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Bathyal benthic fauna of the Mid-Atlantic Ridge between the Azores and the Reykjanes Ridge

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The composition, taxonomic structure and distribution patterns of bathyal benthic fauna of the northern Mid-Atlantic Ridge between the Azores and the southern tip of the Reykjanes Ridge were studied from specimens collected on the 'G.O. Sars MAR–ECO' expedition in July 2004. Material was obtained from 16 Campelen 1800 trawls taken north of the Azores (42°N) and in two areas around the Charlie-Gibbs Fracture Zone (CGFZ) (51°N and 53°N) at depths 1237–3527 m. A total of 192 species were recorded. Overall the MAR–ECO benthic fauna was dominated by echinoderms (49.5% of the total species sampled), sponges (18.2%) and anthozoans (16.7%). Between-station species similarity was analysed using non-metric multidimensional scaling. Our analysis revealed differences between stations from the CGFZ and the Azorean regions. Stations from the Azores formed one cluster whereas stations from the CGFZ separated into two groups related to depth: stations from depths 1263 m to 1916 m and those from 2350 m to 3512 m. The taxonomic structure of the bathyal fauna was also different in the Azores than in the CGFZ areas. At the CGFZ, taxa with the highest percentage of species present were different above and below the 2000 m bathymetric contour, in contrast close to the Azores taxa with the highest percentage of species were the same shallower and deeper than 2000 m. Our results point at turnover in benthic bathyal fauna between the Charlie-Gibbs Fracture Zone and the Azores, which could be related to the presence of the Sub-Polar Front.

Keywords: benthic fauna, bathyal, composition, taxonomic structure, Mid-Atlantic Ridge, Charlie-Gibbs Fracture Zone, MAR–ECO, Azores

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INTRODUCTION

Mid-ocean ridges are undersea mountain ranges forming the largest continuous topographic feature on Earth; a global network almost 85,000 km long (Kennett, 1982). Ridges play an important role in the distribution of benthos in the open ocean. It is hypothesized that they are stepping stones and pathways for the dispersal of slope fauna into the open ocean, but that they can also act as barriers to the dispersal of abyssal seafloor fauna (Wilson & Kaufman, 1987; Vinogradova, 1997; Dinter, 2001; Mironov, 2006). Characterized by high relief, rough topography and remoteness from land, ridges are very difficult to access even with modern oceanographic technologies. Few previous investigations have been dedicated to the targeted study of benthic fauna of ridge systems, except those which have focused on hydrothermal vent habitats.

The Mid-Atlantic Ridge (MAR) is the spreading zone between the Eurasian and American plates. As a result of volcanic and tectonic processes, new seafloor is continually being formed as the two plates spread at a rate of 2–4 cm yr^{-1} (Fornari & Embley, 1995). Between Iceland and the Azores the ridge extends over 1500 nautical miles (nm), and is characterized by rough bottom topography comprising underwater peaks (minimum depth 700–1000 m), a central rift valley, recent volcanic terrain, fracture zones, and seamounts. The northern Reykjanes Ridge is wide (the inner rift is 15–17 km at 58°N) and relatively shallow (500–1000 m deep) and extends from Iceland to the Charlie-Gibbs Fracture Zone (CGFZ) at approximately 52°N where the ridge is offset 5° to the east (see Figure 1). The CGFZ at its deepest is ~4500 m (Felley *et al.*, 2008) and is the deepest connection between the north-east and north-west North Atlantic. South of the CGFZ there are two more significant fracture zones—the Faraday and Maxwell at 50°N and 48°N, respectively.

The MAR has an important influence on the deep-water circulation of the North Atlantic, it separates the eastern and western basins of the North Atlantic along the majority of its length, but there is flow of deep-water between the basins through the CGFZ (Lackschewitz *et al.*, 1996). The dominating deep water mass at bathyal depths is the North Atlantic Deep Water (NADW) which is formed by mixing of the overflowing water masses from the Norwegian and Greenland Seas with Labrador Sea Water. The near surface circulation is complex, but it is dominated by the North Atlantic Current (NAC) which is one of the major currents originating from the North Atlantic Drift. The NAC crosses the MAR in two to four branches flowing in a north-easterly direction between 45°N and 52°N (Lackschewitz *et al.*, 1996;

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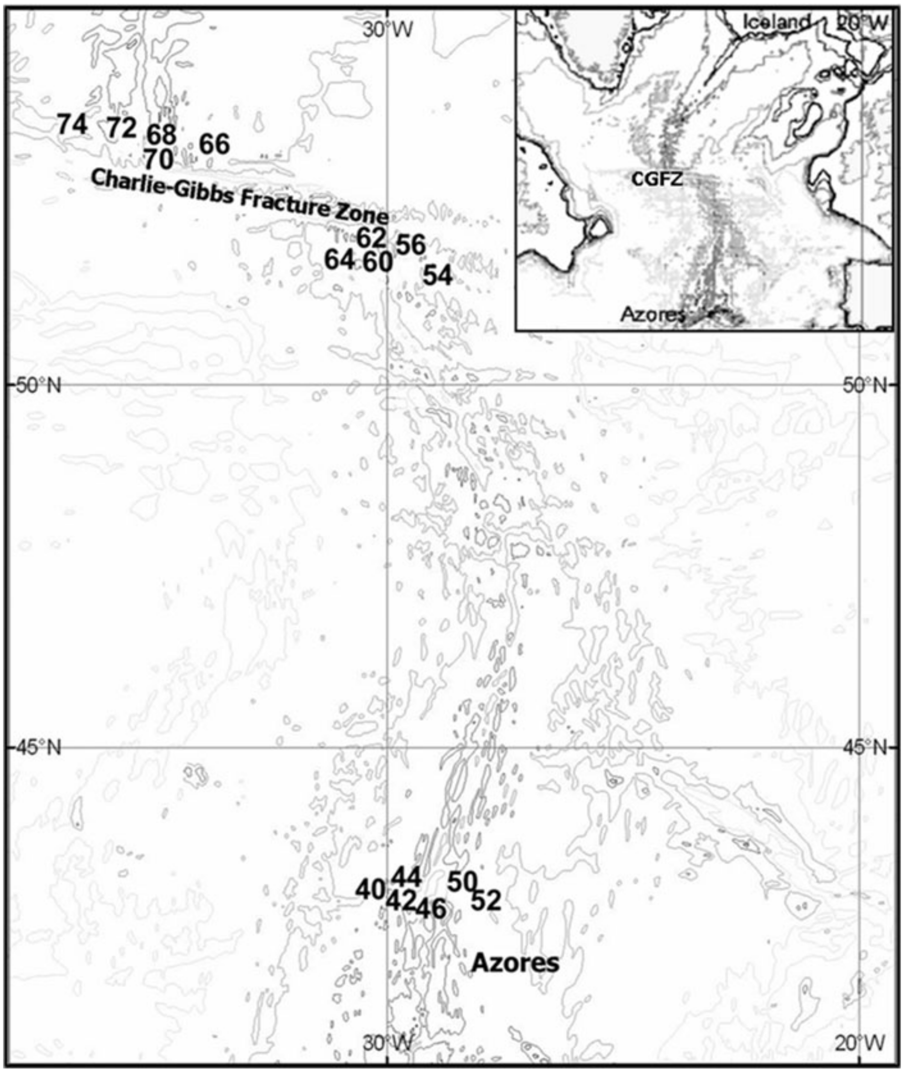

Fig. 1. Map of the study area indicating the position of each sampling station.

Søiland *et al.*, 2008) carrying warmer, more saline water across the ridge to the European shelf and into the Norwegian Sea. Along the northern boundary of the NAC lies the Sub-Polar Front separating cooler and less saline sub-polar water to the north from warmer Atlantic water to the south (Kraus & Käse, 1984). The frontal zone moves temporally, but normally it is located just south of the CGFZ (Søiland *et al.*, 2008).

The central North Atlantic bathyal fauna of the MAR has been less studied than those of several open ocean seamounts which have been the focus of comprehensive research programmes (Hempel & Nellen, 1972; Mironov, 1994; Rogers, 1994; Pfannkuche *et al.*, 2000; Mironov & Krylova, 2006). Prior studies of benthic fauna on the MAR have been restricted to the Reykjanes Ridge (Kuznetsov, 1985; Copley *et al.*, 1996; Tendal, 1998; for a review see Mironov & Gebruk, 2006), and some of these studies on background benthic fauna were conducted in parallel to investigations on hydrothermal vent habitats on the MAR (Young, 1998). Historical, and somewhat scattered, data on bathyal fauna from the area north of the Azores have been published (Koehler, 1909), but knowledge is limited concerning the general ridge fauna from bathyal depths between the Azores and the CGFZ.

The bathyal fauna of the open central North Atlantic is of great interest to marine biogeographers due to the complex biogeographical history of the region. The North Atlantic was subjected to sharp climatic, geomorphological and hydrological changes in the Pliocene and Pleistocene (references in Mironov & Gebruk, 2006). The region has been invaded by species from remote areas, such as the North Pacific, the Indo-Pacific and the Antarctic. In addition there is a strong relationship with the western Atlantic fauna, especially in the southern part of the central North Atlantic (Dilman, 2006; Mironov & Gebruk, 2006; Mironov & Krylova, 2006). The role of bathyal fauna originating from these different areas and their subsequent redistribution is different in the northern part of central North Atlantic (the Reykjanes Ridge) compared to the south (e.g. the Meteor Seamounts). The hypothesized pathway of dispersal along the Mid-Atlantic Ridge is that fauna invaded from the north and south, and met at moderate latitudes between the Azores and the CGFZ. Mironov & Gebruk (2006) highlighted an important zone of change in the bathyal benthic fauna between the Reykjanes Ridge and the Azores suggesting the presence of a biogeographical boundary which supports this theory. Changes in the Asteroidea from the Reykjanes Ridge to the Azores have also been shown recently by Dilman (2008) by comparing samples from 42–53°N on the MAR and those from the Reykjanes Ridge (Dilman, 2006). Interestingly data on the benthopelagic fish community also support this theory. Hareide & Garnes (2001) suggested the area between 48 and 52°N as a region of high species turnover and this was later narrowed to 50 to 52°N by King *et al.* (2006).

The northern MAR (42–53°N) was the target area of the MAR–ECO project, one of the field projects of the Census of Marine Life programme (Bergstad & Godø, 2003; Bergstad, 2008a; www.mar-eco.no). This pilot project aims to understand the biodiversity, distribution patterns, abundance and trophic relationships of pelagic, benthopelagic and epibenthic fauna inhabiting the mid-oceanic North Atlantic, from Iceland to the Azores. A major field effort of the project was the international expedition on the RV 'G.O. Sars' in June–July 2004. Principal results of this expedition were published in the thematic issue of *Deep-Sea Research Part II* (2008, Volume 55, numbers 1–2) 'Mid-Atlantic Ridge habitats and biodiversity'. Mortensen *et al.* (2008) in that issue considered studies of corals in MAR–ECO. A separate thematic issue of *Marine Biology Research* (2008, Volume 4, numbers 1–2) 'Benthic fauna of the Mid-Atlantic Ridge: results of the MAR–ECO expedition' was dedicated to taxonomic studies of benthic organisms collected on the MAR–ECO cruise.

In the present paper we analyse composition, taxonomic structure and distribution patterns of bathyal[1] benthic fauna from the section of the Mid-Atlantic Ridge between the Azores and southern tip of the Reykjanes Ridge. The analysis is based on trawl samples obtained on the 'G.O. Sars' MAR–ECO cruise in 2004.

MATERIALS AND METHODS

The material used in the present study was obtained on the 2nd leg of the 'G.O. Sars' MAR–ECO cruise in July 2004. The following three areas were sampled: north of the Azores, between 42° and 43°N; south-east of the CGFZ at 51°N and north-west of the CGFZ at 53°N (Figure 1).

Most activities were concentrated at pre-determined locations (deemed 'Super Stations'; 2.5 nm × 2.5 nm). These had been selected to produce a transect of stations traversing the ridge, with one central station at the ridge axis and two to three stations either side of the ridge at depths closest to 1000 m, 2000 m and 3000 m. To locate suitable sites, the best available charts were used in advance of the cruise, in addition to real time bathymetric maps produced by a Simrad EM 300 kHz multi-beam bottom profiler and associated charting software (Olex) whilst at sea (for details see De Lange Wenneck *et al.*, 2008). Sampling sites within these 'Super Stations' were termed 'Local Stations'.

Samples of benthos from trawls taken at 16 Local Stations (Table 1) are included in this analysis. The trawls were taken at depths from 1237 to 3527 m. The trawl at Super Station 74 (north-west of CGFZ, mean depth 3055 m) provided a qualitative sample and therefore this station was excluded from the statistical analysis. Owing to limitations in sampling, specimens within all the trawl catches could not be counted and weighed; therefore the analysis is based on species presence–absence data.

The bottom trawl used was a Campelen 1800 shrimp trawl as described in De Lange Wenneck *et al.* (2008). The horizontal opening between the upper bridles at the wing tips is 17 m at 50 m door spread, and the distance between Danlenos at the tips of the ground gear was 12 m. The vertical opening was 4.5 m at 50 m door spread. The cod-end had a 22 mm mesh in addition to a liner with 5 mm mesh size. The groundgear (rockhopper type, with discs of 35 cm diameter) travelled 3.5 m behind the headrope in the centre of the trawl. There was also 10 m of chain as the first part of the lower bridles in front of the Danlenos. According to video recordings made by low light cameras on the headrope, the rockhoppers travelled within the soft substrate, more than halfway submerged, so that most of the epifauna resting on the bottom was caught. To monitor the trawl configuration and performance a full suite of newly developed wireless SCANMAR (Scanmar AS, Norway) deep-water sensors were applied. Tows were made at a speed of 1.5 knots with a bottom time of 50–60 minutes Catches were standardized according to the distance trawled, i.e. the observed distance at which the trawl had bottom contact.

The fauna was first sorted on the cruise by higher taxa. Samples were then preserved in 80% alcohol or 4% buffered formaldehyde depending on taxon. Selected specimens in the best condition were photographed prior to preservation. All benthic samples were deposited in the Museum of Zoology, University of Bergen (Norway) and have since been identified to species level by relevant taxonomic experts (listed in the Acknowledgements).

To determine patterns of bathyal benthic faunal distribution along the ridge in the MAR–ECO area, we evaluated between-station species similarity using the non-metric multidimensional scaling (nMDS) within the PAST (PAlaeontological STatistics version 1.18) statistical programme (Hammer *et al.*, 2003). Correlation matrices were generated using the Sorensen's index of similarity on presence–absence data.

The east–west division of fauna (across the ridge) was investigated by comparing percentages (from the total in each of the three areas) of species occurring east or west of the ridge, those restricted to the ridge axis and those common at both sides of the ridge. Species were considered as 'axial' if they were found only at axial stations (Station 46 and Station 70). Species found at the ridge axis and east or west of the ridge, were considered as 'eastern' or 'western' respectively. The taxonomic structure of fauna was compared by evaluating the percentage of higher taxa (usually order or class) in the three studied areas (the Azores and south-east and north-west of the CGFZ) and those found shallower or deeper than 2000 m.

RESULTS

Faunal composition

The 16 trawl stations used in the present study (Table 1) were distributed between the three sampled areas as follows: 6 trawls in the Azoren area and 5 each south-east and north-west of the CGFZ respectively. Five trawls were taken at

[1]Lower boundary of bathyal is placed at different depths in different schemes. We follow the scheme of Belyaev *et al.* (1959) who defined bathyal as a depth zone between 200 m and 3000 m (see also Zezina, 1997). In this scheme the horizon between 2500 m and 3500 m is considered as transitional between bathyal and abyssal zones. In other schemes the lower boundary of bathyal lies at a depth of 2000 m (e.g. Gage & Tyler, 1992) or at 4000 m (e.g. Thurman, 1985).

Table 1. Details of MAR–ECO trawl stations used in the analysis. Environmental data were taken near bottom with a CTD sensor (Søiland *et al*., 2008).

Area	Super station	Local (trawl) station	Date	Sampling location		Trawling depth (m)			Environmental data		
				Latitude (N)	Longitude (W)	Mean	Max.	Min.	Temp (°C)	Salinity (psu)	Oxygen (ml l^{-1})
Azores	40	367	7 July 2004	42°55	30°20	2961	2968	2954	3.16	34.92	5.94
	42	368	8 July 2004	42°48	29°38	2078	2107	2063	3.93	34.97	5.78
	44	369	9 July 2004	42°55	29°32	1742	1767	1702	5.01	35.06	5.38
	46	372	11 July 2004	42°46	29°16	3031	3050	3005	3.48	34.93	5.89
	50	373	12 July 2004	43°01	28°33	2600	2607	2593	3.79	34.95	5.82
	52	374	13 July 2004	42°55	28°08	2977	2979	2973	3.18	34.93	5.86
Charlie-Gibbs Fracture Zone, south-east	54	377	16 July 2004	51°19	28°52	3512	3527	3505	2.83	34.94	5.83
	56	378	17 July 2004	51°45	29°33	1916	1950	1872	3.43	34.90	6.13
	60	379	19 July 2004	51°33	30°18	1263	1296	1237	3.91	34.90	6.01
	62	380	20 July 2004	51°55	30°25	1910	1959	1872	3.42	34.90	6.14
	64	381	21 July 2004	51°32	30°58	3461	3465	3452	2.90	34.93	6.04
Charlie-Gibbs Fracture Zone, north-west	66	383	24 July 2004	53°01	33°36	3030	3071	2995	2.91	34.98	5.98
	68	384	25 July 2004	53°08	34°46	2350	2374	2306	2.99	34.98	6.02
	70	385	26 July 2004	52°58	34°52	1650	1670	1630	3.13	34.94	6.10
	72	386	27 July 2004	53°16	35°31	2548	2567	2522	3.08	34.97	6.01
	74	387*	28 July 2004	53°17	36°46	3055	3063	3048			

Max., maximum; min., minimum;*, failed trawl.

depths between 1000 m and 2000 m, 6 trawls between 2000 m and 3000 m and 5 trawls >3000 m.

A total of 192 species of benthic organisms were identified from all 16 trawls, representing 16 higher taxa (family and higher) (see Table 2). Echinoderms (Holothuroidea, Asteroidea, Ophiuroidea and Echinoidea) were represented by 95 species forming 49.5% of the total species number, 18.2% (35 species) were sponges (Demospongiae and Hexactinellida), and 16.7% (32 species) were Anthozoa (Actinaria, Anthipatharia, Octocorallia and Scleractinia). These three taxonomic groups contributed to 84.4% of the total species number. 'Minor' groups (with ≤5 species) included Galatheidae, Echiura, Sipuncula, Pycnogonida, Cirripedia and Polychaeta. The number of species per station ranged from 9 (Station 62) to 46 (Station 72) (Table 2). A species-accumulation curve is shown in Figure 2. By the end of sampling this curve did not reach the saturation point indicating incomplete representation of regional fauna in our samples.

The highest number of species per area was found north-west of the CGFZ with 102 species (mean of 33 per trawl). In the Azores area 95 species were recorded (mean of 27 per trawl), and the lowest number of species were sampled south-east of the CGFZ with a total of 70 species (mean of 20 per trawl).

The total number of species and the mean species number per station were highest between 2000 and 3000 m water depth. A total of 119 species with a mean of 33 species per trawl were sampled from 2000–3000 m. At depths <2000 m the total number of species sampled was 69, with a mean 18.0 per trawl, and at depths >3000 m a total of 76 species were sampled, with a mean 26.25 per trawl. The pattern of change of species number along depth is shown in Figure 3.

Comparison of faunal composition and structure along the ridge

Analysis of similarities between stations using the nMDS revealed three clusters of stations (Figure 4). One cluster was formed by stations from the Azorean area. The two other clusters, stations from the CGFZ (both south-east and north-west stations) grouped according to depth: stations shallower than 2000 m and those deeper than 2000 m.

Considering the depth related clustering of stations around the CGFZ we examined the taxonomic structure of the fauna as a percentage of higher taxonomic classifications in all the three areas for those stations shallower and deeper than 2000 m. The species contributing most to each cluster were different, shallower and deeper than 2000 m (Figure 5). North-west of the CGFZ the three leading taxonomic groups that dominated at depths shallower than 2000 m were sponges Hexactinellida (24% of species), Demospongiae (19%) and Asteroidea (14%). At depths exceeding 2000 m the dominant fauna were the Holothuroidea (21%), Asteroidea (21%) and Ophiuroidea (11%). South-east of the CGFZ at depths less than 2000 m the five dominant faunal groups were the Octocorallia (20%), Hexactinnelida (16%) and three echinoderm taxa; Asteroidea, Holothuroidea and Ophiuroidea, each contributing equally (13%). In contrast deeper than 2000 m the fauna contributing most significantly were the Holothuroidea (28%), Asteroidea (20%) and Echinoidea (11%). In the Azorean region the dominant fauna contributing to the cluster both deeper and shallower than 2000 m were the Holothuroidea (24% and 28%), Ophiuroidea (14% and 13%) and Demospongiae (14% and 13%) (Scleractinia and Pycnogonida also contributed 13% to the faunal composition shallower than 2000 m). Thus, there are some differences in the composition and the taxonomic structure of bathyal benthic fauna between the Azores area and the two areas around the CGFZ.

East–west division of fauna

We also examined whether there were any trends in changes of bathyal fauna across the ridge (in the east–west direction). The percentage of species occurring east or west of the ridge axis was compared in all the three areas (Figure 6). In the Azores area and south-east of CGFZ we found relatively high and similar

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Table 2. Inventory of benthic invertebrates sampled by the MAR–ECO expedition. For published details on taxonomy and distribution of MAR–ECO benthos see: [1]Tabachnik & Collins (2008); [2]Molodtsova *et al.* (2008); [3]Murina (2008); [4]Dilman (2008); [5]Martynov & Litvinova (2008); [6]Mironov (2008); [7]Gebruk (2008). *Station 74 was excluded from most of the analyses as the trawl failed.

Species/station	40	42	44	46	50	52	54	56	60	62	64	66	68	70	72	74
area	Azores						CGFZ south-east					CGFZ north-west				
Mean depth, m	2961	2078	1742	3031	2600	2977	3512	1916	1263	1910	3461	3030	2350	1650	2548	3055
No. of species per station	37	21	15	19	43	27	35	15	13	9	24	26	23	37	46	7*
No. of species per area	95						70					102				
Mean No. of species per station/±SD	27.0±SD 10.95						19.6±SD 10.64					33.0±SD 10.55				
				Axial										Axial		
HEXACTINELLIDA[1]																
Amphidiscella atlantica															+	
Asconema fristedti nordazoriensis									+					+		
Asconema sp.	+											+				
Chonelasma choanoides	+				+					+				+		
Dictyaulus marecoi										+				+		
Doconestes aff. *sessilis*														+		
Euplectella gibbsa													+			
Euplectella suberea				+	+											
Farrea aff. *laminaris*														+		
Farrea sp.														+		
Hertwigia falcifera									+	+				+		
Heterotella midatlantica								+								
Lophocalyx atlantiensis														+		
Malacosaccus aff. heteropinularia															+	
Rossella nodastrella														+		
Saccocalyx pedunculata												+				
DEMOSPONGIAE																
Craniella sp.			+											+		
Forcepia sp.						+										
Geodia barretti														+		
Geodia macandrewi														+		
Geodia megastrella					+											
Geodia nodastrella					+											
Iotroata varidens	+															
Isops phlegraei															+	
Polymastia corticata														+		
Sidonops atlantica					+											
Sidonops cf. *mesotriaena*					+										+	
Stelletta rhaphidiophora														+	+	
Stelletta tuberosa	+				+	+								+	+	
Stryphnus fortis					+											
Stylocordyla borealis					+											
Tetilla longipilis	+	+			+											
Thenea cf. *levis*														+		
Thenea muricata			+													
Thenea valdiviae	+	+		+		+										
ACTINIARIA[2]																
Amphianthus inornata					+											
Amphianthus michaelsarsi		+			+	+				+						
Amphianthus sp.						+										
Chondrophellia coronata														+		
Paracalliactis consors	+	+														
Phelliactis robusta		+								+						
Phelliactis michaelsarsi							+									
Sicyonis ingolfi					+										+	
ANTHIPATHARIA[2]																
Schizopathes affinis		+														
OCTOCORALLIA[2]																
Acanella arbuscula					+											
Anthoptilum murrayi								+								
Anthomastus agaricus															+	
Anthomastus cf. *canariensis*														+		
Chrysogorgia agassizi															+	

Continued

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Table 2. Continued

Species/station	40	42	44	46	50	52	54	56	60	62	64	66	68	70	72	74
area	**Azores**						**CGFZ south-east**					**CGFZ north-west**				
Mean depth, m	2961	2078	1742	3031	2600	2977	3512	1916	1263	1910	3461	3030	2350	1650	2548	3055
No. of species per station	37	21	15	19	43	27	35	15	13	9	24	26	23	37	46	7*
No. of species per area	95						70					102				
Mean No. of species per station/±SD	27.0±SD 10.95						19.6±SD 10.64					33.0±SD 10.55				
				Axial										**Axial**		
Dendrobrachia multispina				+												
Funiculina quadrangularis								+		+						
Heteropolypus cf. *insolitus*					+											
Kophobellemnon macrospinosum							+	+								
Paramuricea biscaya								+								
Pennatula phosphorea							+					+				
Scleroptilum grandiflorum					+	+										
Umbellula durissima											+					
Umbellula encrinus								+								
Umbellula thompsoni							+	+								
SCLERACTINIA[2]																
Caryophyllia ambrosia		+														+
Caryophyllia cornuformis											+					
Flabellum alabastrum			+													+
Flabellum angulare	+				+										+	
Fungiacyathus fragilis	+	+				+			+							+
Lophelia pertusa													+			
Placotrochides frustra														+		
Stephanocyathus moseleyanus			+													
POLYCHAETA																
Paradiopatra ehlersi					+											
Eunice pennata					+				+					+		
Leptoecia sp.		+														
SIPUNCULA[3]																
Golfingia anderssoni						+	+				+	+	+			
Phascolosoma agassizii agassizii						+								+		
Sipunculus norvegicus					+	+						+	+		+	
ECHIURA[3]																
Jacobia edmondsi							+				+	+			+	+
BIVALVIA																
Astarte sp.	+															
Cetoconcha sp.															+	
Cetomya tonata											+					
Cetomya sp.							+									
Cuspidaria sp.	+															
Delectopecten vitreus									+					+		
Halicardia flexuosa														+		
Limopsis tenella				+												
Policordia sp.	+														+	
Rhinoclama sp.							+				+					
GALATHEIDAE																
Munidopsis antonii					+											
Munidopsis aries												+				
Munidopsis bairdii															+	
Munidopsis bermudezi												+				
Munidopsis rostrata					+							+			+	
CIRRIPEDIA																
Catherinum recurvitergum						+									+	
Noescalpellum debile							+				+					
Poecilasma kaempferi			+													
Trianguloscalpellum regium	+															
PYCNOGONIDA																
Colossendeis colossea			+											+	+	
Colossendeis macerrima			+	+												
Colossendeis cucurbita							+	+								

Continued

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Table 2. Continued

Species/station area	40 Azores	42	44	46	50	52	54 CGFZ south-east	56	60	62	64	66 CGFZ north-west	68	70	72	74
Mean depth, m	2961	2078	1742	3031	2600	2977	3512	1916	1263	1910	3461	3030	2350	1650	2548	3055
No. of species per station	37	21	15	19	43	27	35	15	13	9	24	26	23	37	46	7*
No. of species per area	95						70					102				
Mean No. of species per station/±SD	27.0±SD 10.95						19.6±SD 10.64					33.0±SD 10.55				
				Axial										**Axial**		
Colossendeis minuta							+						+			
ASTEROIDEA[4]																
Bathybiaster vexillifer													+	+	+	
Benthopecten spinosissimus														+	+	
Benthopecten spinosus							+								+	
Caulaster cf. *dubius*													+			
Caulaster pedunculatus												+				
Cheiraster (Cheiraster) sepitus							+		+							
Dytaster grandis grandis	+			+		+										
Freyella elegans	+	+		+	+	+									+	
Hydrasterias sexradiata					+									+		
Hymenaster anomalus	+			+												
Hymenaster coccinatus													+			
Hymenaster modestus													+			
Hymenaster pellucidus				+			+								+	
Hymenaster regalis															+	
Hymenasterides mironovi														+	+	
Hyphalaster inermis							+				+	+				
Lophaster furcifer															+	
Mediaster bairdi bairdi																
Myxaster sol									+					+		
Paragonaster subtilis	+															
Pectinaster filholi													+		+	
Plutonaster agassizi notatus		+	+		+	+	+	+	+	+						
Porcellanaster ceruleus							+				+	+	+		+	
Pseudarchaster gracilis gracilis								+								
Solaster cf. *abyssicola*							+									
Styracaster armatus							+				+					
Styracaster chuni							+				+					
Zoroaster fulgens	+			+												
OPHIUROIDEA[5]																
Astrodia tenuispina					+											
Asteroschema inornatum								+								
Ophiacantha aculeata					+	+										
Ophiacantha cf. *cosmica*	+															
Ophiacantha fraterna									+				+	+		
Ophiocamax patersoni					+	+									+	
Ophiothamnus chariis									+							
Ophiactis abyssicola		+			+				+	+				+		
Ophiura irrorata				+	+	+									+	
Ophiura ljungmani	+						+					+			+	
Ophiura nitida							+						+		+	
Ophiura saurura	+	+				+										
Ophiura violainae														+		
Ophiocten hastatum		+	+												+	
Amphiophiura convexa											+					
Ophioplinthus tesselata					+		+				+				+	
Ophioplinthus pseudotessellata	+															
Ophiomusium lymani			+										+	+		
ECHINOIDEA[6]																
Aeropsia rostrata							+				+	+			+	
Araeolampas atlantica					+	+										
Echinosigra (Echinogutta) fabrefacta											+					
Echinosigra (Echinosigra) phiale											+	+	+		+	
Echinus alexandri									+					+		

Continued

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Table 2. Continued

Species/station area	40 Azores	42	44	46	50	52	54 CGFZ south-east	56	60	62	64	66 CGFZ north-west	68	70	72	74
Mean depth, m	2961	2078	1742	3031	2600	2977	3512	1916	1263	1910	3461	3030	2350	1650	2548	3055
No. of species per station	37	21	15	19	43	27	35	15	13	9	24	26	23	37	46	7*
No. of species per area	95						70					102				
Mean No. of species per station/±SD	27.0±SD 10.95						19.6±SD 10.64					33.0±SD 10.55				
				Axial										**Axial**		
Hygrosoma petersii									+							
Pourtalesia sp. nov. 2											+					
Pourtalesia sp.nov. 1													+			
Salenocidaris sp.	+	+		+	+	+										
Sperosoma grimaldii		+	+		+											
Tromikosoma koehleri	+				+	+	+					+			+	
Urechinus naresianus												+	+		+	+
Solenocystis imitans															+	
HOLOTHUROIDEA[7]																
Abyssocucumis abyssorum						+	+									
Amperima furcata	+		+			+										
Amperima rosea					+											
Bathyplotes natans								+								
Benthodytes lingua	+			+	+											
Benthodytes sanguinolenta	+						+	+			+	+	+			+
Benthodytes gosarsi	+						+									
Benthodytes typica	+	+		+	+	+	+									
Benthodytes valdiviae				+												
Benthothuria funebris	+					+	+				+	+				+
Benthothuria sp.					+											
Deima validum	+															
Gephyrothuria sp.							+				+		+		+	
Kolga sp.											+					
Mesothuria cathedralis															+	
Mesothuria maroccana	+	+			+						+					
Mesothuria sp.			+													
Molpadia musculus							+				+	+				
Molpadia sp.												+				
Oneirophanta mutabilis	+			+												
Paelopatides grisea								+		+		+	+		+	
Paroriza palens												+				
Peniagone azorica					+											
Peniagone diaphana													+			
Peniagone sp.	+															
Peniagone marecoi		+	+	+	+	+	+								+	
Peniagone longipapillata	+			+	+	+							+		+	
Penilpidia midatlantica		+														
Pseudostichopus globigerinae														+		
Pseudostichopus marenzelleri													+		+	
Psychropotes depressa	+	+		+								+		+	+	
Psychropotes longicauda	+						+									
Synallactes crucifera								+						+		
Thyone sp.												+				
Ypsilothuria talismani							+				+	+				
Zygothuria lactea			+													

percentage of species restricted to either the eastern or western side of the ridge: 38–39% of western species and 34–36% of eastern species respectively. Species found on both sides of the ridge in these two areas constituted 24% in the Azorean region and 25% south-east of the CGFZ. These results indicate that the bathyal invertebrate fauna do have some differences in their faunal composition east and west of the ridge.

The pattern was different on the transect north-west of the CGFZ where 30% of species were found east of the ridge, 24% in the west, 19% on both sides and 27% on the ridge axis. A very high percentage of species found at the ridge axis in this area is probably due to sampling bias: only one trawl conducted west of the ridge on the north-west transect was successful, the second western trawl (Station 74) suffered from technical problems and the number of species in that catch was very low (7 spp.). Therefore, the true pattern of faunal change across the ridge in this area remains unknown due to undersampling on the western side of the ridge.

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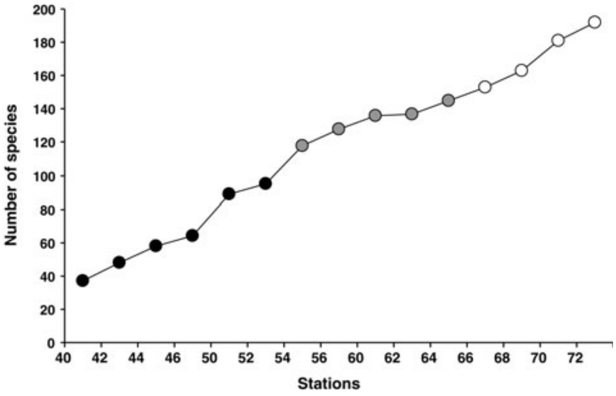

Fig. 2. Species accumulation curve. Black symbols, the Azores; grey symbols, south-east of the Charlie-Gibbs Fracture Zone (CGFZ), white symbols, north-west of CGFZ.

DISCUSSION

The MAR–ECO expedition obtained the first data on the bathyal invertebrate fauna of the Mid-Atlantic Ridge between the Azores and the Charlie-Gibbs Fracture Zone. In total 192 species of benthic fauna were identified. This number is relatively high for a limited number of trawls (16) which were not geared toward sampling invertebrates. Mironov & Gebruk (2006) report a total of 201 species from the Reykjanes Ridge from 1000 to 3000 m based on a series of Russian expeditions, though it does not include the most recent studies in this area by other programmes such as BIOICE (Tendal, 1998). These studies therefore appear to confirm that the MAR–ECO samples have undersampled the invertebrate benthic fauna species present on the MAR, and this is further confirmed by the species accumulation curve (Figure 2).

The bathyal fauna was dominated by echinoderms (49.5% of the total species number), sponges and anthozoans over all three transects. These three taxonomic groups jointly gave 84.4% of the total species number sampled. The data are in agreement with Copley *et al.* (1996) who showed that the same three taxonomic groups dominated the bathyal fauna of the northern Reykjanes Ridge: 81.2% of 101 species (identified from 102 dredge samples between 225 and 2600 m depth) were represented by sponges (38.6%), anthozoans (21.8%) and echinoderms (20.8%). However, Mironov & Gebruk (2006) present a conflicting image of the distribution of invertebrate species of the MAR. Of 201 species sampled on the Reykjanes Ridge between 1000 m and 3000 m depth by Sigsbee trawl (22 samples) and Okean grab (66 samples) the most dominant faunal group were polychaetes with 84 species (41.2% of the total number of species), followed by anthozoans (19.4%) and echinoderms (17.9%). The discrepancy in the dominance of fauna presented is most likely due to a difference in a sampling gear: the Mironov & Gebruk (2006) data were collected using a method which sampled more infauna.

Despite the opportunistic collection of these samples some taxa from this study were new to science and they have since been described. These include the genus *Solenocystis* from the

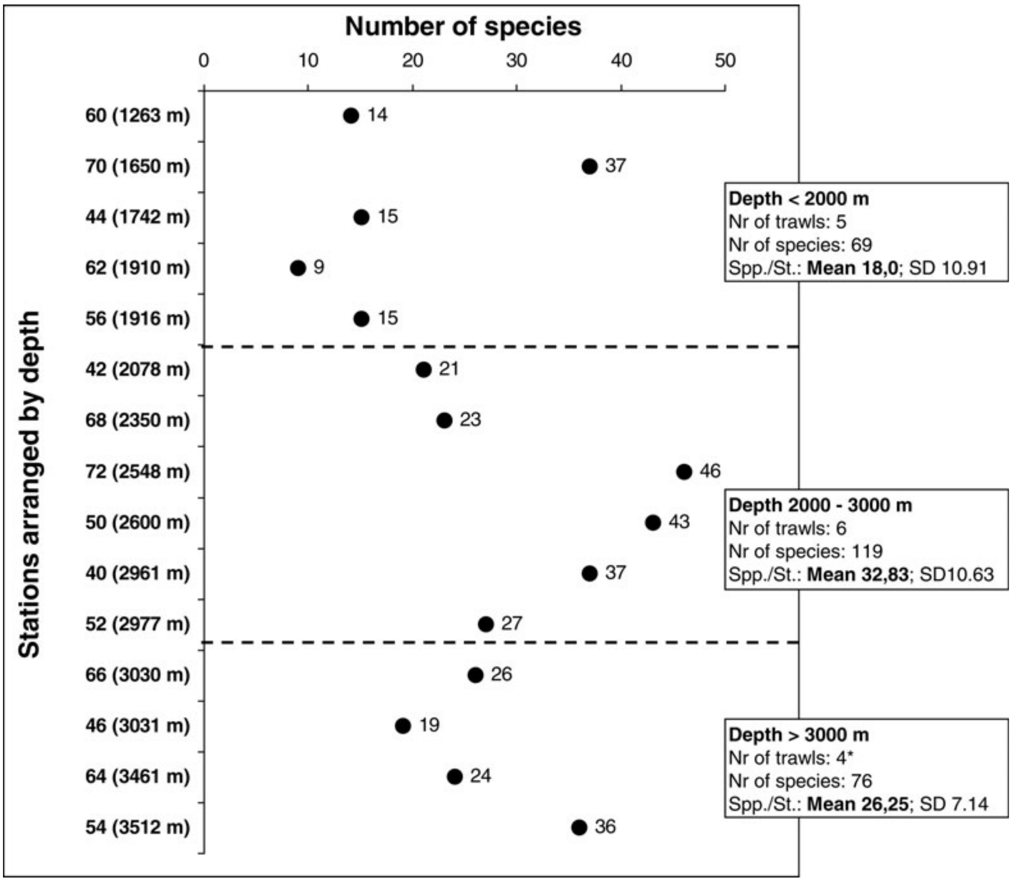

Fig. 3. Change in the number of benthic species with depth in MAR–ECO samples. *Station 74 (3055 m) excluded from analysis.

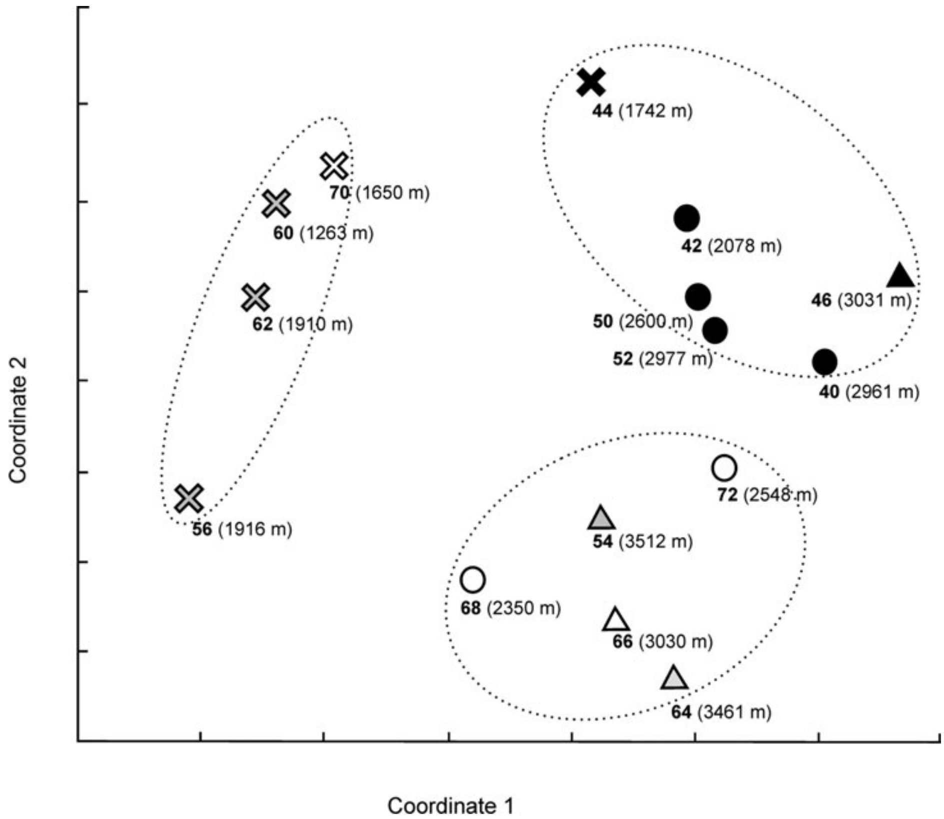

Fig. 4. Between station similarity based on non-metric multi-dimensional scaling (nMDS). Correlation matrices were generated using the Sorensen's index o presence–absence data. Symbols correspond to depth strata: crosses, stations <2000 m; circles, stations between 2000 and 3000 m; triangles, stations >3000 m. Colour of symbols corresponds to the sampling region: black symbols, the Azores; grey symbols, south-east of the Charlie-Gibbs Fracture Zone (CGFZ), white symbols, north-west of CGFZ.

echinoid family Pourtalesiidae (Mironov, 2008) and a further 15 new species, including five species of glass sponges (Tabachnik & Collins, 2008), four species of elasipodid holothurians (Gebruk, 2008), three species of ophiuroids (Martynov & Litvinova, 2008), and one species of Asteroidea (Dilman, 2008), Echinoidea (Mironov, 2008) and Echiura (Murina, 2008). The new species comprise ~8% of the total species, however, this number may increase since not all specimens in the collection have been identified to species level (Table 2).

When comparing each sampling area by species richness, the northernmost sampling region (the southern tip of the Reykjanes Ridge) had the highest species richness. The 102 species recorded in this area is relatively high for only four successful trawls compared with the 201 species reported by Mironov & Gebruk (2006) for the Reykjanes Ridge (see details above). The diversity of bathyal invertebrate fauna is known to be significantly higher on seamounts south of the Azores, e.g. Mironov & Krylova (2006) report ~400 species from the Meteor Seamount area. More comparable, quantitative samples taken along the ridge (at similar depths and with similar gear) are needed for a thorough understanding of how biodiversity changes along and across the MAR.

The peak of species number in our samples and the highest mean number of species per station occurred between 2000 and 3000 m. The mean species number was lower >3000 m compared with the 2000–3000 m depth-range, and much lower at depths <2000 m. Such a trend has been illustrated for the North Atlantic before. In the north-west Atlantic Rex (1983) reported a peak (of expected number of species) at depths 2500–3000 m. A similar trend was shown by Gage *et al.* (2000) for the Rockall Trough in the north-east Atlantic. At the same time in the Goban Spur area in the north-east Atlantic species diversity (the number of species per number of individuals) was shown to increase with increasing water depth from 200 m to 4115 m (Flach & De Bruin, 1999).

The nMDS analysis of between-station species similarity revealed differences between stations in the CGFZ area (51°N–53°N) and the Azores (42°N). The stations from the Azores formed a separate cluster to those samples from the CGFZ, which separated out by depth. The taxonomic structure of the benthic fauna supports the nMDS results with differences in the faunal composition between the Azores and the CGFZ areas. In the two transects in the CGFZ region the dominant taxonomic groups with the highest percentage of species were different, shallower and deeper than 2000 m. In contrast in the Azores area the same groups dominated both shallower and deeper than 2000 m. However, in the Azores area only one trawl was conducted shallower than 2000 m (Station 44) and the number of species at this station was low (15). North-west of the CGFZ had only one station shallower than 2000 m (Station 70), but yielded a high number of species (37). The low number of species shallower than 2000 m in the Azores area may be an artefact of insufficient sampling and therefore more samples are required to conduct rigorous analysis and draw firm conclusions as to the faunal trends present.

Overall the results of the present study point at some turnover in bathyal benthic fauna between the CGFZ and the Azores and are in agreement with the suggestion that a

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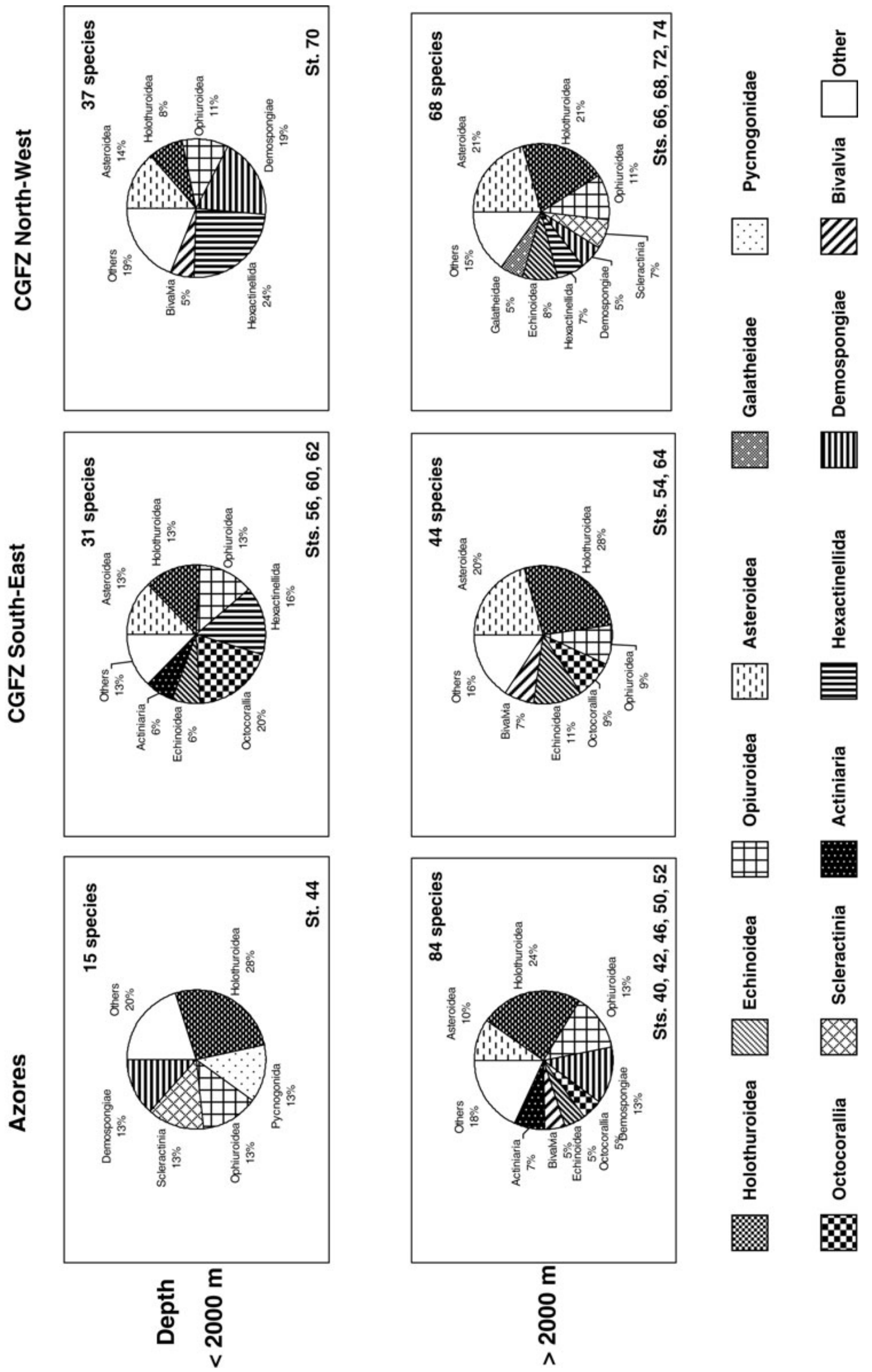

Fig. 5. Taxonomic structure shown as percentage of taxa in the three sampling areas. Stations are separated by depth; those shallower than 2000 m and those deeper than 2000 m.

biogeographical boundary exists in this area. Mironov & Gebruk (2006) speculated that a biogeographical boundary at bathyal south of the Reykjanes Ridge may correspond approximately to the position of the Sub-Polar Front. The front lies south of the CGFZ at about 51°–52°N along the northern boundary of the warm North Atlantic Current, representing a major hydrographical boundary separating cold sub-polar water from warmer Atlantic water (Søiland *et al.*, 2008). The front is a surface feature and may only directly influence near-bottom waters in the shallower areas of the MAR, however, food supply to the seafloor is likely to reflect productivity in epi- and mesopelagic layers.

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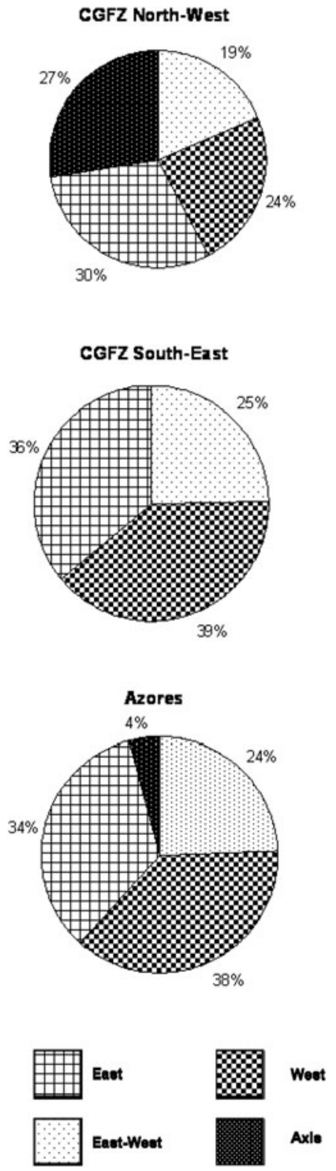

Fig. 6. Percentage of species with different patterns of distribution across the ridge (east–west division). Species indicated as axial were not found east or west of the ridge. Species found at the ridge axis and east or west of the ridge were considered as 'eastern' or 'western' correspondingly. Species observed both east and west of the axial valley are termed east–west.

Observations from leg 1 of the MAR–ECO expedition show that surface chlorophyll concentration (Gaard *et al.*, 2008), zooplankton abundance (Opdal *et al.*, 2008), and meso- and bathypelagic nekton density (Sutton *et al.*, 2008) were considerably higher in the cool waters north of and in the frontal zone compared with the warmer waters to the south. The food supply to the seafloor is therefore likely to differ between these two areas and can be an important factor controlling the composition and structure of benthic fauna. As highlighted by King *et al.* (2006) and Bergstad *et al.* (2008b) productivity and abundance patterns in the overlaying water masses are one of the most important factors structuring composition of demersal fish fauna on MAR.

In the pelagic realm, the Sub-Polar Front forms a boundary between two provinces: the Arctic and the North Atlantic Drift province (Sathyendranath *et al.*, 1995). According to Briggs (1995) at approximately 50°N there is a boundary between the Warm-Temperate and South Boreal plankton groups in the Atlantic (see also Dinter, 2001). However, further data are required to validate and investigate such a biogeographical boundary.

The two transects of stations north and south of the CGFZ were designed to examine the potential barrier effect of the fracture zone on the distribution of fauna. Results of our between-station similarity analysis did not reveal such an effect on the bathyal fauna: stations north and south from the fracture show little separation and tend to cluster according to depth (Figure 4). Notably, in all the three areas at stations deeper than 2000 m the taxonomic structure was more uniform compared to shallower stations: four classes of echinoderms (Asteroidea, Holothuroidea, Echinoidea and Ophiuroidea) dominated the species composition over all transects.

Near-bottom temperature and salinity showed very limited variation among our sampling locations, therefore, it appears unlikely that these physical factors are directly affecting the species composition. At all sites, the O_2 concentration was above levels likely to influence species presence. The highest temperature and lowest O_2 concentration was observed at the shallowest southern location (mean depth 1742 m) placed at a depth corresponding to the bottom of a pelagic oxygen minimum zone.

Our data on changes in bathyal fauna across the ridge showed that the fauna had some differences east and west from the ridge in two of the transects: the Azores and south-east of the CGFZ. The percentage of species occurring only east or only west of the ridge in these two areas was relatively high (72 and 75% respectively) and also it was very similar, indicating that the ridge may structure local faunas in the east–west direction. However, the number of trawls analysed in each area was too small to make firm conclusions. At the southern tip of the Reykjanes Ridge (north-west of the CGFZ) the pattern of change across the ridge was unclear with 27% of species found only at the ridge axis. Since only one station was taken west of the ridge, this result is most likely a sampling bias.

There were no east–west differences found for the Chaetognatha based on the MAR–ECO data (Pierrot-Bults, 2008). The demersal fish trawling data from MAR–ECO revealed some east–west differences in species composition and occurrence indicating that the ridge may act as a barrier to the east–west distribution of some species (Bergstad *et al.*, 2008b) although, as noted by the authors, they were concerned by the lack of replication.

In conclusion, results of the present work indicate presence of a biogeographical boundary in benthic fauna between the Azores and southern end of the Reykjanes Ridge, which may be the result of a change in the overlying regime of surface productivity and its export. That hypothesis could be tested by a future synthesis of MAR–ECO and ECOMAR data. The ECOMAR project (Ecosystems of the Mid-Atlantic Ridge at the Charlie-Gibbs Fracture Zone and Sub-Polar Front; www.oceanlab.abdn.ac.uk/ecomar) is a multidisciplinary consortium of UK scientists focusing on the region from 48 to 54°N on the MAR. ECOMAR, over five years from 2007 to 2011, will conduct targeted sampling of the benthic fauna (vertebrates and invertebrates) at four fixed locations on either side of the ridge at 48°N and 54°N. This project will provide additional data to determine the processes driving the biogeography of the communities found on the MAR. A further facet would be to compare this data with

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that from bathyal depths on the North Atlantic continental slopes. A synthesis study will help to gain a fuller understanding of the biogeographical patterns of bathyal benthic megafauna in the central North Atlantic.

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