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Polychaete abundance, biomass and diversity patterns at the Mid-Atlantic Ridge, North Atlantic Ocean



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ABSTRACT

Recent studies have revealed that the Mid-Atlantic Ridge (MAR) in the North Atlantic Ocean accounts for a large proportion of available bathyal soft-sediment habitat. When comparing the MAR to the continental margins of the North Atlantic, it is apparent that very little is known about the soft-sediment macrofaunal community associated with the MAR. In the present study, as part of the ECOMAR (Ecosystems of the Mid-Atlantic Ridge at the Sub-Polar Front and Charlie–Gibbs Fracture Zone) project, the polychaete component of the MAR macrofaunal community was investigated. A total of 751 polychaete specimens and 133 species were identified from megacorer samples collected at four MAR sites (48–54°N, depth: 2500–2800 m) sampled during the RRS James Cook 48 cruise in the summer of 2010. Polychaetes were the most abundant member of the macrofaunal community, and there was no significant difference in polychaete abundance, biomass and diversity between any of the MAR sites. In addition, the MAR did not appear to provide a physical barrier to the distribution of bathyal polychaetes either side of the ridge.

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1. Introduction

Our understanding of the diversity of deep-sea benthic communities is greatest at the continental margins, in particular in the North Atlantic Ocean (Rex and Etter, 2010). Across the continental margins the distribution of species is influenced by recognised gradients in abiotic parameters with increasing water depth, such as a reduction in light penetration, increasing hydrostatic pressure, decreasing temperature and often the presence of oxygen minimum zones (Carney, 2005). Macrofaunal species diversity is known to reach its maximum at mid-slope depths (Carney et al., 1993) and species diversity is influenced by environmental parameters, such as primary productivity and food supply, bottom water oxygen, sediment heterogeneity and deep-sea currents (Levin et al., 2001). Environmental parameters can covary with depth and it is, therefore, not always easy to predict or interpret how a change in an environmental parameter will influence diversity (Narayanaswamy et al., 2010a).

A limited number of studies have considered macrofaunal diversity and functional ecology at similar depths along-slope of the continental margins (Schaff et al., 1992; Schnack, 1998; Brandt and Schnack, 1999; Budaeva et al., 2008; Shields and Hughes, 2009; Narayanaswamy et al., 2010b). Observed differences in

macrofaunal species richness along slope of continental margins has been linked to the availability of food (Schaff et al., 1992). In the marine environment there appears to be a unimodal relationship between diversity and food availability (Levin et al., 2001) while the standing stock of macrofauna in the deep North Atlantic can reflect primary productivity and export flux (Cosson et al., 1997; Flach, 2002; Hughes and Gage, 2004; Johnson et al., 2007).

When investigating diversity patterns it can be beneficial to focus on a single taxonomic group (Rex et al., 1993). Polychaetes are often the most abundant and species rich members of deep-sea macrofaunal communities (Fauchald and Jumars, 1979; Gage and Tyler, 1991; Grassle and Maciolek, 1992). Furthermore polychaetes exhibit all major feeding strategies and therefore different polychaete species will benefit from differences in food source and availability (Fauchald and Jumars, 1979; Grassle and Maciolek, 1992). Polychaetes are, therefore, an ideal component of the macrofaunal community for investigating abundance, biomass, diversify and feeding type patterns in relation to environmental parameters (Glover et al., 2001, 2002; Narayanaswamy et al., 2005).

Our knowledge of the macrofaunal community associated with mid ocean ridges is fairly limited, particularly when compared to the continental margins (Bergstad et al., 2008; Shields et al., in press). Recent studies have revealed that the Mid Atlantic Ridge (MAR) accounts for a large proportion of available bathyal benthic habitat in the North Atlantic Ocean and comprises mostly of soft-sediment (Niedzielski et al., 2013). Consequently the MAR is

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an important but often overlooked source of suitable bathyal soft-sediment habitat for benthic macrofauna in the North Atlantic Ocean. Furthermore the MAR may provide a barrier to species dispersal, therefore helping to facilitate the distribution of species in the North Atlantic (Priede et al., in press).

The presence of the MAR in the North Atlantic influences deep-water circulation by restricting deep-water flow between the eastern and western basins (Bower et al., 2002). A number of fracture zones dissect the MAR with the largest being the Charlie Gibbs Fracture Zone at 52–53°N (CGFZ; Fleming et al., 1970). The location of the CGFZ approximately coincides with the location of the Sub-Polar Front, a near surface frontal zone where cold subpolar water from the north meets warmer subtropical waters from the south (Søiland et al., 2008). To the south of the CGFZ there is a weak eastward flow of the subtropical water characterised by large mesoscale eddy variability, while to the north there is a weak mean westward flow of the colder sub-polar water (Read et al., 2010). Primary productivity at the MAR is complex (between 51 and 4700 mg C m⁻² d⁻¹) as a result of the different oceanographic conditions north and south of the CGFZ (Tilstone et al., 2009).

In the present study polychaete abundance, biomass and diversity at four similar depth sites on the MAR were investigated in the summer of 2010. In addition the influence of the MAR on species distribution was investigated to determine if the MAR provides a physical barrier to the distribution of bathyal macrofaunal species. Work was undertaken as part of the ECOMAR (Ecosystem of the Mid-Atlantic Ridge at the Sub-Polar Front and Charlie-Gibbs Fracture Zone) project with the aim of addressing our limited understanding of the ecological influence of mid ocean ridge systems (Priede et al., 2013).

2. Material and methods

2.1. Study sites

Four sites (NW, NE, SW, and SE), located at ~2500 m water depth on the Mid-Atlantic Ridge (MAR), were studied during the RRS James Cook cruise 48 (JC048; May–July 2010) (Table 1). Two of the sites were located to the north of the Charlie-Gibbs Fracture Zone (CGFZ), with one site located on the western flank of the MAR and the other on the eastern flank. The other two sites were located to the south of the CGFZ, again with one site located on either flank of the MAR (Fig. 1). Measured mean water temperature (3.01–3.15 °C) and oxygen concentration (281.28–282.43 μmol l⁻¹) near the seabed were comparable between sites (Gooday et al., 2013). Mean organic carbon flux from sediment traps at 2400 m water depth were comparable between sites

((NW, 0.77 g m⁻²y⁻¹; NE, 1.18 g m⁻²y⁻¹; SW, 0.82 g m⁻²y⁻¹; SE, 1.16 g m⁻²y⁻¹) (Abell et al. (2013)).

2.2. Sample collection

A total of 11 samples were collected from four stations during the JC048 expedition in the summer of 2010. Replicate samples were collected with a megacorer fitted with eight core tubes (internal diameter 100 mm) from each of the four stations. Three replicate megacorer deployments were collected at each of the sites with the exception of the NW site where only two successful replicate samples were obtained from four deployments of the megacorer. The number of individual core tubes obtained from a deployment for each replicate sample ranged from 3 to 8 (Mean no. core tubes=6) (Table 1). There was a difference in total area of seabed sampled at each site, most notably at the NW station where a much smaller area of seabed was sampled compared to the other three sites (Table 1). Only six individual core tubes from two replicates were recovered at NW from a total deployment of 32 individual core tubes (eight core tubes per deployment, four deployments). The NW site proved to be extremely problematic for sampling with the megacorer, believed to be due to a high water content for a very fine mud.

Each individual core tube from a megacorer deployment was sliced at 0–2, 2–6 and 6–10 cm sediment depth horizons and then pulled into a single sample for the corresponding sediment depth horizon. Pulled core tube slices were washed through a nest of 500 and 300 μm mesh sieves with filtered sea water. Material retained on each sieve was then washed into individual 500 ml Nalgene bottles and fixed with 10% buffered formalin solution. In the laboratory macrofaunal samples were stained with Rose Bengal 24 h prior to sorting of material under a stereo microscope (Nikon SMZ-10). All polychaetes recovered were identified to the lowest possible taxonomic level (Genus or Species). Following identification all specimens were preserved in 70% ethanol solution.

Analysis of the polychaete community was based on all sediment depth horizons combined from a single megacorer deployment down to a sediment depth of 10 cm. Polychaete biomass (wet weight) was obtained prior to species identification. Specimens were aggregated according to family and weighed on a Mettler Toledo AB265-5 top loading balance. Wet weight biomass was measured for specimens retained only on the 500 μm sieve fraction, as measuring smaller animals adds very little to macrofaunal biomass estimates (Gage et al., 2002). Polychaete wet weight biomass was then converted to ash free dry weight using commonly employed conversion factors (Rowe, 1983). All polychaetes at each site were also assigned to feeding types from similar shallow water species (Fauchald and Jumars, 1979; Gaston, 1987).

Table 1

Megacorer samples collected for macrofaunal community analysis. Station key: NW=North West; NE=North East; SW=South West; and SE=South East.

Site	Sample	Date	Latitude	Longitude	Depth (m)	No. of cores	Area sampled (m ²)
NW	MGC007	02.vi.2010	54°01.00N	36°08.20W	2619	3	0.023
	MGC010	02.vi.2010	54°01.01N	36°08.36W	2619	3	0.023
NE	MGC022	09.vi.2010	54°00.65N	34°10.42W	2510	8	0.062
	MGC025	10.vi.2010	54°00.65N	34°10.42W	2508	8	0.062
	MGC027	12.vi.2010	54°00.67N	34°10.42W	2508	8	0.062
SW	MGC034	16.vi.2010	48°45.76N	28°38.50W	2564	8	0.062
	MGC037	19.vi.2010	48°45.76N	28°38.50W	2520	7	0.054
	MGC042	21.vi.2010	48°45.70N	28°38.56W	2563	3	0.023
SE	MGC049	24.vi.2010	49°05.34N	27°50.22W	2768	6	0.047
	MGC050	24.vi.2010	49°05.40N	27°50.23W	2770	7	0.054
	MGC052	27.vi.2010	49°05.41N	27°50.19W	2775	8	0.062

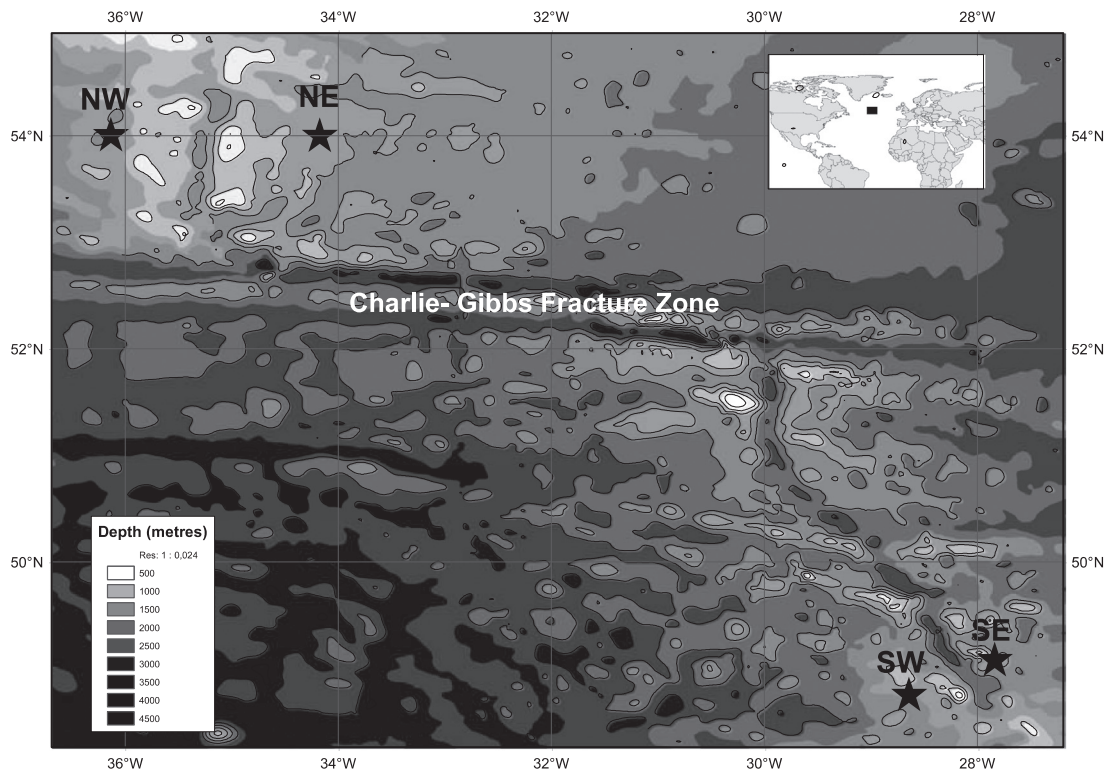


Fig. 1. Location of stations on the Mid Atlantic Ridge. Inserted map show study region location in the North Atlantic Ocean. Stations: NW=North West; NE=North East; CGFZ=Charlie-Gibbs Fracture Zone; SW=South West; and SE=South East.

Megacorer samples revealed that sediment at the two northern sites comprised of very soft mud, with patches of phytodetritus a few mm thick observed at the sediment surface. Sediment at the NE site was characterised by the presence of sponge spicules down through the sediment column. At the southern sites sediments from the megacorer samples were coarser, silty muds with a variable coverage of pteropod tests at the sediment surface. ROV video surveys undertaken with the ROV Isis during the cruise revealed that pteropod coverage on the seafloor was extremely patchy at the SW and SE sites. At the NE, SW and SE sites there was evidence of burrowing megafauna from the megacorer samples, most notably horizontal burrows about 1 cm in diameter at a sediment depth of about 9 cm were observed at each of these sites. No specimens were recovered from the 1 cm diameter burrows and it remains unknown if the burrows extended to the sediment surface. There were no observations of the 1 cm horizontal burrows at the NW site, although this could be an artefact of the small sample size at this site.

3. Polychaete community analysis

Prior to analysis polychaete abundance and biomass data were standardised to 1 m² for comparison between the four sites. Expected species accumulation curves against abundance were estimated by randomising the sample order 100 times (Gotelli and Colwell, 2001) for each site using EstimateS 8.2.0 (Colwell, 2009), and the rarefaction curves plotted using Sigmaplot version 11. Univariate analyses of diversity were undertaken for untransformed species data using “DIVERSE” in Primer version 5 (Clarke and Warwick, 2001). The univariate analyses selected to measure diversity were Shannon's diversity (H') and Pielou's evenness (J') (Magurran, 2004). All polychaete abundance and biomass data and all univariate diversity analyses were normally distributed and had equal variances. Anderson–Darling normality test, Levene's equal

variance test and one-way analysis of variance were carried out using Minitab version 15 statistical software.

Group average clustering and of Bray–Curtis similarities for untransformed species data were produced using Primer version 5. Employing untransformed species data for the multivariate analysis meant that observed similarity between sites was weighted towards the common species (Clarke and Warwick, 2001). Focusing on common species would help reduce the error associated with the under-sampling of rarer species, particularly as there was variation in sample size between sites (Clarke and Warwick, 2001). However, it was important not to overlook the influence of the rare species on the diversity patterns of the polychaete community at each site; a potential drawback of employing untransformed data. To investigate the similarity between samples and sites for all species a reduction of quantitative data were required, and so species data were transformed to presence/absence data to provide rarer species equal weighting as common species. Two separate analysis of similarities (ANOSIM) were undertaken for untransformed and presence/absence data to investigate if there was a greater difference in species composition within sites than between sites. Similarity Percentage (SIMPER) analysis was undertaken on species abundance data to help identify the main species contributing to observed dissimilarity between sites. Species data has been deposited with and is freely available from British Oceanographic Data Centre.

4. Results

4.1. Abundance, biomass and feeding types

In total 715 individual specimens representative of 133 polychaete species belonging to 32 families were recorded from all four sites on the MAR (total sampled area 0.54 m²). A list of species is provided in Table 1. The majority of polychaete specimens

recovered were from the upper 2 cm of sediment at all sites. The dominant polychaete families in terms of abundance were the Spionidae, Cirratulidae, Syllidae and Glyceridae (percentage total abundance for each family $\geq 5\%$). In particular Spionidae accounted for more than 40% (295 specimens) of all polychaetes sampled from the MAR, with *Auospio dibranchiata* and *Prionospio* sp 1 the most abundant species. There was no significant difference in total abundance of polychaetes at each of the four sites on the MAR ($F_{3,7}=1.0, P=0.448$) (Fig. 2). Mean abundance of polychaetes from all four sites combined was 1285 (± 464 SD) ind. m^{-2} . In addition, there was no significant difference in total polychaete biomass between sites ($F_{3,7}=1.32, P=0.342$) (Fig. 2), with a mean polychaete biomass of 19.60 (± 13.27 SD) mg C m^{-2} for the MAR.

All sites were similar in terms of the relative abundance of polychaete feeding types, with little variation between sites (Fig. 3). The polychaete community of the MAR was characterised by surface deposit feeders, representing more than 70% of polychaete abundance at each of the sites. Carnivore/scavenger species also accounted for more than 15% of relative abundance at all sites with the exception of NW. There was, however, a more pronounced difference between sites for relative biomass of polychaete feeding types (Fig. 3). All sites had more than 40% of biomass associated with surface deposit feeders, representing more than 70% of biomass at NE. In contrast the relative biomass of subsurface deposit feeders was less than 5% at NE and SW but more than 50% at NW, largely due to the presence of the species

Notomastus latericeus, belonging to the polychaete family Capitellidae, at NW.

4.2. Diversity patterns

Species richness was investigated with a rarefaction curve for each site for expected species accumulation against the number of individuals for each of the sites (Fig. 4). It appeared that the number of expected species with number of individuals sampled was higher at NE than at any other site. Univariate analyses of diversity were measured for each of the sites. One-way ANOVA for these measures of diversity revealed no significant differences in the measures of diversity between the sites ($H':F_{3,7}=2.08, P=0.191; J':F_{3,7}=0.14, P=0.935$). Variation in species composition between sites was investigated with multivariate statistics. Group average clustering for untransformed species abundance data revealed that the NE site appeared to be distinct in terms of species composition (Fig. 5). However, the similarity between the NE replicates was less than 50% for untransformed polychaete species abundance. The ANOSIM for untransformed data indicated no significant difference in polychaete species composition between sites than between samples within a site (Global $R=0.238, P=0.078$). Focussing our analysis solely on the presence and absences of polychaete species revealed no distinct clustering according to sites (Fig. 6). Further analysis with ANOSIM for

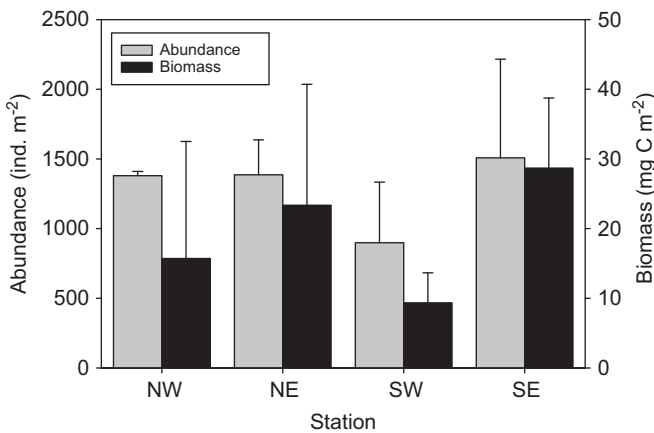


Fig. 2. Abundance and biomass of polychaetes on the MAR. Error bars represent standard deviation. NW=North West; NE=North East; SW=South West; and SE=South East.

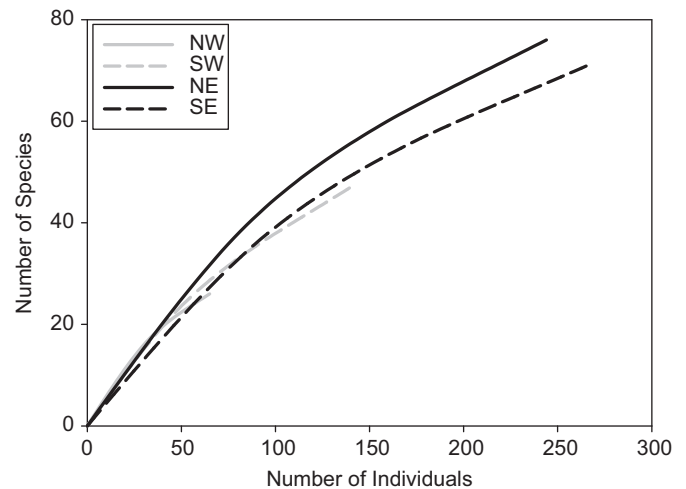


Fig. 4. Rarefaction of the number of species against number of individuals for each site. NW=North West; NE=North East; SW=South West; and SE=South East.

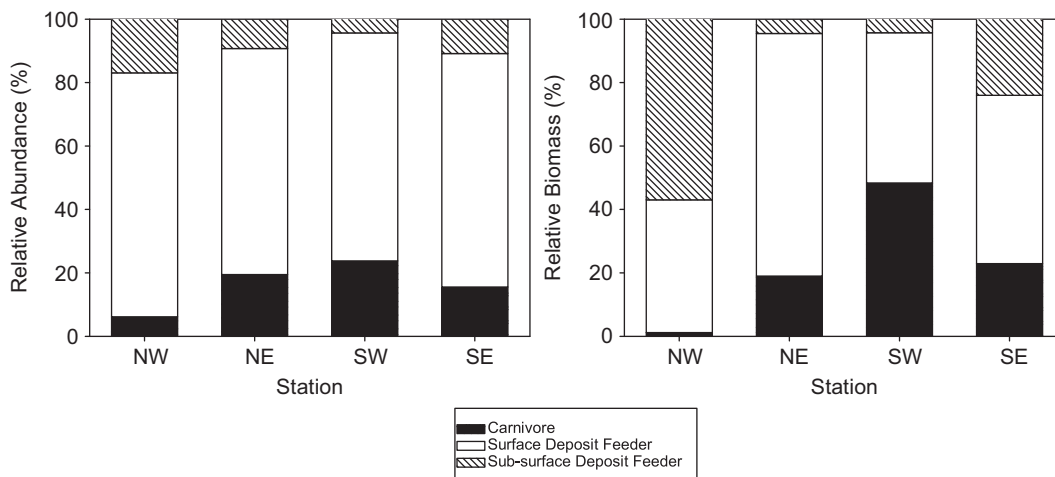


Fig. 3. Relative abundance and biomass of polychaete feeding types at each site. NW=North West; NE=North East; SW=South West; and SE=South East.

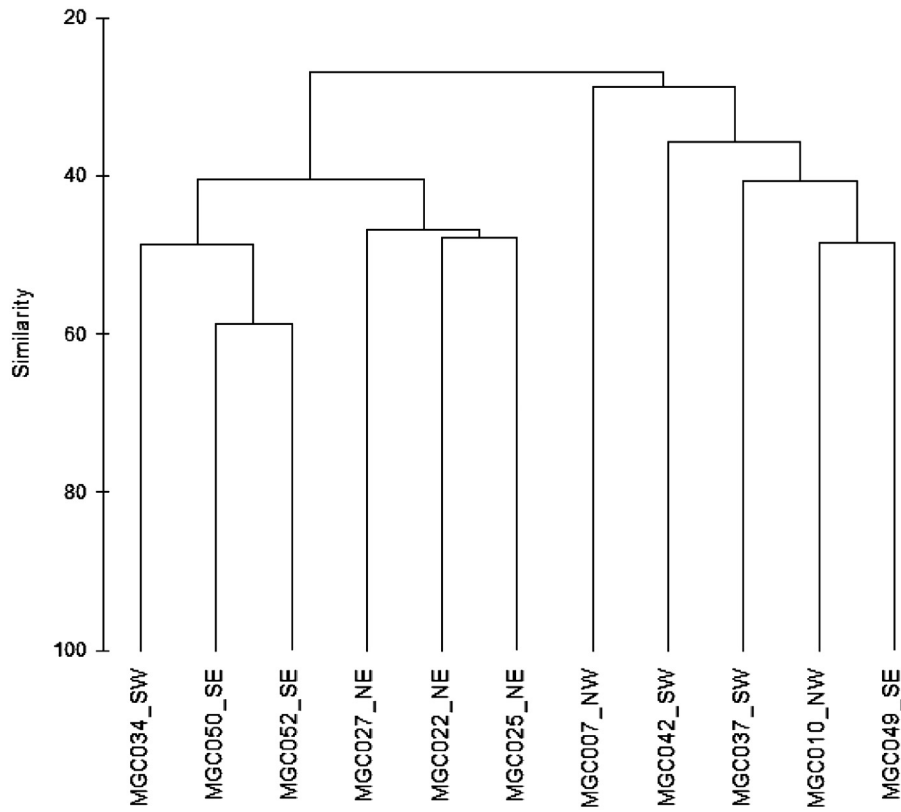


Fig. 5. Bray Curtis similarity for group average clustering of untransformed polychaete species abundance. NW=North West; NE=North East; SW=South West; and SE=South East.

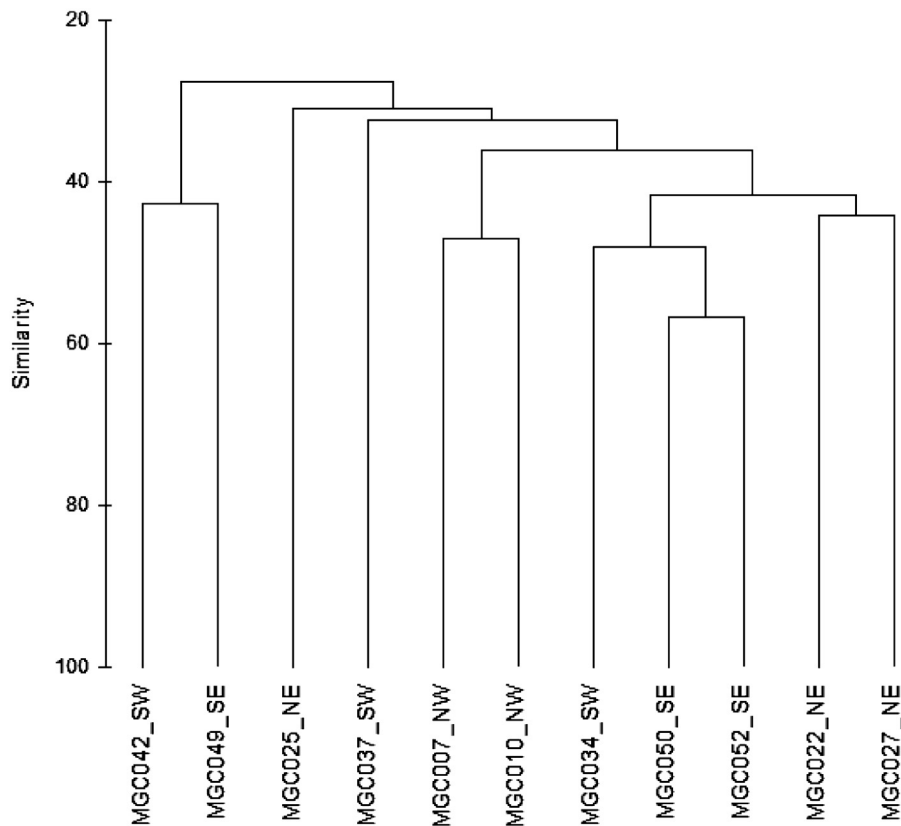


Fig. 6. Bray Curtis similarity for group average clustering of presence and absence of polychaete species. NW=North West; NE=North East; SW=South West; and SE=South East.

Table 2
List of polychaete species sampled at each site. Data presented has not been standardised to 1 m⁻².

Species name	Number of individuals										
	NW		NE			SW			SE		
	NW007	NW010	SW034	SW037	SW042	NE022	NE025	NE027	SE049	SE050	SE052
<i>Abyssoninoe</i> sp.	0	0	1	1	0	1	0	1	0	0	2
Acrocirridae indet.	0	0	0	1	0	0	0	0	0	0	0
Acrocirridae indet.4	0	1	0	0	0	1	1	1	0	0	0
<i>Ammotrypane abranziata</i>	0	0	0	0	0	1	0	0	0	1	2
<i>Ammotrypanella</i> sp	0	0	0	0	0	0	2	1	0	0	0
<i>Ampharete</i> sp.	0	0	0	0	0	0	0	0	0	1	0
<i>Anguillosyllis</i> sp.	1	0	3	0	1	0	0	1	0	1	4
<i>Aphelochaeta</i> sp.	3	0	0	0	0	0	0	0	0	0	0
<i>Aphelochaeta</i> sp.2	0	0	1	1	0	0	0	0	0	0	0
<i>Aphelochaeta</i> sp.3	0	0	0	0	0	0	0	0	0	0	1
<i>Apherusa</i> sp.	0	0	0	0	0	0	1	0	0	0	0
<i>Aricidea abranziata</i>	1	2	0	0	0	1	1	2	0	2	2
<i>Aricidea</i> sp.	0	0	2	0	0	0	0	0	0	0	0
<i>Aricidea</i> sp.1	0	0	0	1	0	0	0	0	0	0	0
<i>Aricidea</i> sp.2	0	0	0	0	0	0	1	0	0	1	0
<i>Aricidea</i> sp.3	0	0	0	0	0	0	0	0	2	0	0
<i>Augeneria</i> sp.	0	0	1	0	0	1	0	0	0	0	0
<i>Aurospio dibranziata</i>	2	7	14	5	4	13	13	10	6	17	16
Capitellidae indet.	0	0	0	0	0	3	0	0	0	1	0
Capitellidae indet.1	0	0	0	0	0	1	0	0	0	0	0
Capitellidae indet.2	0	0	0	0	0	0	1	0	0	0	0
Capitellidae indet.3	0	0	0	0	0	0	1	0	0	0	0
Capitellidae indet.6	0	0	0	0	0	0	0	1	0	0	2
Capitellidae indet.7	0	0	0	0	0	0	0	0	0	0	1
<i>Ceratocephale</i> sp.	0	0	0	0	0	0	0	1	0	0	0
<i>Chaetozone</i> sp.	0	4	0	3	0	0	0	0	3	0	0
<i>Chaetozone</i> sp.1	0	0	0	0	0	2	2	0	0	6	11
Cirratulidae indet.	0	0	0	0	0	0	0	1	0	0	0
Cirratulidae indet.1	0	0	4	1	0	1	0	3	0	4	3
Cirratulidae indet.2	0	0	1	0	1	0	0	4	1	1	5
Cirratulidae indet.5	0	0	0	0	0	0	0	0	0	0	1
Cirratulidae indet.6	0	0	0	0	0	0	0	1	0	1	0
Cirratulidae indet.7	0	0	0	0	0	0	0	2	0	0	0
<i>Cossura</i> sp.	2	0	0	0	0	0	0	0	0	0	0
<i>Diplocirrus</i> sp.	0	0	0	0	0	0	0	0	0	1	0
<i>Eclysippe</i> sp.	0	0	1	0	0	0	0	0	1	1	2
<i>Ephestiopsis</i> sp.	0	0	0	0	0	0	3	0	0	0	0
<i>Euchone</i> sp.1	0	0	0	0	0	1	0	0	0	0	0
<i>Eumida</i> sp.	0	0	0	0	0	0	1	0	0	1	1
<i>Exallopus</i> sp.	0	0	0	0	0	0	1	0	0	0	0
<i>Flabelligella</i> sp.	0	0	0	0	0	1	0	0	0	0	0

<i>Flabelligena</i> sp.1	0	0	0	0	0	0	2	0	0	0	0
<i>Flabelligena</i> sp.2	0	0	1	0	0	0	0	2	0	0	0
<i>Flabelligena</i> sp.4	0	0	0	0	0	0	0	0	0	0	1
<i>Flabelligena</i> sp.5	0	0	0	0	0	0	1	0	0	0	0
<i>Galathowenia</i> sp.	0	0	2	1	1	1	5	0	0	1	0
<i>Glycera mimica</i>	0	1	8	4	1	2	2	6	1	2	1
<i>Glycera</i> sp.1	0	0	0	0	0	5	2	3	0	0	0
Hesionidae indet.	0	0	5	0	0	0	0	0	0	0	0
Hesionidae indet.1	0	0	0	1	0	0	0	0	0	0	0
Hesionidae indet.2	0	0	0	0	0	0	3	3	0	0	0
Hesionidae indet.3	0	0	0	0	0	0	1	1	0	0	2
<i>Hyalopomatus</i> sp.	0	0	0	1	0	0	0	0	0	0	0
<i>Jasmineira</i> sp.1	0	0	0	0	0	0	1	0	0	0	0
<i>Laonice</i> sp.1	0	0	0	0	0	1	0	1	0	1	2
<i>Laonice</i> sp.2	0	0	0	1	0	0	3	1	0	2	3
<i>Laonice</i> sp.3	1	1	3	0	0	2	4	0	3	5	2
<i>Laubieriopsis brevis</i>	0	0	0	0	0	1	0	1	0	2	1
<i>Leanira</i> sp.	0	1	1	0	0	0	0	0	0	0	1
<i>Leanira</i> sp.1	0	0	0	0	0	1	0	0	0	0	1
<i>Leanira</i> sp.2	0	0	0	0	0	0	0	0	1	1	0
<i>Levinsenia</i> sp.	0	0	0	0	0	0	0	0	0	2	0
Lumbrineridae indet.	0	0	0	0	0	1	0	0	0	0	0
Lumbrineridae indet.3	0	0	0	0	0	0	0	0	1	0	0
<i>Lysippe</i> sp.	0	0	1	0	0	0	0	0	0	1	0
<i>Mastobranchus</i> sp.	0	0	0	0	0	0	0	1	0	0	0
<i>Mastobranchus</i> sp.1	0	0	0	0	0	0	0	0	0	1	0
<i>Micronephthys</i> sp.	0	1	0	0	0	1	0	2	0	3	2
<i>Micronereides</i> sp.	0	0	0	0	0	1	1	0	0	0	0
<i>Monticellina</i> sp.	0	0	0	0	0	0	1	0	0	0	0
<i>Mystides</i> sp.1	0	0	0	0	0	0	0	0	0	0	1
Nereididae indet.1	0	0	3	0	0	0	0	0	0	1	2
Nereididae indet.2	0	0	0	1	0	0	0	0	0	0	3
<i>Noanelia</i> sp.	1	0	0	0	0	0	0	0	0	0	1
<i>Notomastus latericeus</i>	6	1	3	0	0	0	0	0	0	1	2
<i>Notoproctus</i> sp.	0	0	0	0	0	0	0	0	0	0	2
<i>Oligobregma</i> sp.	1	0	0	0	0	0	0	0	0	3	6
Opheliidae indet.	0	0	0	0	0	1	0	0	0	0	0
Opheliidae indet.1	1	0	0	0	0	0	0	0	0	0	0
<i>Ophelina abranchiata</i>	0	0	0	0	0	0	0	1	0	0	0
<i>Ophelina</i> sp.3	0	0	0	0	0	0	1	1	0	0	0
Orbiniidae indet.	0	0	1	0	0	0	0	0	1	1	2
Orbiniidae indet.1	0	0	0	0	0	0	0	0	1	0	0
Orbiniidae indet.2	0	0	0	0	0	0	0	1	0	0	0
Orbiniidae indet.3	0	0	0	1	0	0	0	0	0	0	0
Oweniidae indet.	2	0	1	2	0	0	3	3	0	3	1
<i>Paradoneis abranchiata</i>	1	0	0	0	0	0	0	0	0	0	0
<i>Paraonides monilaris</i>	1	0	0	0	0	0	0	0	1	0	0
<i>Paraonis</i> sp.	0	2	2	0	0	0	0	0	1	0	0
<i>Paraonis</i> sp.1	0	0	0	0	0	1	0	0	0	0	0
<i>Paraonis</i> sp.1b	0	0	0	0	0	0	0	1	0	0	0
<i>Parexogone</i> sp.	1	1	1	1	0	4	4	1	0	0	1
<i>Parexogone</i> sp.1	0	0	0	0	0	0	1	0	0	0	0
<i>Parexogone</i> sp.2	0	0	0	0	0	1	0	0	0	2	0
<i>Pholoe</i> sp.1	0	0	0	0	0	0	0	0	0	2	6
<i>Phyllococe</i> sp.1	0	0	1	0	0	1	0	0	0	1	0
Phyllodocidae indet.2	0	0	1	0	0	0	0	0	0	0	0
Polynoinae indet.1	0	0	0	0	0	0	1	1	0	0	0
<i>Prionospio</i> sp.	2	1	2	1	0	1	4	4	0	2	3
<i>Prionospio</i> sp.1	5	5	6	6	1	5	6	9	2	6	7
<i>Prionospio</i> sp.2	1	2	5	1	1	5	0	2	1	10	8

Table 2 (continued)

Species name	Number of individuals										
	NW		NE			SW			SE		
	NW007	NW010	SW034	SW037	SW042	NE022	NE025	NE027	SE049	SE050	SE052
<i>Prionospio</i> sp.3	0	0	2	0	0	0	0	0	2	2	0
<i>Proceraea</i> sp.	0	0	0	0	0	0	0	0	0	1	0
<i>Pseudodysponetus</i> sp.	0	0	0	0	0	0	1	1	0	0	0
<i>Pseudomystides</i> sp.1	0	0	0	0	0	0	0	1	0	0	0
Sabellidae indet.1	0	0	0	0	0	0	1	0	0	0	0
Sabellidae indet.2	0	0	0	0	0	0	0	1	0	0	0
Sabellidae indet.3	0	0	0	0	0	0	0	0	0	0	1
Scalibregmatidae indet.	0	0	0	0	0	0	0	1	0	0	0
Scalibregmatidae indet.1	1	0	2	0	0	1	0	1	0	0	5
<i>Scoletoma</i> sp.	0	0	0	0	0	0	0	0	0	0	3
<i>Siboglinum</i> sp.	0	0	0	0	0	1	1	0	0	0	0
<i>Sphaerephesia</i> sp.	0	0	0	2	0	0	0	0	0	0	0
<i>Sphaerosyllis</i> sp.	0	0	3	0	0	0	0	0	0	0	0
<i>Sphaerosyllis</i> sp.1	0	0	0	3	0	0	0	0	0	0	0
Spionidae indet.	0	0	0	0	0	0	0	0	0	1	0
Spionidae indet.1	1	0	0	0	0	5	1	3	0	0	0
Spionidae indet.2	0	0	0	0	0	0	0	3	0	0	0
Spionidae indet.3	0	0	0	0	0	0	0	0	0	1	0
<i>Spiophanes</i> sp.	0	0	1	0	0	3	0	3	0	1	0
<i>Spiophanes</i> sp.1	0	0	0	1	0	0	0	0	0	0	0
<i>Spiophanes</i> sp.2	0	0	0	1	1	0	2	0	1	0	0
<i>Spiophanes</i> sp.3	0	0	0	0	0	0	0	0	0	0	3
<i>Syllis</i> sp.	0	0	0	1	0	0	0	0	0	3	3
<i>Syllis</i> sp.1	0	0	1	0	0	0	0	0	0	0	0
<i>Tachytrypane jeffreysii</i>	0	0	0	0	0	0	0	0	1	0	0
Terebellidae indet.	0	0	1	1	0	0	0	0	0	0	0
Terebellidae indet.1	0	0	0	0	0	0	1	0	0	0	0
Terebellidae indet.2	0	0	0	0	0	0	0	0	0	0	2
Terebellidae indet.3	0	0	0	0	0	0	1	0	0	0	0
<i>Terebellides</i> sp.	0	1	0	0	0	1	0	0	0	0	0
<i>Terebellides</i> sp.1	0	0	0	0	0	0	0	1	1	1	0
<i>Terebellides</i> sp.2	0	0	0	0	1	0	0	0	0	0	2

presence and absence data revealed that between site differences were significantly greater than between samples within site (Global $R=0.46$, $P=0.013$). SIMPER analysis revealed that the contribution of species to the dissimilarity between sites varied between two site comparisons. However, the abundance of the spionid species, *A. dibranchiata*, always had the greatest influence on dissimilarity between each site.

5. Discussion

5.1. Abundance, biomass and functional ecology

Little is known about the macrofaunal community associated with mid ocean ridges (Bergstad et al., 2008; Shields et al., in press) and the present study provides an important insight into the polychaete community of the MAR. Polychaetes were the most abundant component of the macrofaunal community at all four sites on the MAR (Relative abundance of polychaetes from the macrofaunal community: NW–68%; NE–55%; SW–55%; and SE–61%). There was no significant difference in polychaete abundance and biomass between the four MAR sites. Previous analysis of the MAR macrofaunal community, from the same samples, has revealed no significant difference in abundance and biomass between sites (Priede et al., in press).

The polychaete family Spionidae accounted for more than 40% of polychaete individuals recovered from the MAR, with a relative abundance ranging from 33% to 58% in all samples. Spionidae is typically one of the most commonly found Polychaeta families in deep-sea soft sediments (Glover et al., 2002; Hughes and Gage, 2004; Shields and Hughes, 2009). In the NE Atlantic a comparably high relative abundance of spionids (>40%) was reported from a depth of over 3500 m west of Ireland at one of the BENBO study sites (Hughes and Gage, 2004). Spionids are often classed as interface feeders, meaning the animals can switch from surface deposit feeding to suspension feeding as water current speeds and the flux of suspended food increases (Taghon et al., 1980). The ability to take advantage of both deposited and suspended food could provide spionids with a competitive advantage over other polychaetes at the MAR, particularly important due to the complex primary productivity regime (Tilstone et al., 2009). The most abundant spionids from the MAR were *Prionospio* spp. and the widespread deep-sea species *A. dibranchiata* Maciolek, 1981. As the samples collected for the present study represent one sample in time it remains unclear how the abundance of polychaete species varies seasonally and interannually at the MAR. Size class data for *A. dibranchiata* from the NW Atlantic continental margin indicates little evidence of seasonal recruitment for this species although seasonal variation in egg size does suggest there may be seasonal reproduction patterns (Blake and Watling, 1994).

In terms of functional ecology all sites on the MAR were characterised by the high abundance of surface deposit feeders. Surface deposit feeders are commonly the most abundant polychaete and macrofaunal feeding mode in deep-sea sediments (Gage and Tyler, 1991). The relative abundance of all feeding types was comparable between the four MAR sites and similar to macrofaunal community observations from depths of about 2000 m on the Northeast Atlantic continental margin (Flach et al., 1998; Hughes and Gage, 2004). No bathymetric distribution data is presented here for the MAR. However, studies from the NE Atlantic suggest that the relative abundance of surface deposit feeders is highest at mid-slope bathyal depths, while subsurface deposit feeders become more abundant at lower slope bathyal depths and on the abyssal plain (Flach et al., 1998; Hughes and Gage, 2004).

The NW site was the only location on the MAR where subsurface deposit feeders represented more than 40% of total polychaete biomass. The high biomass of subsurface deposit feeders at NW was due to the presence of the Capitellidae, *N. latericeus* Sars, 1851 representing >40% of polychaete biomass. Sub-surface deposit feeders are believed to favour sediments with large quantities of refractory organic matter (Rice and Rhoads, 1989; Rosenberg, 1995; Dauwe et al., 1998). *N. latericeus* has been found at bathyal depths on the western and eastern Atlantic continental margins and it would appear that the MAR does not provide a physical barrier to the distribution of this species in the North Atlantic (Smith et al., 1986/87; Romero-Wetzel and Gerlach, 1991; Shields and Hughes, 2009).

Results presented here suggest that the MAR can support a similar standing stock of polychaete community as the continental margins of the North Atlantic in terms of both abundance and biomass (Flach and Heip, 1996; Flach et al., 1998; Flach, 2002; Hughes and Gage, 2004; Wei et al., 2010a; Rex and Etter, 2010). Total abundance and biomass of the macrofaunal community of the continental margins in the North Atlantic can reflect annual primary production and export flux (Cosson et al., 1997; Flach, 2002; Hughes and Gage, 2004; Johnson et al., 2007). Export flux on the MAR at 1000 m water depth is comparable to long term measurements from the Porcupine Abyssal Plain, NE Atlantic at the same depth (Priede et al., in press). There are differences in the primary production north and south of the CGFZ (Tilstone et al., 2009), suggesting a combination environmental parameters are influencing the availability of organic matter supporting the polychaete community at the MAR.

Both macrofaunal and polychaete abundance and biomass estimates for the MAR fall within the range of global estimates at comparable water depths (Priede et al., in press; Wei et al. 2010b). Global estimates for bathyal macrofaunal abundance and biomass are predominately based on data compiled from the continental margins with very little data available from mid oceanic ridges (Wei et al., 2010b). It does, however, remain unclear how the abundance and biomass of macrofauna varies with depth across the MAR. There is no significant difference in macrofaunal abundance and biomass with depth between the eastern and western continental margins of the north Atlantic (Rex and Etter, 2010). The presence of the same species either side of the MAR (Table 2) and north and south of the CGFZ suggests the MAR does not provide a physical barrier to the distribution of bathyal polychaete species either side of the ridge (Shields et al., in press). It would appear that the MAR does not provide a physical barrier to other taxa either, and that the species associated with the MAR can be found on both the eastern and western Atlantic continental slopes (Priede et al., in press). The MAR, however, may provide a physical barrier for some species, particularly if the larvae or adults cannot pass over the ridge if the required vertical migration would be beyond their physiological tolerance limit (Rex and Etter, 2010). Therefore it would be expected that the MAR might provide a physical barrier to the distribution of species normally found below bathyal depths. The MAR, however, does provide a large proportion of available bathyal soft sediment habitat in the North Atlantic (Niedzielski et al., 2013) and may actually help facilitate the distribution of bathyal species found living on both the western and eastern Atlantic continental slopes (Priede et al., in press).

5.2. Diversity patterns

There was a difference in samples size between sites and differences in sample size can potentially impact on measures of diversity. As there was no significant difference in total polychaete abundance between sites it was assumed that the species accumulation curves should provide a good indication of species

richness independent of sample size (Fig. 4). It should be noted that the species accumulation curves had not reached an asymptote at any site and it is, therefore, extremely unlikely that all polychaete species have been sampled. Increasing the number of samples and/or sample size would increase the likelihood of the expected species accumulation curve reaching an asymptote. There was, however, no significant difference in species richness between sites, based on 95% confidence intervals for the rarefaction (Gotelli and Colwell, 2001; Magurran, 2004). Typically, macrofaunal samples yield 24–56 species per hundred individuals from deep-sea sediments (Snelgrove and Smith, 2002). However, estimating the expected number of species from a sample of individuals is dependent on the relative abundance of different species (Gage and May, 1993; May, 1993). Issues associated with rarefaction analysis are now well documented and can be addressed by other measures of diversity that can corroborate results (Levin et al., 2001). Both Shannon's diversity (H') and Pielou's Evenness (J') further supported the theory of no significant difference in diversity or evenness between sites. Despite there being no difference in diversity and evenness between sites there was clearly a difference in the species composition between samples and between sites.

Multivariate analysis weighted towards common species resulted in the NE site clustering separately from the other sites. Results based on present and absence data indicated a higher dissimilarity between sites than between site samples even though there was no clear clustering of samples according to site. The higher dissimilarity between sites suggests that there are distinct polychaete communities at each site, despite similarities in the presence of the most common species. SIMPER analysis indicated that the relative abundance of the most abundant species were responsible for the greater dissimilarity between sites. The most abundant species at each site belonged to the spionid family and *Prionospio* sp1 and *A. dibranchiata* as mentioned earlier. While the influence of rarer species on dissimilarity between sites could be a direct result of the smaller sample size at some sites, reducing the likelihood of rarer species being successfully sampled. Variation in sample size can influence data on the distribution of species, which in turn will influence the identification of diversity patterns (Warwick and Clarke, 1996).

5.3. Summary

The MAR does not appear to provide a physical barrier to the distribution of the bathyal polychaete community associated with the MAR. Diversity patterns on the MAR are comparable to the continental margin of the North Atlantic (Rex and Etter, 2010). However, it is difficult to draw direct comparisons between the MAR samples and other North Atlantic locations for a number of reasons. Firstly diversity indices are dependent on a complex combination of sampling gear, size of area sampled, size distribution of animals, sieve size and fixation of samples prior to sieving (Warwick and Clarke, 1996). It is therefore not easy to directly compare the present study with previous studies on the western and eastern continental margins. In order to address direct comparison issues it has been recently recommended that there should be the adoption of standardised sampling methods and sorting techniques for future macrofaunal community studies in European waters to permit direct comparison between studies in the future (Narayanaswamy et al., 2010b). Secondly benthic communities are known to vary seasonally and interannually (Ruhl, 2007; Ruhl et al., 2008) and often there can be decades between samples collected from the same location (Shields and Hughes, 2009). If there are differences in the sampling techniques employed and a significant length of time between studies then it can be difficult to determine if any observed differences between

studies are a result of a changing benthic community and/or result of different sampling techniques. Lastly the relationship between the macrofaunal community to depth and environmental factors will vary at each location and needs to be considered independently for each study site (Wei et al., 2010a).

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