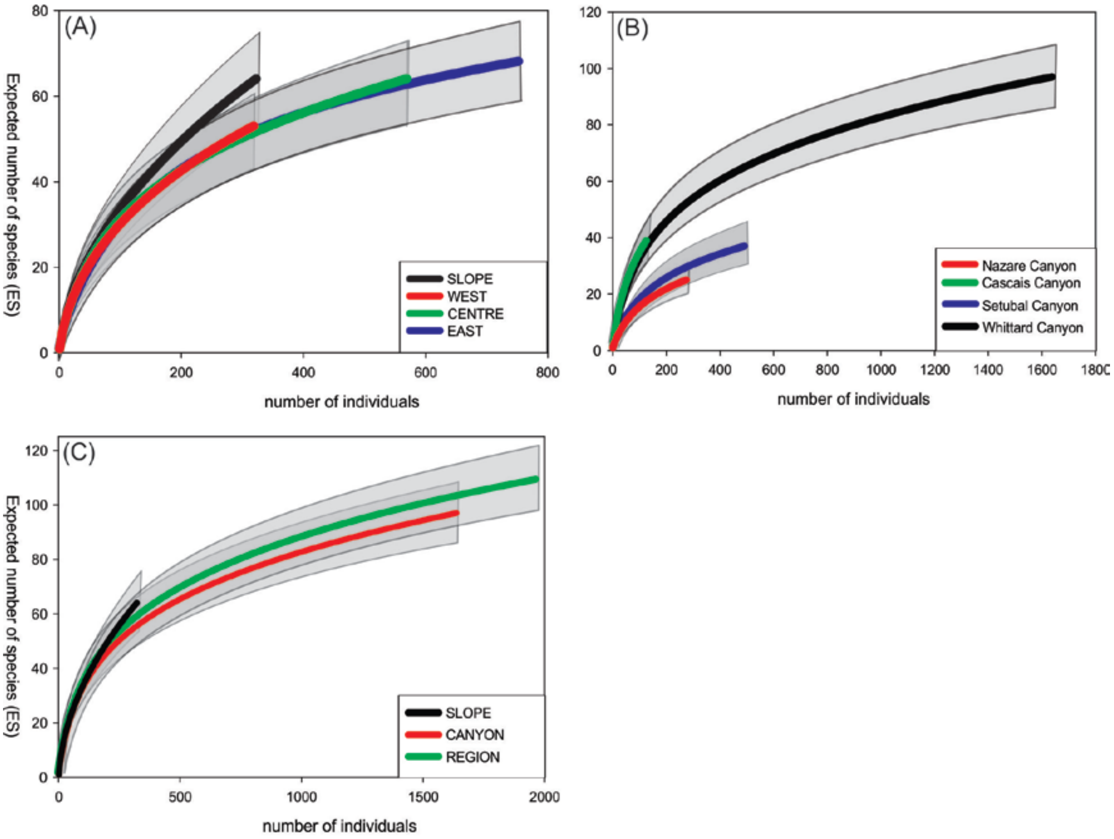
(A)
Expected number of species (ES)
80
60
40
20
0
0
200
400
600
800
number of individuals
SLOPE
WEST
CENTRE
EAST
(B)
120
100
80
60
40
20
0
0
200
400
600
800
1000
1200
1400
1600
180
number of individuals
Nazare Canyon
Cascais Canyon
Setubal Canyon
Whittard Canyon
(C)
Expected number of species (ES)
120
100
80
60
40
20
0
0
500
1000
1500
2000
number of individuals
SLOPE
CANYON
REGION

Fig. 5 a,b&c

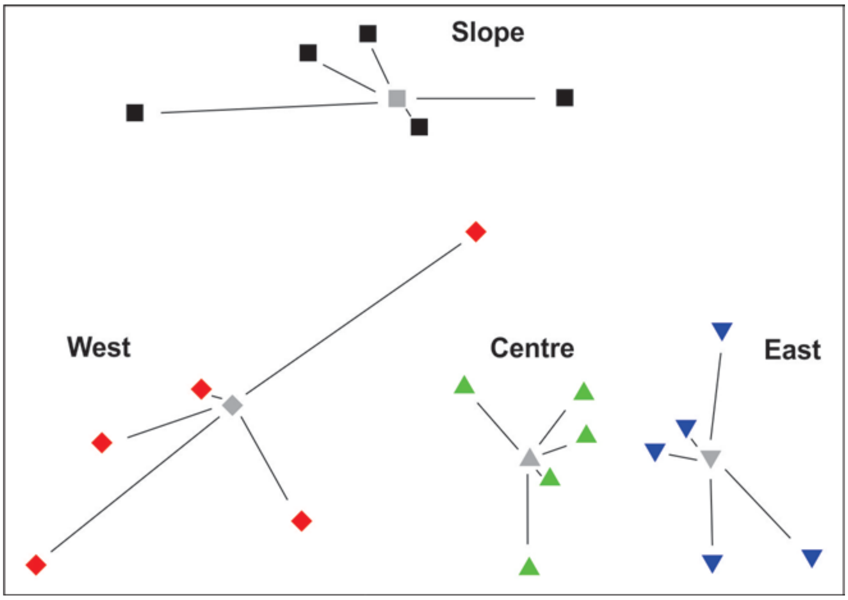

Fig. 6

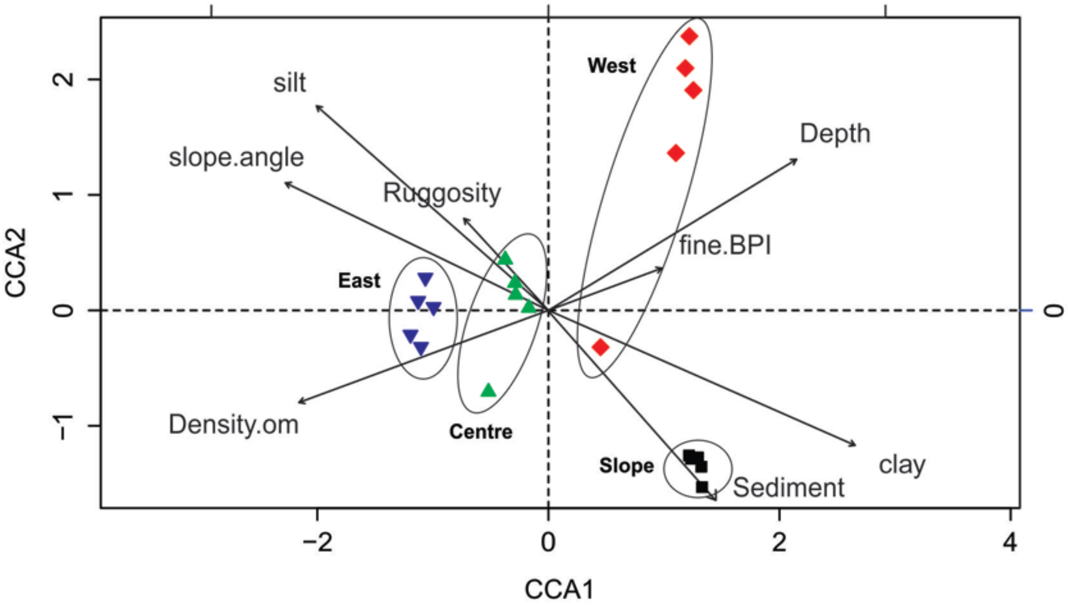
silt
slope.angle
Ruggosity
Depth
fine.BPI
West
East
Centre
Density.om
Slope
Sediment
clay
CCA2
CCA1
2
1
0
−1
−2
0
2
4
0

Fig. 7

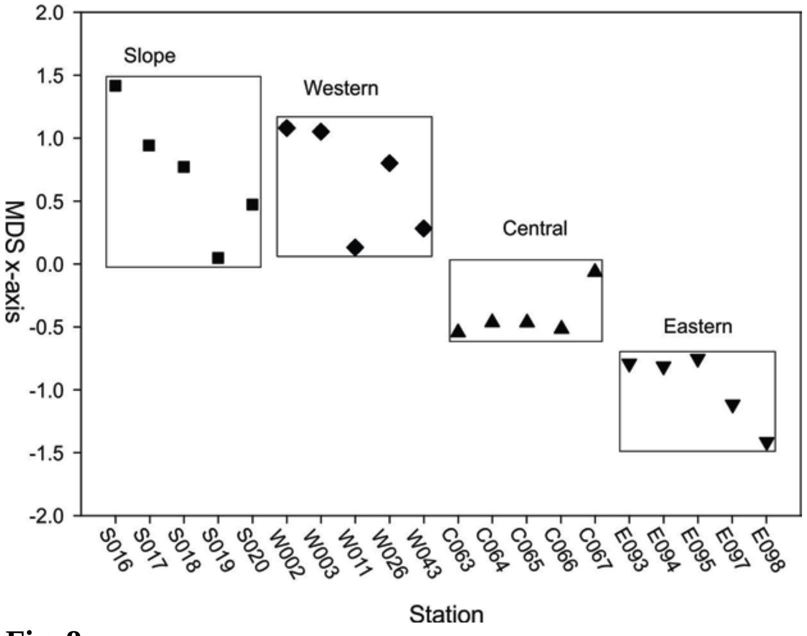
2.0
1.5
1.0
0.5
0.0
-0.5
-1.0
-1.5
-2.0
MDS x-axis
Slope
Western
Central
Eastern
S016
S017
S018
S019
S020
W002
W003
W011
W026
W043
C063
C064
C065
C066
C067
E093
E094
E095
E097
E098
Station

Fig. 8

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