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Macrofaunal abundance and community composition at lower bathyal depths in different branches of the Whittard Canyon and on the adjacent slope (3500 m; NE Atlantic)

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ABSTRACT

We studied benthic macrofaunal abundance and community composition in replicate Megacorer samples obtained from three sites in different branches of the Whittard Canyon (NE Atlantic) and one site on the adjacent slope to the west of the canyon system. All sites were located at a depth of ~3500 m. Abundance (macrobenthos sensu stricto, $>300\,\mu m$) varied significantly ($p<0.001$) among sites, and decreased from east to west; highest in the Eastern branch (6249 ± standard deviation 1363 ind. m^{-2}) and lowest on the slope (2744 ± SD 269 ind. m^{-2}). Polychaetes were the dominant taxon, making up 53% of the macrofauna, followed by isopods (11%), tanaids (10%), bivalves (7%) and sipunculans (7%). Among the polychaetes, the Amphinomidae was the dominant family (27%), followed by the Spionidae (22%). Assemblage composition changed across the sites. From east to west, the proportion of polychaetes and isopods decreased (by 6% in each case), while sipunculans and tanaids increased (by 13% and 8%, respectively). The ranking of the two dominant polychaete families reversed from east to west (Eastern branch—Amphinomidae 36%, Spionidae 21%; Slope—Spionidae 30%, Amphinomidae 10%). Ordination of faunal groups (macrofaunal higher taxa, and polychaete families) revealed that the Central and Eastern branches were substantially similar, while the Western branch and slope sites were relatively distinct. A very similar pattern was evident in a corresponding ordination of environmental variables across the sites. An analysis of faunal similarities (ANOSIM) indicated that the Western branch/slope and Central branch/Eastern branch groups displayed the highest similarity. The clearest separation was between the slope and the Eastern branch. We conclude that, when compared at the same water depth, macrofaunal abundance and composition varies between open slope and canyon location, as well as among canyon branches. These differences probably reflect the influence of organic enrichment together with hydrodynamic activity, both of which are influenced by the topographic profile of individual canyon branches.

1. Introduction

Submarine canyons are major topographic features on continental margins. They play an important role as fast-track conduits for the transport of material from the shelf to abyssal depths (Vetter and Dayton, 1998). Organic carbon in the form of macrophyte detritus (Rowe et al., 1982; Vetter and Dayton, 1999), sediment (Arzola et al., 2008) and even pollutants (Palanques et al., 2008) are transported through canyons out onto the adjacent abyssal plain. Active canyons are believed to be very unstable environments that are subject to tidal currents, episodic slumps, sediment gravity flows, turbidity flows and periodic flushing events (Gardner, 1989; Canals et al., 2006; de Stigter et al., 2007). Topography (Shepard and Dill, 1966) and proximity to a fluvial source will also influence the disturbance regime. Although they have been known for over a century and a half (Dana, 1863), the rugged topography of canyons and the difficulty of sampling within them have limited multidisciplinary studies to the last 20 years (Ramirez-Llodra et al., 2010b). As a result, current knowledge of canyon benthic biology is poor.

Deep-sea macrofauna abundance decreases with depth (Rowe, 1983; Rex et al., 2006). However, this decline in abundance is far from uniform (Gage, 2003) and regions of high productivity can show elevated benthic abundance regardless of depth (Rex and Etter, 2010). In this regard, submarine canyons have been referred to as biomass and productivity ‘hotspots’ (De Leo et al., 2010; Vetter et al., 2010). Canyon sediments are reported to be richer in

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fresh organic carbon, total nitrogen, phytopigments (Garcia et al., 2007) and lithogenic (Romano et al., 2013) material than sediments on the adjacent slope. High organic enrichment inside canyons compared with the open slope has been linked to increased megafaunal (Vetter and Dayton, 1999; Ramirez-Llodra et al., 2010; Vetter et al., 2010; De Leo et al., 2010), macrofaunal (Rowe et al., 1982; Vetter and Dayton, 1998; Tyler et al., 2009; Duineveld et al., 2001; Paterson et al., 2011), meiofaunal (Ingels et al., 2009; Soetaert et al., 1991) and foraminiferal (Duros et al., 2011) densities. On the other hand, depressed faunal abundance inside canyons may be linked to frequent physical disturbance and high sedimentation rates (Gage et al., 1995; Koho et al., 2007).

As with faunal abundance, benthic community composition and diversity is influenced by the quality and quantity of food inputs (Gooday and Turley, 1990; Ruhl and Smith, 2004) and hydrodynamic disturbance (Thistle et al., 1985; Grassle and Morse-Porteous, 1987), as well as by water depth (Jumars and Gallagher, 1982; Flach et al., 2002), sediment grain size (Etter and Grassle, 1992; Leduc et al., 2012), sediment mobility (Levin et al., 1994) and bottom-water oxygen concentration (Levin et al., 2000). Many of these factors are thought to interact, regulating biological communities within canyons (McClain and Barry, 2010).

Evidence from the High Energy Benthic Boundary Layer Experiment (HEBBLE) site (Thistle and Sherman, 1985; Thistle and Wilson, 1987, 1996; Thistle et al., 1991, 1999) suggests that elevated levels of disturbance inside canyons, such as those caused by currents, will structure the faunal assemblage differently compared with more quiescent slope environments. Taxa such as tanaids that are able to burrow into the sediment and hide from disturbance (Reidenauer and Thistle, 1985) gain an advantage, while suspension-feeding organisms (sponges and corals) benefit from enhanced bottom currents inside canyons (Rowe, 1971) and deposit-feeding organisms can benefit from the increased levels of macrophyte detritus (Okey, 1997). Opportunistic species will also be favoured in areas of high disturbance (Paterson et al., 2011). The diverse current regimes, varying substratum types, and detrital funneling from the continental shelf, will combine to enhance habitat heterogeneity within canyons (Levin et al., 2010). Large sessile megafauna add to the habitat complexity, and cold-water corals provide habitats and refuges from predators for a variety of taxa (Buhl-Mortensen et al., 2010). Thus, a greater diversity of microhabitats is available to canyon inhabitants compared with those living on the open slope. Such factors may explain differences in community composition between canyons and adjacent slopes sites located at similar depths (Vetter and Dayton, 1998; Duineveld et al., 2001; Garcia et al., 2007).

The Whittard Canyon is a dendritic submarine canyon system on the NW European continental margin. Previous studies have shown that this feature hosts increased foraminiferal (Duros et al., 2011) and nematode (Ingels et al., 2011) abundances compared with the open slope. Hunter et al. (2013) reported high macrofaunal abundances inside the canyon. Duineveld et al. (2001) reported a significantly higher macro- and mega-faunal biomass inside the canyon compared with the slope, but no significant difference in macrofaunal abundance. Increased taxon richness and abundance in the Whittard Canyon have also been reported for cold-water corals (Morris et al., 2013). There are no previous studies, however, of macrofaunal abundance and community composition across the canyon system. With this in mind, the present study investigates these faunal parameters at the higher taxon level for the macrofauna as a whole, and at the family level for the dominant macrofaunal group (polychaetes) at the same water depth within different branches of the Whittard Canyon and on the adjacent slope. We aim to test whether (1) macrofaunal abundance is enhanced inside the Whittard Canyon relative to the adjacent slope, (2) community composition inside the canyon is distinct from that on the adjacent slope, and (3) canyon assemblages are distinct on an intra-canyon scale.

2. Material and methods

2.1. Study area

The Whittard Canyon is located on the Irish margin, southwest of the British Isles and southeast of the Goban Spur, and is not directly connected to any rivers. It starts around the shelf break at about 200 m water depth and extends to a depth of 4000 m over a distance of about 110 km. Three main branches, the Western, Central and Eastern, are recognised within the canyon system (Fig. 1). These branches coalesce around 3700 m to form a single canyon that opens out on to the Porcupine Abyssal Plain. The upper part is very steep-sided with walls reaching a height of up to 800 m, but at depths of around 3600 m the walls are lower (Hunter et al., 2013). The mouth of the canyon discharges into a large fan, 148 km long by 111 km wide (Reid and Hamilton, 1990).

The sediments in the upper part of the canyon are coarse compared with those further down (Hunter et al., 2013). The sediment is characterised by silty clay and fine sand in the Western branch (~3000 m), whereas sandy silt and fine sand predominate in the Eastern branch (~3000 m). The slope to the west of the canyon system is characterised by sand and silt (Duros et al., 2012). Some of the canyon sediments are derived from the shelf, which presumably provides a significant proportion of the material that passes down the canyon system at present (Reid and Hamilton, 1990; Cunningham et al., 2005).

Evidence about the levels of activity within the Whittard Canyon is ambiguous. Reid and Hamilton (1990) report small slope failures and a semi-diurnal tidal current only strong enough to transport fine-grained material. However, there is also evidence for active down-slope sediment transport in the form of turbidity currents, as well as mud-rich flows large enough to overspill the canyon system and form overbank deposits (Cunningham et al., 2005). Near-bottom currents reaching a maximum speed of 16 cm s^{-2} have been reported at 3752 m depth inside the canyon (Reid and Hamilton, 1990). Tidal currents with speeds up to 40 cm s^{-1} at 1000 m and up to 20 cm s^{-1} at 2000 m were recorded in the Eastern and Western branches (de Stigter in Duros et al., 2011). Sediment fluxes down the Whittard Canyon have not been well quantified and how they vary between the different branches remains unknown.

The present study focuses on sites located at the same depth (~3500 m) in the Western, Central and Eastern branches. Previous studies reported differences in environmental parameters between the Western and Eastern branches at similar depths. These published data are summarised in electronic Supplementary information (Table S1).

2.2. Field sampling

Macrofauna were collected from three sites in different branches of the canyon and one site on the adjacent slope (Fig. 1) using a Megacorer (Gage and Bett, 2005) during the RRS *James Cook* cruise 036 in June and July 2009. Samples were taken from 22 deployments (Table 1), between 3373 and 3670 m depth. In general, the Megacorer was fitted with eight large (100 mm internal diameter) core tubes. However, for one deployment at each site, one of the large tubes was replaced with a single smaller (59 mm internal diameter) tube. This collected a core that was used for sediment grain-size analysis.

Five replicate deployments were conducted in the Western branch, six in the Central branch, six in the Eastern branch and five

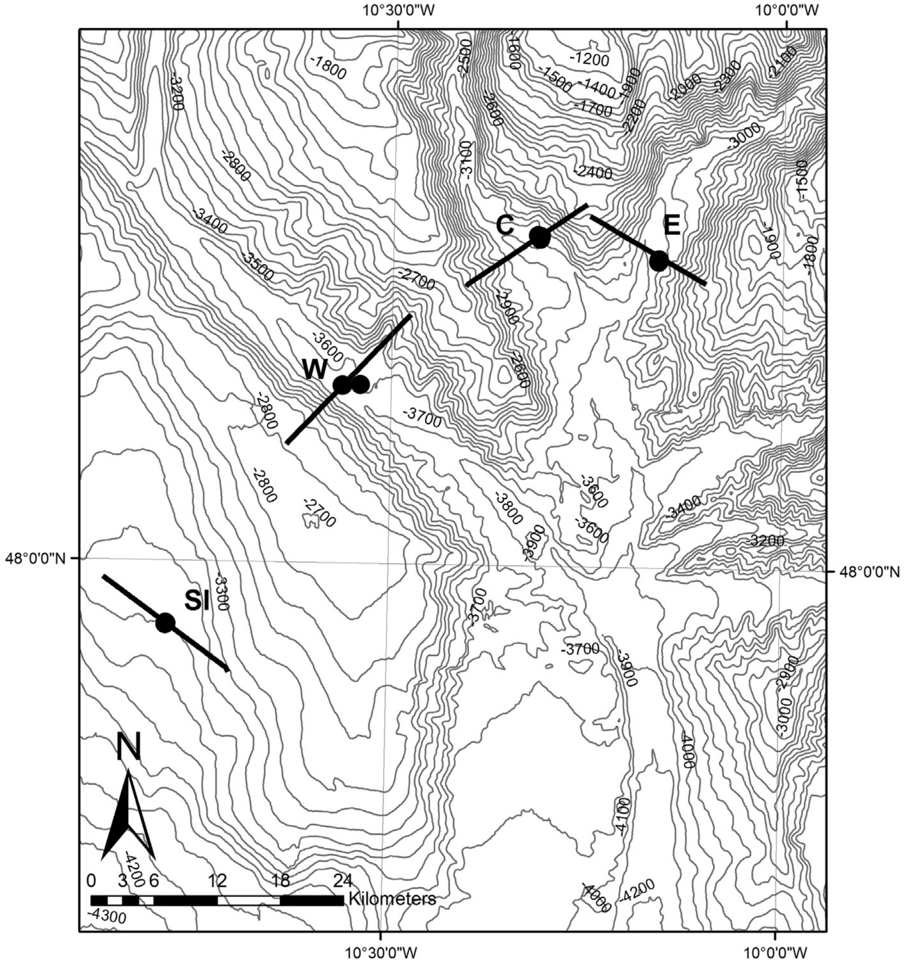

Fig. 1. Bathymetric chart of Whittard Canyon, based on data provided by the Geological Survey of Ireland (www.gsiseabed.ie). The four study sites are indicated: Western branch (W), Central branch (C) and Eastern branch (E) of the canyon and one site on the adjacent slope (Sl). Contour lines are given in metres. Solid lines represent transverse bathymetric profiles shown in Fig. 2.

Table 1
Station list. Megacore deployments on RRS *James Cook* cruise 36, Whittard Canyon and adjacent slope. W, Western branch; Sl, Slope site; C, Central branch; E, Eastern branch. MGS, mean grain size. Percentage clay, silt and sand (Wentworth, 1922).

Deployment	Date (dd/mm/09)	Latitude North	Longitude West	Depth (m)	Area sampled (m^{-2})	Slope angle (°)	Rugosity × 10^{-6}	Fine-scale BPI	MGS (μm)	Clay (%)	Silt (%)	Sand (%)
Sl016	24/06	47°56.79	10°46.85	3511	0.063	0.93	14	−20				
Sl017	24/06	47°56.78	10°46.85	3512	0.055	0.93	15	−20				
Sl018	24/06	47°56.81	10°46.91	3514	0.047	0.93	6	−20				
Sl019	24/06	47°56.74	10°46.94	3505	0.063	0.93	11	−17	71.8	16.5	56.7	26.8
Sl020	25/06	47°56.78	10°46.85	3514	0.055	0.93	14	−20				
W002	20/06	48°09.18	10°33.70	3670	0.063	2.36	161	3	28.8	13.3	74.2	12.5
W003	21/06	48°09.17	10°33.70	3661	0.055	2.36	165	3				
W011	23/06	48°09.22	10°32.36	3582	0.047	0.20	6	30				
W026	27/06	48°09.18	10°33.73	3670	0.039	2.36	138	−10				
W043	08/07	48°09.15	10°33.76	3657	0.047	2.36	113	−10				
C063	13/07	48°16.89	10°18.74	3375	0.047	2.49	140	−81	26.9	12.0	77.9	10.1
C064	13/07	48°16.97	10°18.65	3382	0.063	2.49	610	−109				
C065	13/07	48°17.04	10°18.89	3373	0.055	3.35	239	−118				
C067	13/07	48°16.98	10°18.72	3376	0.055	3.88	448	−106				
C066	13/07	48°16.83	10°18.72	3381}	0.063	2.75	187	−91.5				
C068	13/07	48°17.01	10°18.83	3375								
E093	21/07	48°15.89	10°09.56	3424	0.063	3.15	92	−27	32.7	10.6	75.5	13.9
E094	21/07	48°15.78	10°09.57	3429	0.053	3.36	92	−23				
E095	21/07	48°15.78	10°09.58	3429}	0.063	3.35	1150	−23				
E096	22/07	48°15.76	10°09.60	3424								
E097	22/07	48°15.89	10°09.54	3425	0.039	3.15	88	−28				
E098	22/07	48°15.76	10°09.60	3432	0.031	3.35	131	−23				

at the slope site. The additional deployment in the Central and Eastern branches was made to compensate for the failure to recover enough cores during earlier deployments. On deck, the individual cores from each deployment were sliced into five sediment layers (0–1, 1–3, 3–5, 5–10 and 10–15 cm). Core slices from the same layer of the different cores from one deployment were placed in the same 20 l bucket. The contents of the bucket were then homogenised to produce one combined sample for each layer (i.e. five combined samples for each deployment). The overlying water was added to the 0–1 cm layer. The combined samples (one for each sediment layer) were then carefully washed with filtered (mesh size 125 μm) seawater on 500 and 300 μm sieves. The >500 μm residues from each combined sediment layer from one deployment were placed in one 5 l plastic tub and fixed with 10% borax-buffered formalin. The same was done for the 300–500 μm residues. Thus each deployment yielded two combined sieve fractions for each of the five sediment layers.

2.3. Environmental data

A post-processed bathymetry map of the Whittard Canyon (cell size 10×10 m) was downloaded from the INFOMAR website (www.gsiseabed.ie/). The steepness of the terrain at each site was calculated using the ArcMap 10 (ESRI) Spatial Analyst geoprocessing tool ‘Slope’ applied to the bathymetry map. The Slope tool calculates the maximum rate of change between each cell and its immediate neighbours in a 3×3 cell window. The Benthic Terrain Modeler ArcGIS Desktop Extension alpha version (Wright et al., 2005) was used to calculate the fine-scale bathymetric position index (BPI) and vector ruggedness measure (VRM) from the bathymetry data. BPI is a scale-dependent index representing a grid cell’s topographic location within a benthic landscape relative to its local surroundings; the fine-scale BPI allows the identification of smaller features within the benthic landscape (Wright et al., 2005). VRM is the variation in three-dimensional orientation of grid cells within a neighbourhood (3×3 window). Transverse bathymetric profiles of the canyon branches and the slope were derived using the ArcMap profile view tool.

Cores for sediment particle-size analysis (Table 1) were sliced on deck into 12 layers (0.5 cm layers between 0 and 2 cm depth and 1 cm layers between 2 and 10 cm). Each layer was placed in a 500 ml bottle and fixed in 10% buffered formalin. Only the 0–0.5, 1–1.5, 2–3 and 4–5 cm sediment layers were analysed as other layers were not available. Each layer was first homogenised (particles >2 mm removed), dispersed using a 0.05% $(NaPO_3)_6$ solution and mechanically agitated before being analysed using a Malvern Mastersizer 2000 laser diffraction particle size analyser (Abbireddy and Clayton, 2009).

2.4. Macrobenthos processing

The top three sediment layers (0–1, 1–3, 3–5 cm) were analysed for this study. The samples were transferred from the formalin onto a 300-μm-mesh sieve, rinsed with 70% ethanol to remove the formalin and then sorted for macrofauna, also in 70% ethanol. The 300–500 μm and >500 μm fractions were processed separately. All specimens were sorted to major taxa (phylum or class) under a Leica MZ9.5 stereomicroscope. We followed common practice in deep-sea studies by considering only the macrofauna sensu stricto (Gage and Tyler, 1991; Bett, 2014), i.e. meiofaunal taxa (foraminifera, copepods, nematodes, and ostracods) were excluded.

The polychaetes were identified to family level based on morphological characters visible under a light microscope and identified by reference to taxonomic keys (Hayward and Ryland, 1996; Beesley et al., 2000). Where fragmented specimens were encountered, only head fragments were counted.

2.5. Data analyses

Macrofaunal counts were standardised to unit seafloor area sampled (i.e. density, ind. m^{-2}), and subject to a log $(x+1)$ transformation prior to analysis. Before analyses were performed, the ANOVA assumptions of normality and homogeneity of variance were evaluated using Anderson-Darling and Levene’s tests, respectively. Density data satisfied tests of ANOVA assumptions. Thus, ANOVA and Tukey Pairwise tests were performed on density data. Mood’s Median tests were used to test for significance of slope, rugosity and fine-scale BPI. These univariate tests were carried out using the Minitab statistical software package (v16, LEAD Technologies, 2010).

Multivariate analyses were executed using the PRIMER software package (Clarke and Gorley, 2006; v6, PRIMER-E Ltd). Macrobenthos data were assessed via non-metric multidimensional scaling (MDS) based on Bray Curtis similarity of log transformed density. Global and pair-wise analysis of similarities (ANOSIM) was employed to assess the distinctiveness of canyon and slope study sites. Environmental data were assessed via principal components analysis (PCA) of normalised data (i.e. transformed to zero mean, and unit variance). In the absence of direct measurement, macrofaunal abundance was used as a proxy for organic matter input. Global macrofaunal abundance in the deep sea has been predicted from the incoming flux of organic matter (Rex et al., 2006; Wei et al., 2010). Similarly, the metabolic theory of ecology (Brown et al., 2004) predicts that carrying capacity (faunal abundance) is directly related to resource supply where habitat and temperature are constant. Organic matter supply to the seafloor is normally estimated from surface primary productivity and water depth (e.g. Lutz et al., 2007), but this would fail to account for the funnelling action of the canyon system.

3. Results

3.1. Environmental characteristics

3.1.1. Bathymetry and derivatives

The slope angle of the seafloor at sites sampled inside the canyon branches was fairly uniform, ranging from means of 2.36° (Western branch) to 3.27° (Eastern branch) (Table 1). The angle on the adjacent slope was much lower (mean 0.93°). There was a statistically significant difference in slope between all four sites (Mood’s Median Test: Slope versus Location $p<0.001$). Bathymetric position index (BPI) values were higher in the Western branch and on the slope (representing higher points/crests in terrain compared with the surroundings) than in the Eastern and Central branches, and statistically different between all four sites (Mood’s Median Test: BPI versus location $p<0.001$). Rugosity was highest in the Central branch and lowest on the slope (Table 1); again the differences were significant between all four sites (Mood’s Median Test: rugosity versus location $p=0.015$). Canyon profiles are approximately “U” shaped (Fig. 2), most clearly so in the case of the Eastern branch, which has the narrowest branch width. The Western branch is wider with a flatter floor than the Eastern and Central branches. The flat slope profile in Fig. 2 is included for comparison.

3.1.2. Sedimentology

The three canyons sites (Western, Central and Eastern branches) had similar mean particle sizes (28.8, 26.9 and 32.7 μm, respectively) (Table 1). The slope site had a significantly coarser sediment (mean particle size 71.8 μm) (Fig. 3). At all four sites the sediment was composed predominantly ($>56\%$) of silt (grain size 4–63 μm). The Central branch sediment had a slightly higher percentage of silt

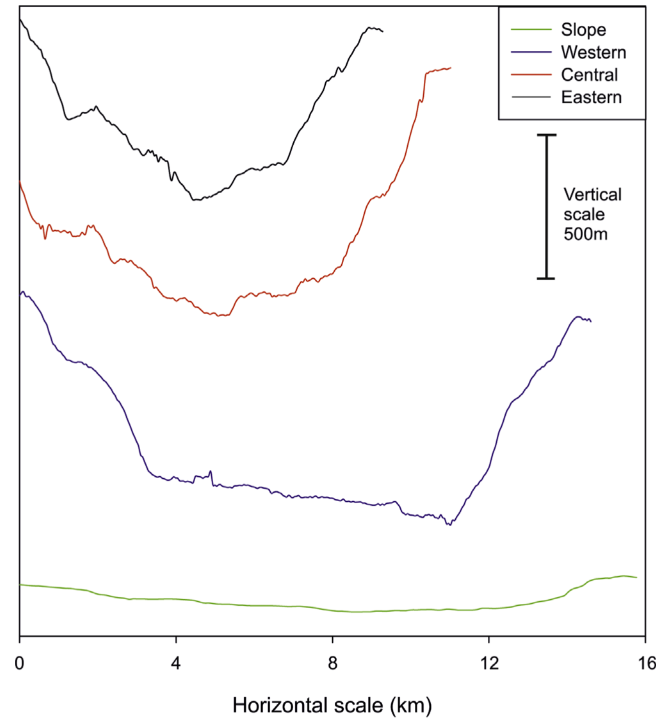

Fig. 2. Slope-normal bathymetric profiles through the study sites in the Eastern, Central and Western canyon branches, and on the adjacent open slope.

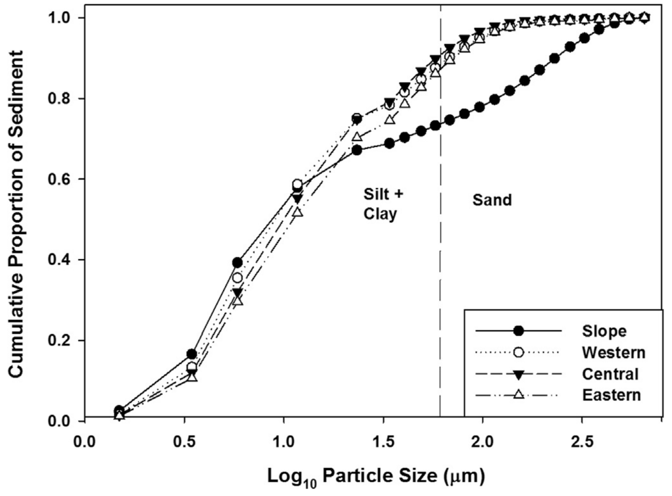

Fig. 3. Cumulative sediment particle size distribution at three canyon branch sites and adjacent open slope site.

(77.9%), than the Eastern (75.5%) and the Western (74.2%) branches, while the slope sediment had a much lower silt content (56.7%) (Table 1). Clay content (grain size < 4 μm) was highest on the slope (16.5%) and decreased inside the canyon from the Western (13.3%) to the Eastern (10.6%) branches. The slope sediment had a distinctly higher percentage of sand (26.8%) compared with the canyon sites ($< 13.9\%$), where the percentage was lowest in the Central branch (10.1%).

3.1.3. Principal component analysis

A PCA was performed on the following environmental variables (Fig. 4): sediment grain size, slope angle, fine-scale BPI, VRM and station depth (Table 1), with macrofaunal density used as a proxy for organic matter (OM) input. The four study sites were quite discrete in the ordination space formed by the first two axes. The differentiation of canyon and slope sites appeared to align with the environmental vectors of sediment grain size, rugosity, slope angle and fine-scale BPI. Differentiation of the Western from the Central and Eastern branches appeared to align with water depth and proxy organic matter supply (macrofaunal density).

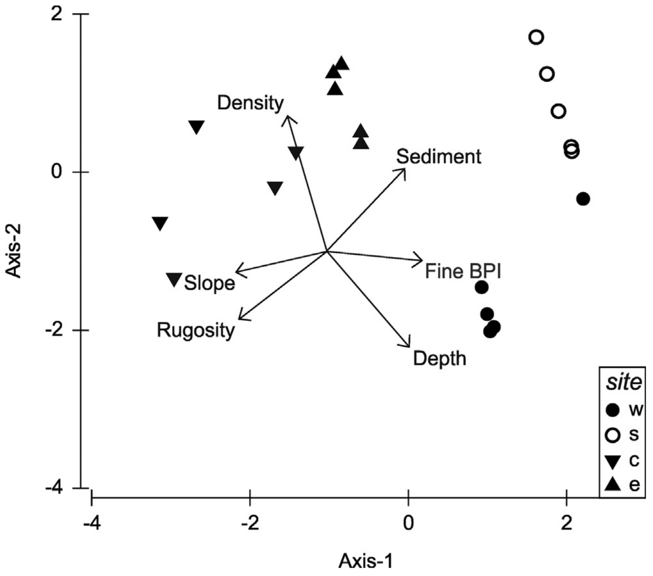

Fig. 4. Principal components analysis of normalized environmental variables at canyon and slope sites. The variables are depth, mean grain size (sediment), slope angle, rugosity, fine-scale Bathymetric Position Index (BPI) and macrofaunal density (as a proxy for organic matter supply).

3.2. Macrobenthos

3.2.1. Total abundance

In total, 4444 macrofauna individuals were picked from the samples. Fifty-three percent of the fauna was retained on the 500 μm sieve. There was a significant differences in abundance between sites (One-way ANOVA, $p < 0.001$, R^2 (adj)=76.32%). Pairwise comparison revealed that the Central and Eastern branches were significantly different ($p < 0.05$) from the Western branch and slope. The Eastern branch had the highest abundance of macrofauna (6249 ± SD 1363 ind. m^{-2}). Values were intermediate in the Central branch (4461 ± SD 856 ind. m^{-2}) and lowest in the Western branch (2900 ± SD 538 ind. m^{-2}) (Table 2). The abundance decreased across all sites from east to west, with the slope site having the lowest value (2744 ± SD 269 ind. m^{-2}) (Table 2).

3.2.2. Major taxon composition

Sixteen higher taxa were recognised in the canyon and slope samples (Table 2). Polychaeta was always the most abundant taxon, making up just over 50% of the macrofauna with 2255 individuals in total and an average density of 2191 ind. m^{-2} for the 0–5 cm layer. The tanaids (10%; 397 ind. m^{-2}), isopods (11%; 432 ind. m^{-2}), sipunculans (7%; 297 ind. m^{-2}) and bivalves (7%; 288 ind. m^{-2}) were also important faunal components.

Although polychaetes always represented $> 50\%$ of the assemblage in each branch, the proportion of other taxa varied between branches (Fig. 5A). The percentage of sipunculans (13%) was higher in the Western branch compared with Eastern (4%) and Central (5%) branches. The Eastern and Central branches had higher percentages of isopods (11% and 16% respectively) than the Western branch (6%). The tanaids maintained fairly similar percentages throughout the branches, as did the bivalves. The slope fauna was more similar to the

Table 2
Density of macrofaunal taxa at three canyon sites and on the adjacent slope. Values are mean densities ($n=5$) for the 0–5 cm sediment layer, based on the >300 μm sieve size fraction.

Taxon	Abundance (ind. m^{-2})			East
	Slope	West	Central	
Amphipoda	14.9	96.7	291.8	241.3
Aplacophora	18.5	21.3	37.9	18.3
Ascidiacea	0.0	0.0	0.0	5.1
Bivalvia	58.5	246.2	309.0	538.7
Cumacea	35.2	10.6	23.7	26.8
Echinoidea	0.0	5.1	7.3	8.3
Gastropoda	0.0	5.1	0.0	0.0
Holothuroidea	0.0	0.0	0.0	5.1
Isopoda	136.4	197.2	723.8	670.0
Nemertea	0.0	3.6	3.6	0.0
Ophiuroidea	70.2	111.7	83.2	164.8
Polychaeta	1386.9	1468.7	2236.6	3557.4
Scaphopoda	0.0	0.0	45.3	227.2
Sipuncula	329.0	362.2	233.8	263.2
Tanaidacea	562.5	235.6	326.1	461.8
Indet. worm	62.6	50.1	112.8	49.4
Unknown	69.7	85.6	26.4	16.6
Total	2744	2900	4461	6249

Western branch than to the Central and Eastern branch fauna and in this sense it fitted in with a gradient of change of macrofauna composition across the four sites. The slope had a high percentage of sipunculans (12%) and tanaids (20%) but a low percentage of isopods (5%) and bivalves (2%). These percentages were similar to the Western branch values: sipunculans (13%), tanaids (10%), isopods (6%) and bivalves (7%).

The numerical abundance of macrofauna displayed some of the same trends as the percentage abundance data (summarised in Table 2). Isopods had a high abundance in the Central and Eastern branches, but a much lower abundance in the Western branch, whereas sipunculans had a higher abundance in the Western branch compared with the Eastern and Central branches. Different trends were seen in other higher taxa. Tanaids were most abundant in the Eastern branch and less abundant in the Central and Western branches. Bivalves exhibited a similar east to west decline.

Numbers at the slope and Western branch sites were fairly similar for the sipunculans and isopods (summarised in Table 2). For other taxa there were larger differences. The tanaids were almost twice as abundant on the slope compared with the Western branch. Bivalves were four times more abundant in the Western branch than on the slope.

3.2.3. *Multidimensional scaling analysis of major taxa*

Differences between canyon branches in the major macrofaunal taxon composition are reflected in the corresponding MDS plot (Fig. 6A), which shows samples from the Central and Eastern sites intermingled and quite distinct from the Western branch and slope site samples. Two macrofaunal samples (SI019 and SI020) from the slope were distinct from the rest of the slope samples. The Western branch and remaining slope sites formed separate but adjacent grouping. ANOSIM global assessment indicated statistically significant ($p=0.001$) variation among the sites. Significant ($p<0.05$) pairwise differences were detected between Western/Central branches, Western/Eastern branches, slope/Central branch and slope/Eastern branch (Table 4).

3.2.4. *Polychaete family composition*

In total, 2225 individual polychaetes were picked from the samples. Their abundance showed significant differences between sites (One-way ANOVA: $p<0.001$, R^2 (adj)=70.92%) and followed the same patterns as the macrofauna. A Tukey pairwise test revealed that the Eastern and Central branches were significantly ($p<0.05$) different from the Western branch and slope. The polychaetes represented 26 families (Table 3). The most abundant were the Amphinomidae, with an overall average density of 582 ind. m^{-2} (27%), followed by the Spionidae (480 ind. m^{-2}; 22%), Paraonidae (202 ind. m^{-2}; 9%), Cirratulidae (196 ind. m^{-2}; 9%) and Opheliidae (172 ind. m^{-2}; 8%).

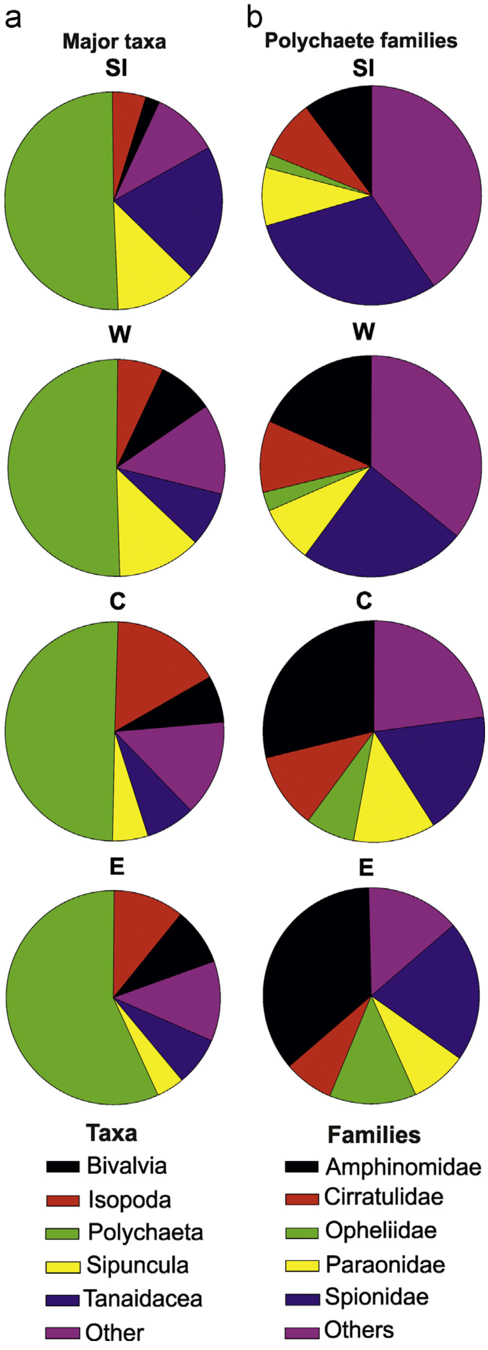

Fig. 5. Relative abundance of top five taxa at the three canyon branch sites (W, E, C) and adjacent slope site (SI). (A) Macrofaunal major taxa, (B) polychaete families.

Polychaete composition differed between branches (Fig. 5B). The Eastern branch had the highest numbers of Amphinomidae (1270 ind. m^{-2}) compared with the other sites. This family represented 36% of the polychaetes compared with 29% in the Central branch and 18% in the Western branch. The same pattern was seen in the Ophellidae; 13% in the Eastern branch and 3% in the

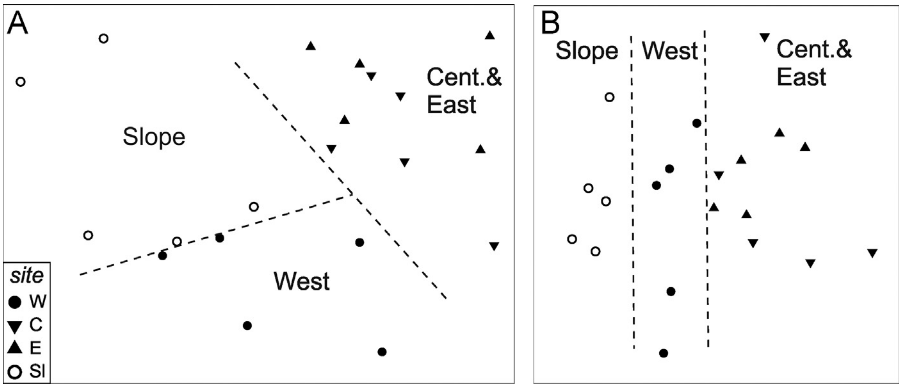

Fig. 6. Non-metric multidimensional scaling ordinations of (A) macrofaunal major taxa, and (B) polychaete families, for five replicate samples at each of the three canyon branch sites (W, E, C) and adjacent slope site (Sl).

Table 3
Density of polychaete families at three canyon sites and on the adjacent slope. Values are mean densities ($n=5$) for the 0–5 cm sediment layer, based on the > 300 μm sieve size fraction.

Family	Abundance (ind. m^{-2})			East
	Slope	West	Central	
Acrocirridae	99.6	57.7	41.7	57.6
Ampharetidae	93.5	22.1	10.0	9.6
Amphinomidae	140.4	265.2	651.1	1269.5
Capitellidae	7.9	0.0	12.7	0.0
Cirratulidae	120.7	169.3	239.1	262.5
Chrysopetalidae	0.0	0.0	11.5	3.2
Dorvilleidae	6.4	0.0	4.2	0.0
Glyceridae	49.1	40.6	48.7	74.4
Hesionidae	0.0	4.2	0.0	0.0
Lumbrineridae	21.7	21.1	26.4	48.4
Maldanidae	7.4	43.6	51.4	54.3
Nephtyidae	3.2	23.1	46.4	82.9
Onuphidae	6.8	0.0	0.0	0.0
Opheliidae	27.3	39.9	161.3	458.6
Orbiniidae	20.5	44.8	41.8	47.6
Paraonidae	118.9	120.5	272.3	298.3
Phyllodocidae	3.2	0.0	0.0	0.0
Pilargidae	0.0	0.0	3.6	0.0
Scalibregmatidae	23.2	19.0	16.8	27.8
Sigalionidae	33.8	69.5	25.0	17.3
Sphaerodoridae	3.2	0.0	91.0	0.0
Spionidae	417.1	351.6	405.2	746.8
Sternaspidae	0.0	3.6	6.4	3.2
Syllidae	139.5	161.9	30.6	67.9
Terebellidae	7.4	0.0	0.0	0.0
Poly. indet.	36.2	7.4	0.0	15.6
Larval poly. indet.	0.0	0.0	30.8	18.5
Total	1387	1469	2237	3557

Table 4
ANOSIM pairwise tests of macrofauna major taxa and polychaete families across four sites. Western branch (W), Central branch (C), Eastern branch (E) and adjacent slope (Sl). n/s, not significant.

Groups	Major taxa		Polychaete families	
	R statistic	*p* Value	*R* statistic	*p* Value
W, Sl	0.240	n/s	0.276	0.048
W, C	0.576	0.008	0.204	n/s
W, E	0.724	0.008	0.248	n/s
Sl, C	0.784	0.008	0.684	0.008
Sl, E	0.868	0.008	0.864	0.008
C, E	0.032	n/s	0.048	n/s

Western branch. The Cirratulidae displayed the opposite pattern. The Western branch had the highest percentage (12%), the Eastern branch the lowest (7%) with intermediate values in the Central branch (11%). The Spionidae exhibited a similar pattern (Western 24%, Central 18% and Eastern branch 21%).

The slope site followed cross-canyon trends in polychaete family composition in being more similar to the Western branch than to the Central and Eastern branches. The slope assemblage was dominated by Spionidae (30%), Amphinomidae (10%) and Syllidae (10%). These percentages were similar to those from the Western branch; Spionidae (24%), Amphinomidae (18%) and Syllidae (11%). The ranking of the two dominant families on the slope was reversed in the Central (Amphinomidae 29%, Spionidae 18%) and Eastern branches (Amphinomidae 36%, Spionidae 21%).

The actual family abundance values followed the same trends between branches, except for the Spionidae, which reached their highest abundance in the Eastern and their lowest in the Western branch (summarised in Table 3). The slope site was generally more similar to the Western branch than to the other canyon branches in terms of the absolute abundance of the families Amphinomidae, Cirratulidae and Paraonidae. This was not true for all families; in particular the abundance of Spionidae on the slope was more similar to the Central branch values than to that of the Western branch.

3.2.5. Multidimensional scaling analysis of polychaete families

Polychaete family data revealed significant differences in assemblages between the sites. An MDS plot (Fig. 6B) grouped the Central and Eastern branch assemblages together, whereas the Western branch and slope sites were quite distinct. ANOSIM global assessment indicated statistically significant ($p=0.001$) variation among the sites. Significant ($p < 0.05$) pairwise differences were detected between the slope site and all canyon branches (Table 4).

4. Discussion

4.1. Comparison with earlier studies

4.1.1. Macrofaunal abundance

Macrofaunal abundance decreased across the Whittard Canyon from the Eastern branch to the Western branch and was lowest on the adjacent slope. This pattern is consistent with the data of Hunter et al. (2013). At similar depths (3500 m) in the Whittard Canyon, they observed a higher abundance of macrofauna in the Eastern branch (5352 ± SD 2583 ind. m^{-2}) compared with the Western branch (3416 ± SD 2069 ind. m^{-2}). An earlier study by Duineveld et al. (2001), however, reported a much lower abundance in the Western branch (1339 ind. m^{-2} at 3760 m) compared with the present study (2900 ± SD 538 ind. m^{-2}). At larger spatial scales, our macrofaunal densities can be compared with those in the extensively studied canyons on the Portuguese Margin (Tyler et al., 2009). Values from around 3500 m depth in the Setúbal Canyon (2241 ind. m^{-2}), and particularly in the Nazaré Canyon (4600 ind. m^{-2}) (Cunha et al., 2011), are comparable to those reported in the present study (average 4536 ± SD 1676 ind. m^{-2}). On the slope, macrofaunal densities are higher (2744 ± SD 269 ind. m^{-2}) at our site to the west of the Whittard Canyon than on the nearby Goban Spur (500 ind. m^{-2} at 3700 m; Flach et al., 2002) and Porcupine Abyssal Plain (1465 ind. m^{-2} at 4850 m depth; Galeron et al., 2001), but comparable to those from 3600 m depth on the Goban Spur (2420 ind. m^{-2}) reported by Duineveld et al. (2001). These differences may reflect sampling and sample processing techniques. Flach et al. (2002), Galeron et al. (2001) and Duineveld et al. (2001) used box corers and 500, 250 and 500 µm sieves, respectively, whereas a Megacorer and a 300 µm sieve were used in the present study. Densities in the Western branch based on our 500 µm sieve fractions were far lower (1777 ± SD 220 ind. m^{-2}) and more comparable to those of Duineveld et al. (2001) from the same area (1339 ind. m^{-2}). Box corers collect samples that are more disturbed than those obtained by hydraulically dampened multiple corers, leading to the loss of some meiofaunal and macrofaunal animals (Bett et al., 1994; Gage and Bett, 2005), while a larger sieve size would retain fewer animals.

Our macrofaunal densities from the canyon site considerably exceed the value (369 ind. m^{-2}) predicted by the regression equation of Rex et al. (2006) (Fig. 7); which was derived by plotting published global macrofaunal abundances against depth. The values in the present study are likewise far higher than the predicted 657 ind. m^{-2} derived from the formula in Wei et al. (2010) (Fig. 7). Wei et al. (2010) used a machine-learning algorithm, Random Forests, to model the relationship between oceanic properties and seafloor macrofaunal standing stock. They caution that the predicted values should be considered as conservative estimates for soft-bottomed communities relying solely on sinking phytodetritus. Wei et al. (2010) also warn that their model may not hold true for submarine canyons. They argue that organic matter originating from the continental shelf accumulates inside canyons leading, to higher concentrations compared with non-canyon areas. Indeed, when canyon sites and non-canyon sites at similar depths in the NE Atlantic are compared, the Whittard Canyon sites yield some of the highest macrofaunal abundances (Fig. 7). To account for gear bias, as detailed by Bett et al. (1994) and Gage and Bett (2005), box core densities estimates have been increased by a factor of two to improve comparability with multiple corer estimates. The full list of original data is given in the electronic Supplementary information (Table S2).

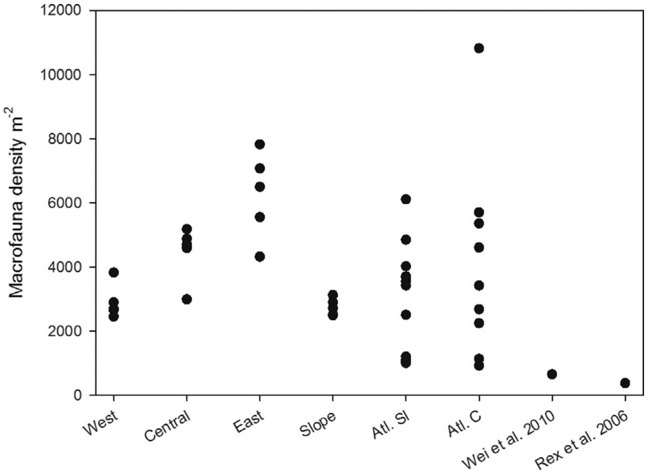

Fig. 7. Benthic abundance comparison of macrofaunal densities among present study sites (Western, Central and Eastern canyon branches and adjacent slope) and published Atlantic slope (Sl) and canyon (C) sites (Table S2). Global predictions for water depth 3500 m of Wei et al. (2010) and Rex et al. (2006) are also included. Data have been approximately corrected for sampling gear bias (see text for details).

4.1.2. Higher taxon composition

An important finding of our study was the clear shift in community composition, even at higher taxonomic levels, between the canyon branches and between the canyon and the adjacent slope. Polychaetes made up more than half of the macrofaunal assemblage at all sites. A lower percentage of polychaetes was reported by Hunter et al. (2013) (Western branch 30%, Eastern branch 20%). However, Hunter et al. (2013) included nematodes in the macrobenthos and, when these are excluded, polychaetes accounted for ~50% of the macrofauna sensu stricto. Our Eastern branch samples were characterised by high abundances of polychaetes, bivalves and isopods whereas the Western branch and adjacent slope yielded high abundances of polychaetes, sipunculans and tanaids. Differences in macrofaunal assemblage composition between branches were also noted by Hunter et al. (2013); polychaetes, crustaceans and macrofaunal-sized nematodes were equally abundant in the Western branch, whereas nematodes were dominant (> 50%) in the Eastern branch.

Our results, and those of previous studies, suggest that there is a remarkable degree of heterogeneity between canyons in terms of their faunal composition, even at higher taxonomic levels. In the Setúbal Canyon, polychaetes were ranked first, crustaceans second and molluscs third (Cunha et al., 2011). In the Nazaré Canyon molluscs were the most abundant higher taxon, representing just under 50% (2500 ind. m^{-2} at ~3400 m) of the total macrofaunal community (Cunha et al., 2011). Polychaetes were ranked second, followed by arthropods and echinoderms. In the Cascais Canyon (~3400 m depth), 45.9% of total abundance was made up of crustaceans, polychaetes were ranked second (~40%), and molluscs were the least abundant taxon (~5%) (Cunha et al., 2011). In contrast, in the Whittard Canyon, polychaetes always made up > 50% of the macrofaunal assemblages, crustaceans were ranked second (25% total across all sites) and molluscs third (9% total across all sites). Potential reasons for these differences in faunal composition are discussed in Section 4.2.

4.1.3. Polychaete family composition

Polychaete family composition differed between the canyon branches. Particularly high numbers of Amphinomidae were observed in the Eastern branch. In contrast, Hunter et al. (2013) reported a high abundance of Amphinomidae in the Western branch and Cirratulidae and Spionidae in the Eastern branch. Duineveld et al.'s (2001) report of numerous small tubiculous Sabellidae in the Western branch is particularly interesting. Sabellidae are filter feeders, which strain food from passing water currents (Fauchald and Jumars, 1979). Dunieveld et al. (2001) suggest their high abundance in the Western branch was caused by a high load of suspended organic particles passing over the canyon floor at that site, providing food for the sabellids. The absence of sabellids in our samples may indicate a reduced load of suspended organic particles in the water column when the samples were taken, or an absence of a suitable substrate for their tubes, or simply the heterogeneity of the canyon system.

Canyons cannot be characterised by one particular polychaete family. For example, the three most abundant families at depths around 3400 m in the Portuguese canyons were: Nazaré Canyon – Spionidae, Fauveliopsidae and Paraonidae; Cascais Canyon – Siboglinidae, Spionidae and Capitellidae; Setúbal Canyon – Spionidae, Ampharetidae and Nephytidae (Cunha et al., 2011). In the present study, the three top-ranked families were the Amphinomidae, Spionidae and Cirratulidae. However, it appears that Spionidae are often common in canyons. They were the top-ranked family overall in the Portuguese canyons (Paterson et al., 2011), second-ranked in the Whittard Canyon (this study) as well as the Cap-Ferret Canyon (Gerino et al., 1999). The Spionidae contain species thought to be opportunistic, such as those within the genus *Prionospio* (Paterson et al., 2011), which may be favoured in disturbed environments such as canyons where they are able exploit new patches of recently disturbed seafloor. Further investigations of species-level data are required to fully understand functional shifts in community composition.

4.2. Environmental controls on macrofauna community structure and composition

4.2.1. Organic matter quantity and quality

The higher abundance of macrofauna in the Eastern branch of the Whittard Canyon compared with that in the other branches may reflect the quality and quantity of organic matter. Duineveld et al. (2001) observed higher concentrations of phytodetritus in cores from stations in the Eastern branch compared with those from the Western branch. Sediment analyses revealed a higher percentage of sedimentary POC in the Eastern (0.7%) compared with the Western (0.5%) branch, although this result was not statistically significant (Hunter et al., 2013). The composition of sedimentary particulate organic matter (POM) was also reported to vary between branches of the Whittard Canyon (Huvenne et al., 2011). Huvenne et al. (2011) record higher total lipid concentration in sediments from the Eastern ($26\,\mu\text{g}\,\text{g}^{-1}$) compared with the Western ($15\,\mu\text{g}\,\text{g}^{-1}$) branch. In the Eastern branch, the lipids included essential fatty acids thought to be derived from phytoplankton or zooplankton sources. In contrast, in the Western branch, sediment POM contained a high proportion of monounsaturated fatty acids (Huvenne et al., 2011), which are associated with mesozooplankton (Kiriakoulakis et al., 2005) and more degraded detritus compared with the “fresher” polyunsaturated fatty acids (Kiriakoulakis et al., 2004). Significantly higher values of sediment total nitrogen (TN) were recorded in the Eastern branch sediment (TN % 0.098 ± 0.006) of the Whittard Canyon compared with the Western branch sediment (TN % 0.076 ± 0.007) (Hunter et al., 2013). Cunha et al. (2011) argued that macrofaunal abundance in the Portuguese canyons (at 3500 m) was positively correlated with sediment TN concentration. Higher sediment TN values indicate better food quality, which Cunha et al. (2011) suggested was the driver for increased macrofaunal abundance. These data suggest that more and higher quality food may be available in the Eastern branch.

The Whittard Canyon stations appear to experience higher levels of organic matter input than the adjacent slope, probably derived from the channeling of organic matter from the shelf through the canyon branches via downslope processes such as turbidity currents. Possibly, channeling is more active through the Eastern branch than the Central and Western branches, although there is no direct evidence for this suggestion. The Eastern branch may also be a more efficient trap of material from along-slope currents. The northerly and north-westerly flow of the NE Atlantic slope current will be topographically steered to flow essentially east to west across our study site (Pingree and Le Cann, 1989). The similarity between the slope and the Western branch and between the Eastern branch and the Central branch may reflect similar organic matter availability and composition at each site given their geographical proximity. Unfortunately, no organic matter data exists for the slope and Central branch.

By comparison with Rex et al. (2006) and Wei et al. (2010), the slope site also exhibited an elevated macrofaunal density for its depth. A possible factor explaining this high abundance is proximity to the canyon system. Cunningham et al. (2005) noted that mud-rich turbidity flows within the Whittard Canyon have been of sufficient magnitude to overspill the canyon walls, depositing fine sediments on the adjacent slope. This could lead to some organic matter enrichment of the area surrounding the canyon.

4.2.2. Disturbance

The higher abundance of macrofauna at 3500 m inside the Whittard Canyon than on the adjacent slope could also reflect disturbance. A high frequency from bottom-currents within canyons is thought to depress infaunal abundance, as suggested for the Nazaré Canyon (Gage et al., 1995; Koho et al., 2007). On the other hand, physical disturbance has been shown to increase macrofaunal abundance at the HEBBLE site, located at 4820 m depth on the Nova Scotia Rise (western North Atlantic). Several times per year, this area experiences intense currents that are strong enough to transport sediment (Thistle et al., 1985, 1991). These “benthic storms” are thought to deliver more nutrients for the fauna. At the HEBBLE site, abundances of macrofaunal polychaetes, bivalves, tanaids and isopods were significantly higher than expected for their depth (Thistle et al., 1991). These macrofaunal groups were also abundant inside the Whittard Canyon. Similarly, the Cascadia Channel in the northeast Pacific Ocean experiences a high frequency of turbidity currents that deliver a significant amount of organic matter. As a result, this area has a benthic macrofaunal density four times that on the adjacent plain (Griggs et al., 1969). Thus, the influence of bottom currents on macrofauna abundance remains ambiguous.

Physical disturbance may also influence the taxonomic composition of the macrofauna. Composition of fauna differs between disturbed and quiescent sites in canyons (Gage et al., 1995) and in the HEBBLE area (Thistle et al., 1991; Thistle and Wilson, 1996). Disturbance events can suspend soft-bottom fauna making them vulnerable to predators and physical damage. “Exposed” isopods (exposed on the sediment surface) were less abundant at disturbed sites in the HEBBLE area than at nearby quiescent sites (Thistle and Wilson, 1996). In this study the abundance of isopods was highest in the Central branch and lowest on the slope, although we have no evidence that the intensity of current flow differed between these sites.

There may be a difference in disturbance regimes between the Western and Eastern branches of the Whittard Canyon. A higher abundance of disturbance-tolerant taxa led Hunter et al. (2013) to conclude that disturbance events were more frequent in the Eastern branch. However, the magnitude and frequency of disturbance inside the Whittard Canyon is poorly understood (Section 2.1) and there is no clear basis for linking macrofaunal patterns to disturbance levels.

4.2.3. Sediment grain size

Mean sediment grain size is higher on the slope than at our three canyon sites. The slope site had a larger proportion of sand and clay, whereas the canyon site sediments were composed predominantly of silt (Table 1). It is possible this difference may be caused by the slope site being more exposed to along-slope currents (Pingree and Le Cann, 1989). Sediment mobility and reworking is a critical factor in explaining the effect of physical disturbance on community structure (Thistle and Levin, 1998). On the summit of a high-energy seamount off the coast of California, areas with stable, coarse-grained sediments supported relatively immobile assemblages whose feeding activities were focused at the sediment-water interface. In contrast, areas of unstable coarse-grained sediments that moved daily supported highly mobile assemblages with well-developed burrowing abilities (Levin et al., 1994). The different characteristics of canyon and slope sediments suggest that they may react differently to current activity, influencing the benthic community.

4.2.4. Other factors

A variety of other factors could influence the density and composition of macrofaunal assemblages. Differences in slope angle at the Whittard Canyon and slope sites are probably too slight (~2°) to have much effect on sediment stability. On the other hand, the bottom profiles of the canyon branches varied substantially. The Eastern branch has a much narrower, steeper-sided channel than the Western branch, which may suggest that sediment and organic matter pass along it more quickly. Steep and V-shaped canyons are thought to experience stronger and more frequent along-canyon currents than their more U-shaped counterparts (Shepard and Dill, 1966), and canyons with low topographic relief are more likely to resemble open-slope environments (Hecker et al., 1983). De Leo et al. (2014) reported that variability in canyon profiles partially explained variations in macrofaunal community structure among Hawaiian canyons.

Preferential predation by megafauna may affect macrofaunal taxonomic composition. Canyons generally have higher abundances of megafauna (De Leo et al., 2010; Vetter et al., 2010) than the surrounding slope and bottom-feeding fish may also exploit the high abundance of invertebrate macrobenthic communities (De Leo et al., 2010, 2012). Reduced oxygen availability has a strong effect on community composition by eliminating hypoxia-intolerant species (Levin, 2003). Ingels et al. (2011) reported signs of oxygen limitation in the upper part of the Whittard Canyon. This was believed to reduce densities of nematodes. However, there is no evidence of reducing environments in deeper parts of the canyon. Similarly, water depth (hydrostatic pressure) is not considered to be an important discriminating factor in this study as all samples were taken from similar depths (~3500 m).

5. Conclusions and future directions

Our results support all three hypotheses posed in the introduction. In summary, at 3500 m water depth the Whittard Canyon (1) has high macrofaunal abundance compared to the adjacent slope (2) contains a distinct community composition and (3) contains distinct within-canyon heterogeneity. These results are similar to those obtained for previous studies of the metazoan meiofauna and foraminifera. Within-canyon heterogeneity is probably explained by a combination of variable organic enrichment and hydrodynamic activity, both of which can be influenced by the topographic profile of individual canyon branches. Canyons are natural deep-sea laboratories for benthic sediment resuspension, disturbance and organic enrichment and as such may be important future locations to investigate fundamental biological processes of relevance to future human impacts in the deep sea, such as those likely to occur through deep-water trawling or mining.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at http://dx.doi.org/10.1016/j.dsr.2014.11.010.

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