Bathyal demersal fishes of Charlie Gibbs Fracture Zone region (49–54°N) of the Mid-Atlantic Ridge, I: Results from trawl surveys

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ARTICLE INFO

ABSTRACT

Demersal fishes were sampled by single-warp otter trawl (OTSB) at three sites on the Mid-Atlantic Ridge (MAR), to the northeast (NE), northwest (NW) and southeast (SE) of the Charlie–Gibbs Fracture Zone at approximately 2500 m depth. The mean abundance was 4109 fish km^{-2} (SD 3714) and biomass 897.1 kg km^{-2} (SD 842.9) compared with 1996 fish km^{-2} (SD 1497) and 721.2 kg km^{-2} (SD 387) at the same depth on the Porcupine Seabight (PSB) segment of the NE Atlantic Ocean margin from previous studies. There was no significant difference in biomass or abundance between the three sites on the MAR, nor in comparison with the ocean margin. A total of fish 22 species were recorded at the three MAR sites with evidence of highest species richness at the SE site. No unique species were found on the ridge; but there were differences in species composition between the PSB and the MAR. *Coryphaenoides brevibarbis* and *Antimora rostrata* were important at both the NE and NW trawl sites on the MAR whereas *Halosauropsis macrochir* was most important in the SE. We conclude that the MAR is an important habitat for species otherwise confined to narrow strips of appropriate depth around the North Atlantic Ocean margins. The MAR supports similar population densities to ocean margin settings but with differences in relative importance of different species between regions.

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1. Introduction

The Mid-Atlantic Ridge (MAR) lies on the spreading zone between the Eurasian and American tectonic plates, separating the Eastern and Western basins of the North Atlantic and providing an area of elevated sea floor with extensive bathydemersal habitat in an otherwise abyssal mid-ocean (Vecchione et al., 2010). The MAR represents ca. 46% of the total lower bathyal area (800–3500 m depth) in the North Atlantic making it the single most important bathydemersal habitat (Niedzielski et al., 2013) in this ocean. The demersal ichthyofauna of the MAR between the Azores and Iceland has been well studied using trawls (Bergstad et al., 2008b), long lines (Fossen et al., 2008) and baited cameras (King et al., 2006). All species found had previously been listed by Haedrich and Merrett (1988) as occurring elsewhere in the North Atlantic Ocean indicating that despite the remote mid-ocean location there are no endemic fish species on the MAR. The MAR is populated by bathyal fishes that are otherwise confined to narrow strips at their preferred depths around the ocean margins (Bergstad et al., 2012). Genetic studies on samples of several

species from the MAR and around the North Atlantic detect a general lack of structure in the populations with a high degree of connectivity across the ocean (e.g. White et al., 2009; Ritchie et al., 2013; Priede et al., 2013).

Along the MAR, differences in fish species composition have been observed in relation to latitude and depth. The Charlie Gibbs Fracture Zone (CGFZ) around 52°N has been noted as an area of latitudinal faunal change (King et al., 2006; Gebruk et al., 2009) with species reaching the northern or southern limits of their distribution. As well as the structural discontinuity of the CGFZ (Fig. 1) the Sub-Polar Front (SPF) at this latitude is where surface northern sub-arctic waters meet warmer more saline waters from the south (Opdal et al., 2008; Søiland et al., 2008) and is marked by flow of the North Atlantic current through the CGFZ (Read et al., 2010). Haedrich and Merrett (1988) concluded that distribution and abundance of deep demersal fishes are influenced by patterns of productivity in overlying waters, a finding further corroborated by Koslow (1993) who linked the distribution of fish assemblages with local circulation and regional water masses. Whereas the ocean margins may receive relatively high organic matter (OM) input as a result of upwelling and terrigenous input (van Weering et al., 2002), the MAR receives no such potential subsidies and organic matter export from the surface is no greater than in surrounding open ocean areas (Abell et al., 2013). This raises the question of comparison of bathyal fish assemblages; are

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population densities on the MAR higher or lower than at corresponding depths on the continental slopes? In this study we used replicated standard otter trawls at ca. 2500 m depth on the MAR. The trawl was equipped with bottom-contact sensors so that swept area could be determined to obtain quantitative estimates of number and biomass of fishes of different species. These were compared with previous data from the Porcupine Seabight (PSB) at 50°N at the same depth using the same fishing gear (Priede et al., 2010). Trawling was carried out at 3 stations within the marine protected area (MPA) designated by the North East Atlantic Fisheries Commission (NEAFC, 2008; O'Leary et al., 2012) Middle MAR Area for protection of vulnerable marine ecosystems (Charlie–Gibbs Fracture Zone and sub-Polar Frontal Region). The stations were near the boundaries of the MPA, two north of the CGFZ at 54°N and one to the south at 49°N (Fig. 1). This enabled comparisons to be made between north and south of the SPF/CGFZ complex as well as east and west of the axis of the MAR. These trawl studies are complementary to surveys at the same stations using baited cameras (Cousins et al., 2013) and video transects from a remotely operated vehicle (Linley et al., 2013).
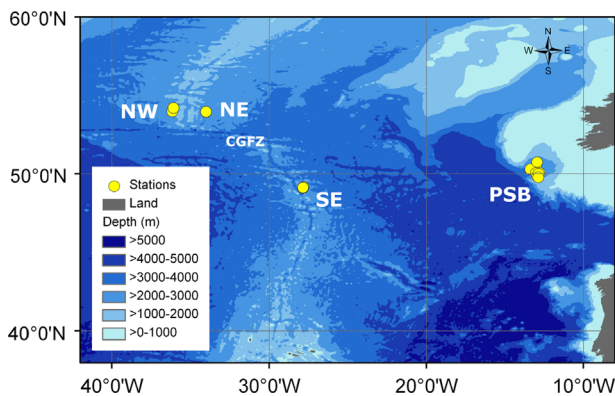

Fig. 1. North East Atlantic Ocean. Locations of trawl stations at ca. 2500 m depth on the Mid-Atlantic Ridge (NW, NE and SE) and the Porcupine Seabight (PSB). CGFZ=Charlie Gibbs Fracture Zone.

2. Materials and methods

2.1. Data collection

2.1.1. Trawl gear

A 14 m semi-balloon otter trawl (OTSB) was fished on a single warp with 120 kg otter boards; the head rope width was 4.2 m and the nominal spread of the mouth of the trawl (the width in contact with the sea floor) 8.6 m. The main area of the net had a 44 mm stretch mesh, the central part a 37 mm stretch mesh and the cod end liner a 13 mm stretch mesh (Gordon and Bergstad, 1992; Merrett and Haedrich, 1997). Acoustic telemetry provided data on the net depth and time in contact with the seabed. The distance run varied between trawls, as did haul duration, therefore data were standardised to abundance and biomass per km^{-2}. The OTSB net is generally effective at catching a wide range of species but due to its small size, limited herding abilities and slow tow speeds, highly mobile species, such as sharks, can often be poorly represented in the trawl catch (Merrett et al., 1991; Gordon et al., 1996; Priede et al., 2010).

Target sampling areas on the flanks of the MAR around 2500 m depth between 49°N and 54°N were surveyed using a Kongsberg–Simrad EM120 multi-beam sonar and OLEX real-time 3D plotting software during the R.R.S. James Cook cruise JC011 from 13th July to 18th August 2007 (Priede et al., 2013). Suitable trawl grounds on flat north–south oriented sedimentary plains located between escarpments of the terrace structure of the ridge were identified at the NW, NE and SE sites (Fig. 1). No suitable trawl ground was found west of the ridge at 49°N. A total of 12 successful trawls were conducted during cruises JC011 (2007) and during JC037 (1 August–9 September 2009) (Table 1). Trawl JC011/017 was damaged and hence excluded from quantitative analysis but provided information on species presence. For the other trawls, swept areas were estimated from the distance towed and the trawl mouth spread resulting in quantitative data from four trawls at the SE superstation, four in the NW and three in the NE.

Fish were identified to the lowest taxonomic level possible on board ship and species identifications confirmed during a subsequent taxonomic workshop aided by taxonomic texts and species lists for the region (Whitehead et al., 1984; Cohen et al., 1990; Bergstad et al.,

Table 1
Details of trawls on the Mid-Atlantic Ridge during R.R.S. *James Cook* cruises JC011 (2007). and JC037 (2009). Depths given are minimum and maximum values on the sea floor.

Station	Date	Depth (m)		Latitude	Longitude	MAR region	Area trawled (km²)
JC011/017[a]	21 Jul 07	C 2700	Start	49°14.68′N	27°42.31′W	SE	N/A
			End	49°03.43′N	27°53.86′W		
JC011/23B	22 Jul 07	2718–2734	Start	48°54.59′N	27°50.00′W	SE	0.03
	23 Jul 07		End	49°15.85′N	27°50.00′W		
JC011/075	5 Aug 07	2615–2630	Start	53°51.10′N	36°11.36′W	NW	0.05
			End	54°06.02′N	36°07.20′W		
JC011/101	10 Aug 07	2405–2435	Start	54°06.33′N	33°58.27′W	NE	0.06
			End	53°47.47′N	34°02.89′W		
JC011/106	11 Aug 07	2410–2445	Start	54°05.68′N	33°58.54′W	NE	0.05
			End	53°46.94′N	34°03.02′W		
JC011/111	12 Aug 07	2404–2430	Start	54°05.68′N	33°58.54′W	NE	0.05
			End	53°47.71′N	34°02.83′W		
JC037/015	10 Aug 09	C 2750	Start	49°05.04′N	27°50.07′W	SE	0.02
			End	49°06.84′N	27°49.84′W		
JC037/019	10 Aug 09	2754–2724	Start	49°04.64′N	27°50.66′W	SE	0.04
	11 Aug 09		End	49°07.16′N	27°50.30′W		
JC037/027	18 Aug 09	2755–2702	Start	49°04.79′N	27°50.29′W	SE	0.05
			End	49°07.86′N	27°50.51′W		
JC037/061	28 Aug 09	2598–2619	Start	54°13.04′N	36°04.07′W	NW	0.05
			End	54°09.83′N	36°05.58′W		
JC037/067	28 Aug 09	2598–2625	Start	54°13.07′N	36°04.03′W	NW	0.05
	29 Aug 09		End	54°09.96′N	36°05.49′W		
JC037/070	29 Aug 09	2604–2615	Start	54°13.00′N	36°04.08′W	NW	0.04
	30 Aug 09		End	54°10.53′N	36°05.24′W		

[a] Trawls in which no swept area measurement was possible are excluded from quantitative analysis.

2008a; Fossen et al., 2008; King et al., 2006). The weight of each fish was recorded on board ship using heave-compensated digital scales with a 0.2 g resolution (M1100, Marel, Iceland). For comparison with North Atlantic continental margin, data were abstracted from the trawl data set for the Porcupine Sea Bight (PSB) (Priede et al., 2010). PSB hauls between 2292 and 2670 m depth and during the months of June to September were selected so as to be comparable with the MAR trawl data. The PSB trawls had been conducted using the same OTSB fishing gear as was used on the MAR. Data from nine PSB hauls were included in the analysis (Table 2 and Fig. 1).

2.2. Statistical analyses

Univariate analyses were conducted using Minitab (v16, Mini-tab, UK). One-way analysis of variance (ANOVA) was used to investigate whether there were significant differences in total abundance, biomass of demersal fishes between sites. Biodiversity and species evenness were examined using the Shannon diversity index (H') and Pielou's evenness (J') (Magurran, 2004). Prior to the one-way ANOVA data were tested for equality of variance using a Levene's test and for normal distribution using an Anderson–Darling test. All data fitted the assumptions required for analysis using an ANOVA. A Tukey's range test was used for post-hoc analysis. Species accumulation curves were produced by randomising the sample order 100 times and calculating the mean species richness for each value to produce a smoothed species accumulation curve (Colwell et al., 2004). The analyses were performed using Estimate S (v8.2.0; R.K. Colwell, http://purl.oclc.org/estimates) and then plotted in Sigma Plot (v11.0).

All multivariate analyses were conducted in PRIMER (v5.0; Clarke and Gorley, 2006). Untransformed abundance data were used to investigate community structure and to reveal spatial groupings without enhancing contributions of rare or absent species. Group average cluster analysis was conducted on Bray–Curtis similarities (Bray and Curtis, 1957). Non-metric, multi-dimensional scaling (MDS) was applied to visualise clusters in 2 dimensions. MDS plots were followed by ANOSIM analysis to determine the significance of any differences between sampling regions. SIMPER was used to determine the species contributing most to the observed similarity within sampling sites and dissimilarity between sampling groups.

3. Results

3.1. The Mid-Atlantic Ridge

3.1.1. Biomass and abundance

There was no significant difference in total fish abundance between the SE, NE and NW sites ($F_{2,8}=1.97$; $P=0.201$; Fig. 2 and

Table 2
Porcupine Seabight Cruises, C516, D255, C505 and C134, C prefix refers to the R.R.S. *Challenger* and D to the R.R.S. *Discovery*. Positions are trawl start locations.

Station	Date	Depth (m)	Latitude	Longitude	Region	Area trawled (km²)
C505/1101	04 Jun 79	2230	50°32′N	13°1′W	PSB	0.08
C516/1101	21 Jul 82	2292	50°17′N	13°24′W	PSB	0.05
C516/1301	21 Jul 82	2420	50°45′N	12°58′W	PSB	0.07
C518/0501	27 Sept 83	2487	49°55′N	12°58′W	PSB	0.06
C134/13408[a]	11 Aug 97	2441	50°2′N	12°48.5W	PSB	n/a
C134/13411[a]	12 Aug 97	2567	50°2.1′N	13°2.9′W	PSB	n/a
D250/13910	21 Sept 00	2462	49°50.55′N	12°58′W	PSB	0.04
D255/14141	20 Aug 01	2567	49°59.3′N	12°53.4′W	PSB	0.05
D255/14143	21 Aug 01	2670	49°45.7′N	12°53.5′W	PSB	0.1

[a] Trawls in which no swept area measurement was possible are excluded from quantitative analysis.
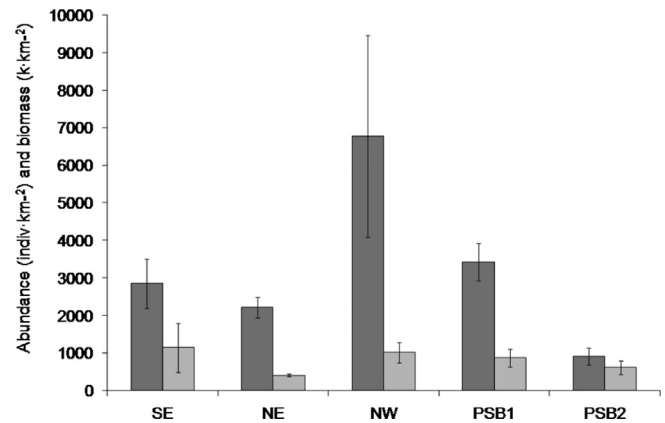

Fig. 2. Comparison of mean trawl catches at each region in terms of abundance (dark shading, individuals km^{-2}) and biomass (light shading, kg km^{-2}). Vertical bars represent standard errors. Mid-Atlantic Ridge stations (NW, NE and SE). Porcupine Seabight stations (PSB1 – early data 1979–1983 prior to commercial fishing, PSB2 – later data 2000–2001 after commercial fishing).

Table 3). There was also no significant difference in total fish biomass found between the three sites ($F_{2,8}=0.67$; $P=0.539$; Fig. 2 and Table 3). Overall mean abundance for the MAR data combined was 4109 fish km^{-2} ($\pm$ 3714 SD) and mean biomass 897.1 kg km^{-2} ($\pm$ 842.9 SD).

3.1.2. Species richness and diversity

A total of 22 individual demersal fish species were sampled on the MAR at all three sites with four taxonomic unit groupings where identifications could not be finalised (Table 3). Four species were unique to the SE, one to the NE and three to the NW, eight species occurred at all three sites. The NE was the least species rich, with only 15 species and taxonomic units; 21 species and taxonomic units, and 19 species and taxonomic units were sampled from the SE and NW sites respectively. Cumulative species richness curves (Fig. 3) indicate a clear trend of higher species richness in the SE.

Biodiversity and evenness of the three regions were measured using the Shannon diversity index (H') and Pielou's evenness (J'; Fig. 4). Significant differences at the 5% level in the H' were found between the three sites ($F_{2,8}=10.15$; $P=<0.01$). Comparison of J' values also revealed significant differences between the MAR sampling sites ($F_{2,8}=10.14$, $P=<0.01$). Tukey's post-hoc analysis showed that the differences were between the SE and the NW site for both H' and J'. The SE site has the highest mean H' and J' values and the NW has the lowest (Fig. 4).

In terms of abundance several species contributed to a high proportion of the SE catch; *Halosauropsis macrochir*, *Polyacanthonotus challengeri*, *Histiobranchus bathybius*, *Alepocephalus agassizii*, *Coryphaenoides armatus*, *Coryphaenoides brevibarbis* and *Antimora rostrata* (Table 3). Both the NE and NW had notably high numbers of three species *C. armatus*, *A. rostrata* and *C. brevibarbis*. *Coryphaenoides brevibarbis* was particularly numerous at the NW site (Table 3). The Macrouridae dominated abundance at all MAR sites (Fig. 5). In the SE there was a significant contribution to biomass from the Ophidiidae, Macrouridae and Moridae, particularly from some large *Spectrunculus* specimens, *C. armatus* and *A. rostrata* (Table 3; Fig. 6). At the northern sites most of the total biomass consisted of *A. rostrata*, *C. armatus* and *C. brevibarbis* (Table 3). Rarer species contributed diminutive proportions to the abundance and biomass (Table 3). *Coryphaenoides armatus*, *C. brevibarbis* and *A. rostrata* were the only species found in consistently high numbers across all sites and no significant differences in biomass or abundance between sites were found (*C. armatus*, abundance,

Table 3
Comparison of species composition of trawl samples from the Mid-Atlantic Ridge and the Porcupine Seabight. Mean abundance (indiv. km^{-2}) and wet-weight biomass (kg km^{-2}) of individual species at each site (transformed data), with SD in parentheses.

| Area	MAR summary						PSB summary	
	SE station mean		NE station mean		NW station mean		PSB mean	
Mean depth (m)	2736		2422		2614			
Swept area (km^2)	0.035		0.053		0.045		0.064	
Species	Abun. (fish km^{-2})	Biomass (kg km^{-2})	Abun. (fish km^{-2})	Biomass (kg km^{-2})	Abun. (fish km^{-2})	Biomass (kg km^{-2})	Abun. (fish km^{-2})	Biomass (kg km^{-2})
Harriotta sp.					16 (22)	0.42 (0.55)		
Bathyraja richardsoni			6 (10)	17.99 (31)			4 (7)	6.03 (14)
Halosauropsis macrochir	744 (117)	71.24 (21)			109 (28)	27.59 (4)	164 (239)	25.26 (36)
Notacanthus bonaparte	8 (17)	0.57 (1)					6 (10)	0.33 (0.33)
Polyacanthonotus challengeri	93 (139)	6.66 (8)			6 (13)	0.51 (1)	4 (9)	0.29 (0.77)
Histiobranchus bathybius	195 (339)	128.39 (218)	6 (11)	3.20 (5)	6 (13)	1.53 (3)	38 (84)	23.83 (52)
Ilyophis brunneus							5 (7)	0.14 (0.26)
Synaphobranchus kaupii	8 (17)	0.17 (0.35)	18 (18)	2.88 (3)			114 (291)	7.99 (21)
Alepocephalidae spp.	8 (17)	7.63 (15)	6 (10)	0.50 (0.87)	11 (12)	7.45 (15)		
Alephocephalus agassizii	247 (212)	31.26 (24)	60 (21)	44.35 (48)	18 (24)	10.21 (13)	6 (12)	6.67 (11)
Alephocephalus australis	53 (41)	34.06 (43)			23 (26)	21.56 (36)		
Alephocephalus bairdii					11 (23)	0.32 (0.64)		
Alephocephalus productus			12 (21)	4.30 (7)	5 (10)	2.24 (4)	12 (23)	8.06 (14)
Alepocephalus rostratus							16 (21)	12.05 (15)
Bathylaco nigricans							3 (8)	3.07 (8)
Bathytroctes macrolepis	5 (10)	0.02 (0.05)						
Bathytroctes microlepis							22 (37)	3.24 (5)
Narcetes stomias					10 (20)	9.59 (19)	18 (24)	20.16 (27)
Conocara macropterum							1 (4)	0.30 (0.79)
Conocara murrayi	5 (10)	0.31 (0.62)					86 (80)	10.57 (7)
Bathysaurus ferox	43 (43)	15.28 (16)	18 (18)	8.03 (9)	10 (12)	10.27 (12)	16 (13)	20.54 (18)
Coryphaenoides armatus	383 (319)	145.12 (170)	140 (104)	38.02 (34)	106 (66)	65.71 (40)	111 (211)	27.18 (46)
Coryphaenoides brevibarbis	436 (107)	17.45 (7)	1519 (399)	96.36 (35)	5748 (5407)	263.79 (269)	66 (107)	1.62 (3)
Coryphaenoides carapinus	125 (96)	8.24 (7)			86 (74)	0.92 (0.95)	18 (47)	2.40 (6)
Coryphaenoides guentheri							725 (967)	68.17 (94)
Coryphaenoides leptolepis	73 (52)	18.77 (9)	12 (10)	1.37 (2)	36 (26)	18.65 (15)		
Coryphaenoides mediterraneus	5 (10)	1.64 (3)	18 (18)	10.90 (10)	15 (30)	0.04 (0.07)		
Juvenile Macrouridae	37 (48)	0.23 (0.4)	84 (75)	0.79 (1)	6 (11)	0.04 (0.07)		
Unidentified Macrouridae	75 (96)	8.82 (17)	30 (21)	1.22 (1)	11 (12)	0.03 (0.04)		
Antimora rostrata	246 (155)	234.97 (148)	188 (39)	144.47 (44)	546 (325)	574.87 (437)	397 (187)	407.41 (256)
Lepidion eques							2 (5)	0.00 (0.00)
Cataetyx laticeps							10 (15)	1.01 (1.59)
Spectrunculus spp.	63 (125)	410.61 (821)	6 (11)	7.39 (13)				
Spectrunculus grandis	5 (10)	3.54 (7)					145 (95)	62.76 (47)
Lycodes terraenovae							4 (9)	0.11 (0.28)
Pachycara crassiceps							3 (8)	2.06 (5)
Total	2849 ($\pm$1312)	1144.40 ($\pm$1316)	2124 ($\pm$473)	408.45 ($\pm$62)	6781 ($\pm$5377)	1015.7 ($\pm$543)	1996 ($\pm$1497)	721.23 ($\pm$378)
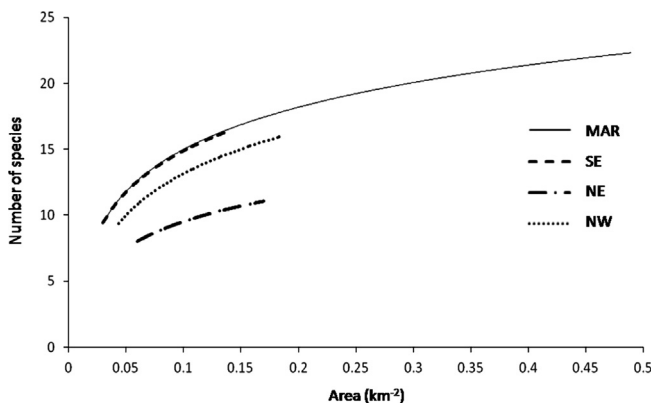
Fig. 3. Species richness on the Mid-Atlantic Ridge. Species accumulation curves calculated based on area of seabed sampled by trawls at each of the super-stations (NW, NE and SE). MAR – combined data for all stations.
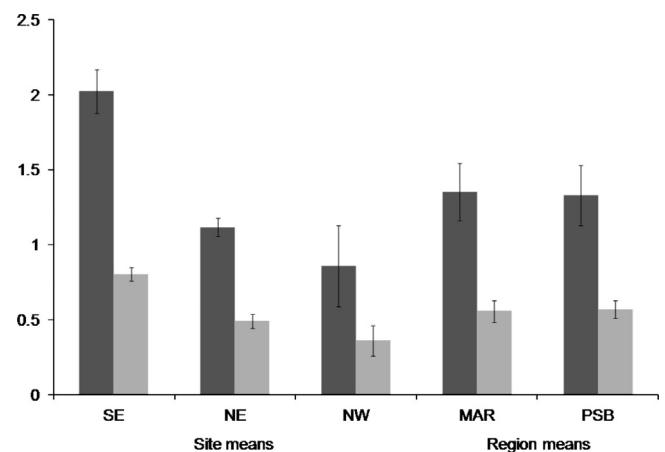

Fig. 4. Comparison of biodiversity on the Mid-Atlantic Ridge (NW, NE, SE and MAR) and the Porcupine Seabight (PSB). Shannon diversity index (H') – dark shading. Pielou's evenness (J') – light shading. Vertical bars represent standard errors.
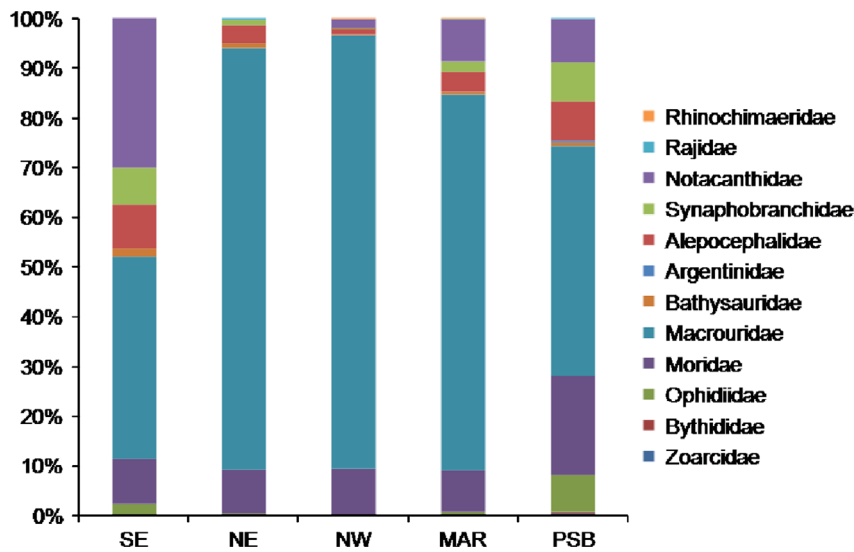
Fig. 5. Numerical percentage catch composition by family on the Mid-Atlantic Ridge (NW, NE, SE and MAR) and the Porcupine Seabight (PSB).
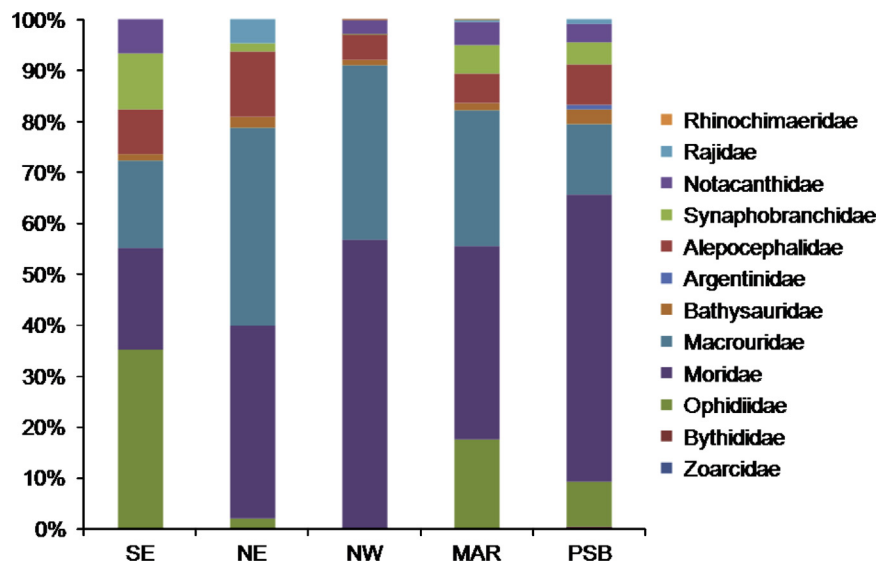

Fig. 6. Biomass percentage catch composition by family on the Mid-Atlantic Ridge (NW, NE, SE and MAR) and the Porcupine Seabight (PSB).

$F2,8=2.09$, $P=0.187$; biomass $F2,8=0.96$ $P=0.422$; *C. brevibarbis*, abundance $F2,8=2.81$, $P=0.119$, biomass $F2,8=2.28$, $P=0.165$; *A. rostrata*, abundance $F2,8=2.46$, $P=0.147$ biomass $F2,8=2.47$, $P=0.146$).

MDS plots of untransformed species abundance and ANOSIM analysis show significant spatially explicit groupings between the SE and both the northern sites (Fig. 7 and Table 4). The northern sites are not significantly spatially distinct from each other (Fig. 7 and Table 4).

SIMPER analysis identified *H. macrochir* and *C. brevibarbis* as contributing 63.26% of the within group similarity for the SE site with *C. armatus* and *Al. agassizii* also typifying the community (Table 5). In the NW and NE sites *C. brevibarbis* and *A. rostrata* are the main species contributing to the within group similarity ($>85\%$ for both sites respectively; Table 5). SIMPER analysis can also be used to identify the species contributing to the between group dissimilarity. SIMPER analysis identified *C. brevibarbis* and *Halosauropsis macrochir* as the two main contributing species to the dissimilarity between the SE and both northern sites (Table 6).

3.2. Comparisons between the MAR and PSB

3.2.1. Biomass and abundance

The PSB were separated into two groups PSB1 included trawls taken between 1979 and 1983 (trawls D505/1101, C516/1101, C516/1301 and C518/0501) and PSB2 from 2000 and 2001(trawls D250/13910, D255/14141 and D255/14143). A significant difference in abundance was found ($F1,5=25.88$; $P=0.004$), but no significant difference in biomass ($F1,5=0.74$; $P=0.429$) was detected between PSB1 and PSB2. Therefore there had been significant change in abundance between the two time periods. The PSB data were treated as two separate groupings for comparison with the MAR data. Overall mean abundance was 918 fish km^{-2} (±443 SD) for PSB1 and 3433 fish km^{-2} (±868 SD) for PSB2. Mean biomass values were 612.5 kg km^{-2} (±372 SD) for PSB1 and 866.2 kg km^{-2} (±406.5 SD) for PSB2.

No significant differences between the MAR and PSB1 and PSB2 were found for abundance ($F2,15=1.60$; $P=0.234$) or for biomass ($F2,15=0.23$; $P=0.796$). MDS plots of untransformed individual species abundance data show differences between the MAR and
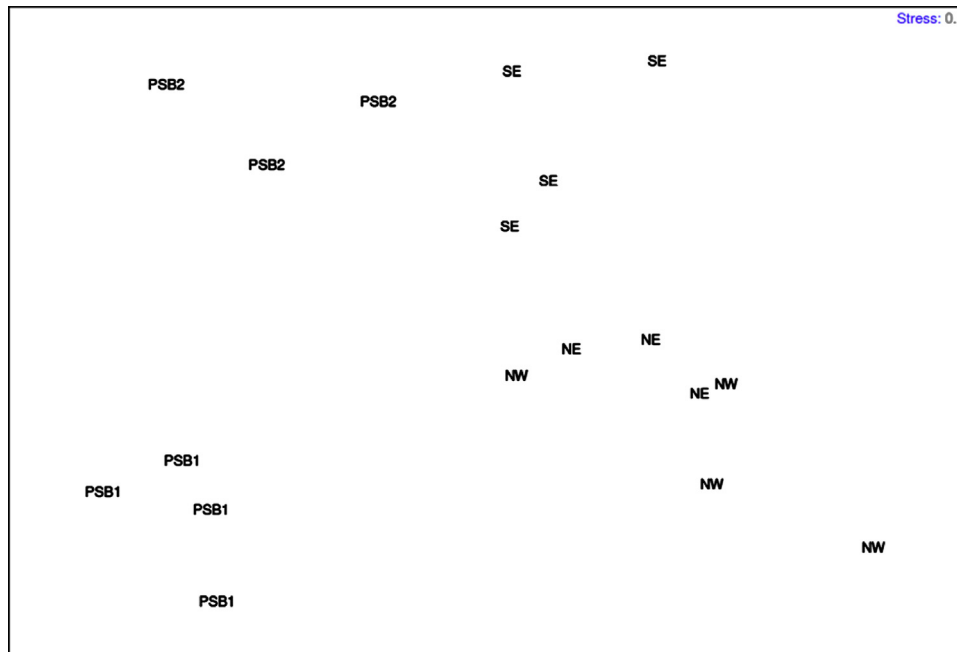
Fig. 7. Multidimensional scaling (MDS) plot of untransformed species abundance data for the Mid-Atlantic Ridge stations (NW, NE and SE) and Porcupine Seabight stations (PSB1 – early data 1979–1983 prior to commercial fishing, PSB2 – later data 2000–2001 after commercial fishing).

Table 4
Pairwise comparisons of demersal fish community similarities between different sampling regions (untransformed abundance data). *R* statistic and *P* values generated from ANOSIM analysis.

Region pair	*R* statistic	*P* value
SE, NW	0.823	0.029*
SE, NE	0.944	0.029*
NW, NE	0.241	0.20
NE, PSB1	1.0	0.029*
NE, PSB2	1.0	0.10
NW, PSB1	0.969	0.029*
NW, PSB2	0.963	0.029*
SE, PSB1	1.0	0.029*
SE, PSB2	0.944	0.029*
PSB1, PSB2	1.0	0.029*

*indicates a significant difference where p < 0.05.

Table 5
SIMPER analysis results showing the species contributing to within-group similarity for the MAR regional sites and PSB temporally explicit samples. Species contributing to > 90% of the cumulative similarities are listed.

Superstation/ region	Untransformed abundance data		
	Species	Av. abundance	Contribution %
SE	*Halosauropsis macrochir*	744.25	40.22[a]
	Coryphaenoides brevibarbis	435.50	23.04[a]
	Coryphaenoides armatus	383.25	11.39[a]
	Antimora rostrata	245.75	7.98
	Alepocephalus agassizii	246.50	6.66[a]
	Coryphaenoides carapinus	125.00	3.33
NW	*Coryphaenoides brevibarbis*	5748.00	78.09[a]
	Antimora rostrata	546.25	12.37
NE	*Coryphaenoides brevibarbis*	1518.67	77.75[a]
	Antimora rostrata	188.00	10.11[a]
	Coryphaenoides armatus	140.00	4.53[a]
PSB1	*Antimora rostrata*	445.50	77.42[a]
	Spectrunclus grandis	150.00	15.86
PSB2	*Coryphaenoides guentheri*	1691.67	60.55[a]
	Halosauropsis macrochir	381.67	11.44[a]
	Antimora rostrata	333.33	9.99[a]
	Conocara murrayi	143.33	4.11[a]
	Coryphaenoides brevibarbis	155.00	3.71
	Coryphaenoides armatus	260.00	3.44

[a] Species with dissimilarity/SD > 1.5. These are species which typify the group.

the PSB (Fig. 7). A separation also appears between the PSB1 and PSB2 datasets. ANOSIM results reveal that PSB1 and PSB2 are significantly spatially distinct from the SE and NW sites and also from each other (Table 4). The NE was found to be significantly different from PSB1 but not from PSB2 (Table 4). In terms of the SIMPER analysis the species which typify the PSB1 and PSB2 groups are different. *Antimora rostrata* accounts for most of the within group similarity in the PSB1 group, whereas for PSB2 *A. rostrata*, *Spectrunculus grandis*, *Alepocephalus rostratus* and *C. guentheri* are determined as the species typifying the within-group similarity (Table 5). There are many species which contribute to the dissimilarity between the MAR sites and the PSB1 and 2 groups; however *C. brevibarbis* are consistently identified as a discriminating species (Table 6).

Fig. 8 shows the biomass estimates for demersal fish on the MAR at 2500 m depth from the present study compared with previously recorded values of mean total biomass from the NE Atlantic, including the PSB, using the same gear type (Godbold et al., 2013; Gordon and Bergstad, 1992; Massutí et al., 2004;

Merrett et al., 1991). The fitted trend line takes the form:

$$Log_{10} B = 3.479 - 0.0002635d \quad R^2 = 0.161$$

where *B* is the trawled biomass (kg km^{-2}) and *d* is the depth (m).

3.2.2. Spatial biodiversity

Thirty-two species were caught across both the MAR and the PSB, with four taxonomic groupings where identifications could not be finalised; 26 species were caught on the PSB over seven

Table 6
Percentage contribution of discriminating species to dissimilarities between different regions of the Mid-Atlantic Ridge and temporally explicit Porcupine Seabight (PSB) samples (untransformed abundance data). Species contributing up to 90% of the cumulative dissimilarities are listed. [*]

Species	SE vs. NW	SE vs. NE	NW vs. NE	SE vs. PSB1	NW vs. PSB1	NE vs. PSB1	SE vs. PSB2	NW vs. PSB2	NE vs. PSB2	PSB1 vs. PSB2
A. rostrata	5.92	4.27[a]	9.06	7.97	5.56	9.86[a]	4.3	4.03	2.9	6.35
Al. agassizii	3.67	5.04		6.40[a]		2.02[a]	5.26[a]			
C. armatus	4.63	7.17	2.34	10.63[a]		5.40[a]	6.6	2.8	4.31	6.66
C. brevibarbis	61.65[a]	34.44[a]	73.38[a]	15.16[a]	75.04[a]	58.75[a]	7.25[a]	54.45[a]	29.67[a]	4.22[a]
C. carapinus		3.69	2.77	3.61	2.25		2.46			
C. guentheri							40.24[a]	23.53[a]	36.52[a]	49.20[a]
C. leptolepis				2.10[a]			1.60[a]			
Con. murrayi							3.37[a]	2.04	3.18[a]	3.11
H. macrochir	11.44[a]	24.59[a]	2.94[a]	25.13[a]	2.29[a]		9.04[a]	3.84	8.32[a]	11.20[a]
Histiobranchus bathybius	2.76	4.71		4.31			4.48		1.88	2.56
Juvenile macrourids		2.31				3.06			1.77	
P. challengeri		2.39		2.27			1.74			
S. grandis				4.71	3.13	5.69	2.99		2.82[a]	3.02
Synaphobranchus kaupii				5.82	3.71	6.88				5.24
Unidentified macrourids		2.41		2.21			1.68			

[a] Species with dissimilarity/SD > 1.5. These are good species for discriminating between groups.
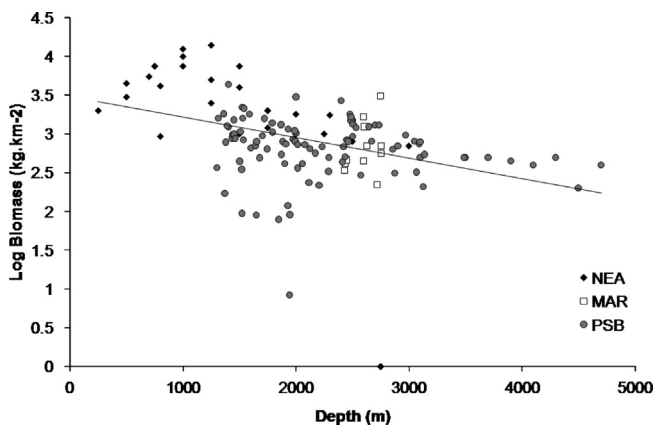

Fig. 8. Demersal fish biomass in the North East Atlantic. MAR – Mid-Atlantic Ridge data from the present study. PSB – Porcupine Seabight data from Godbold et al. (2013). NEA – North East Atlantic from Merrett et al. (1991), Gordon and Bergstad (1992) and Massutí et al. (2004). The trend line is fitted to the entire data set.

trawls (0.45 km^{-2}), compared to the 22 species and four unidentified groups caught on the MAR over 11 trawls (0.48 km^{-2}). Nine species were found only on the PSB and six only on the MAR (excluding the unidentified groups), the remaining species were sampled at both sites (Table 3). *Synaphobranchus kaupii*, *A. rostrata*, *C. armatus* and *C. guentheri* were found in high numbers on the PSB, with *H. macrochir* being found in high numbers on both the MAR and PSB. There were no significant differences in H' or J' between the MAR and PSB1 and PSB2 (H', $F2,15 = 1.1$; $P = 0.359$; J', $F2,15 = 0.32$, $P = 0.734$).

4. Discussion

The present study shows that at lower bathyal depths around 2500 m there is no significant difference between the MAR and the NE Atlantic continental slopes of the PSB in terms of overall mean abundance and biomass of demersal fishes. This is contrary to the findings of Bergstad et al. (2012) who found elevated fish biomass on the MAR compared to other regions. However their study compared data from different types of trawls in which standardisation by swept area may not have eliminated all uncertainties in comparison (Gordon, 1986). Bergstad et al. (2012) also speculated that biomass on the continental slopes may be relatively depleted compared with the MAR. Given the absence of enhanced pelagic to benthic flux of organic carbon over

the MAR (Abell et al., 2013; Priede et al., 2013) elevated fish biomass over the MAR for resident demersal species seems unlikely although migratory pelagic species are certainly attracted to summits of sea mounts (Morato et al., 2010).

Our study shows clear differences in the PSB between the years prior to significant commercial exploitation and more recent sampling in terms of abundance and species composition. There appears to have been a switch to more numerous smaller fishes. These changes may be related to the effects of commercial fishing described by Bailey et al. (2009) and Godbold et al. (2013). It is evident that care must be taken with speculating on ecological explanations of differences in fish assemblages when exploitation may be a compounding factor. Nevertheless we conclude that fish biomass on the MAR is broadly similar to that on the ocean margins at similar depths and this is confirmed by the good fit of our data to the general trend for the North East Atlantic Ocean (Fig. 8).

We detected no significant differences in the biomass or abundance of demersal fishes between sites north of the CGFZ and to the south. Although the sub-polar front is regarded as the boundary between predominantly cold productive waters to the north (NE and NW stations) and warmer oligotrophic regions to the south (SE station) (Longhurst, 1998) the frontal region itself is very complex with numerous eddies containing patches of high productivity (Vecchione et al., 2010) so that resultant export flux from the surface is similar at the northern and southern stations. Abell et al. (2013) found no significant differences in organic carbon export flux in sediment traps at 2400 m at the three stations, NE 1.2 g m^{-2} yr^{-1}, NW 0.8 g m^{-2} yr^{-1} and SE site 1.1 g m^{-2} yr^{-1} with large inter-annual variability.

MDS plots of species abundance revealed spatially explicit groupings between the MAR sites (Fig. 7). The northern sites were dominated by the presence of *C. brevibarbis* which constituted over 70% of the catch at both sites; accounting for most of the reduced species evenness and diversity compared to the south. No significant difference in species composition was found cross ridge between the NE and NW sites; with both sites characterised by *C. brevibarbis* and *A. rostrata*. Bergstad et al. (2008a) also caught high numbers of *C. brevibarbis* and *A. rostrata* at similar depths in their northern study sites and described them as a representative species of the northern MAR. Previous baited camera and trawling studies on the MAR have shown spatially explicit groupings on the MAR using MDS analysis which was attributed to depth and latitude, and ultimately overlying water mass characteristics (King et al., 2006; Bergstad et al., 2008a,b, 2012).

No endemic species were found on the MAR. The SE was shown to be the most diverse, and had the highest species evenness of

the three sites. High diversity in the southern regions of the MAR is in agreement with Bergstad et al. (2008a). The calculated mean values were similar for the NE (1.1) but lower for the NE (0.9) which are in the same range as those indicated by Fossen et al. (2008) for the CGFZ at 2500 m depth.

No significant difference in Shannon diversity index was found between the MAR and PSB at 2500 m in agreement with Bergstad et al. (2012) who found that MAR fish species assemblages are most similar to those from the eastern North Atlantic slopes and rises. Bergstad et al. (2012) also found no unique species to the MAR between 2251 and 3000 m.

The proportion of individual species contributing to total abundance and biomass differed between the MAR and PSB. More than 50% of the abundance of the MAR catch was composed of *C. brevibarbis*, which made up only a small proportion of the PSB catch and contributed significantly to the dissimilarity between the MAR and the PSB sampling regions. There were also other species which were more common on the PSB than on the MAR. Bergstad et al. (2012) state that despite the high species similarity between the MAR and the Eastern North Atlantic that the change of fish assemblage with depth is different between the two regions, indicating that different groups of fish may be dominant at similar depths. In terms of biomass, both sites had high proportions of their catch made up of Moridae and Macrouridae. In particular *A. rostrata* contributed significantly; approximately 56% of the PSB and 37% of the MAR. High abundances of *A. rostrata* at baited cameras on the MAR have previously been reported by King et al. (2006).

5. Conclusion

The MAR and PSB support similar abundances and biomasses of demersal fish species at lower bathyal depths but with significant differences in the species assemblages mainly in terms of relative abundances of the same species. The variation between MAR sites in species diversity indicates that the fish assemblages are most likely influenced by local heterogeneity in overlying hydrographic regime, physical habitat and food supply (King et al., 2006; Mortensen et al., 2008; Opdal et al., 2008; Bergstad et al., 2012).

Acknowledgments

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