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Bathyal demersal fishes of Charlie-Gibbs Fracture Zone region (49–54°N) of the Mid-Atlantic Ridge: II. Baited camera lander observations

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A B S T R A C T

Demersal fishes appearing at baited cameras at 2500 m depth either side of the axis of the Northern Mid-Atlantic Ridge (MAR) at 54°N and 49°, north and south of the Charlie Gibbs fracture Zone respectively, showed significant differences in species composition between north and south. A total of 19 taxa were observed, with *Hydrolagus affinis*, *Bathyraja richardsoni*, *Halosauropsis macrochir*, *Histobranchus bathybius*, *Synaphobranchus kaupii*, *Coryphaenoides armatus*, *Corphaenoides brevibarbis*, *Coryphaenoides mediterraneus/leptolepis*, *Antimora rostrata* and *Spectrunculus crassa* occurring at all locations. The total species assemblage comprised 40% of species captured by trawl at the same locations indicating a high proportion of scavenging species on the MAR. The most abundant was *C. armatus* showing shorter arrival times and larger body size in the north, suggestive of higher population density and higher food availability. The next most abundant species *A. rostrata* however showed faster arrival in the south but larger size in the North. No differences could be discerned between stations at the same latitude east and west of MAR axis.

1. Introduction

The Mid-Atlantic Ridge (MAR) is the most significant topographical feature in the North Atlantic Ocean providing extensive bathydemersal habitat in an otherwise abyssal central North Atlantic basin (Niedzielski et al., 2013). Demersal fish community composition on the MAR has been extensively explored using trawls (Bergstad et al., 2008), long lines (Fossen et al., 2008) and baited cameras (King et al., 2006) over wide latitudinal and depth ranges. Depth and latitude were consistently found to be the primary determinants of species composition at any given location (Bergstad et al., 2008, Fossen et al., 2008, King et al., 2006).

The Charlie-Gibbs Fracture Zone (CGFZ) traverses the MAR at approximately 52°N representing a major discontinuity in the structure of the MAR (Searle, 1981). The CGFZ comprises two transverse canyons, 10–20 km wide in which the sea floor extends to over 4 km depth, but also the ridge axis is displaced ca. 150 km eastwards in the south relative to the north. The CGFZ allows water to circulate between the eastern and western North Atlantic basins (Read et al., 2010, Miller et al., 2013). Above the CGFZ is the Sub-Polar Front (SPF), where northern, sub-arctic waters meet warmer more saline waters from the south (Opdal et al., 2008; Søiland et al., 2008). The frontal region is highly complex (Vecchione et al., 2010) and using satellite remote sensing Miller et al. (2013) show that to the north of the CGFZ conditions are relatively uniform whereas to the south where branches of the North Atlantic Current cross the MAR there is a high frequency of thermal fronts. This combination of topographic and hydrographic discontinuities may result in biogeographic barriers to species distribution. At the CGFZ/SPF region there is evidence of high species turn-over as fauna reach the northern and southern limits of their distribution (King et al., 2006; Gebruk et al., 2009). Bergstad et al. (2012) found that demersal fish within the North Atlantic are broadly distributed in relation to regional circulation and watermass characteristics. A general latitudinal faunal divide at 48–52°N in deep demersal fish assemblages in the North Atlantic Ocean has been proposed by Hariede and Garnes (2001) and King et al. (2006) showed that for scavenging species on the MAR this divide narrows to 50–52°N, potentially implicating a functional barrier in the region of the CGFZ. In addition to these latitudinal differences, Haedrich and Merrett (1988) found significant differences in deep demersal fish assemblages between the eastern and western North Atlantic Ocean. Whilst many species are common to both regions the pattern of occurrence at different depths is variable. The MAR may act as a demarcation zone between western and eastern faunas particular since the shallow crest of the ridge could act as a barrier to movement of deeper-living fish species.

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The primary aim of the present study was to investigate the diversity of scavenging (defined as bait-attending) demersal fishes on the MAR in CGFZ/SPF region. Sampling was conducted using replicated baited lander deployments over several years at bathyal depths distributed between four regional sampling sites; two at 54°N, and two at 49°N. In order to elucidate fine scale latitudinal and longitudinal differences species composition, behaviour and abundance we have sampled at a single depth stratum close to 2500 m. Baited underwater cameras are increasingly used for fishery surveys (Stobart et al., 2007) since they can be used in habitats not accessible by trawl, cause no damage to vulnerable benthic habitats and do not deplete fish populations. In particular in this study it was possible to deploy landers at the SW ECOMAR site where trawling was not possible (Cousins et al., 2013).

2. Material and methods

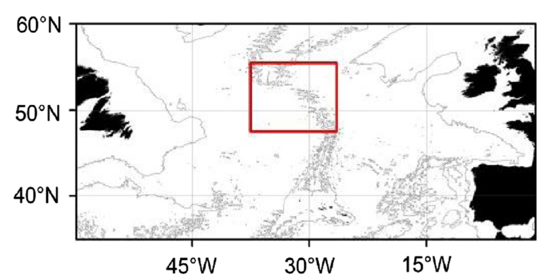
Data were collected during three ECOMAR cruises on board the RRS *James Cook* (JC011, 13th July–19th August 2007, JC037, 1st August–9th September 2009, JC048, 26 May–3 July 2010) at four sample sites between 48°N and 54°N (Fig. 1) designated as SE, SW, NE and NW. A total of 19 deployments were conducted six at the SE site, three at the SW, five at the NW and five at the NE stations (Table 1).

The Photographic and Acoustic Lander (PAL) was equipped with a downward-facing digital stills camera (OE14-208, 5.0 megapixel; Kongsberg Maritime, Norway), a flash unit (OE11-242; Kongsberg Maritime; Norway), and a twin acoustic ballast release system (OCEANO 2500 Universal AR and RT; IXSEA, France). During the JC011 and JC037 cruises PAL was also fitted with a 300 kHz Sentinel ADCP (RDI Teledyne, USA), and a conductivity, temperature and depth unit (SBE 37; SeaBird Electronics, Inc. USA). The camera was programmed to take digital photographs at 60 s intervals from a height of 2 m above the seafloor, with the ballast, bait (500 g mackerel *Scomber scombrus*) and reference cross (1 m × 1 m marked at 10 cm intervals) in the centre of the field of view. Ribbons were attached to the end of each arm of the scale cross to visually corroborate current direction.

The mean number of images per deployment was 1771, varying between 509 and 3028 corresponding to time lapse imagery durations of 29.5 h, 8.4 and 50.5 h respectively. Fish attending the bait were identified to the lowest possible taxonomic level using morphological characteristics visible in the images. Voucher specimens caught at the SE, NE and NW stations using the OTSB14 trawl system were used to verify identification (Cousins et al., 2013). Arrival time of the first individual (t_{arr}), maximum number of fish present in the field of view (N_{max}) and percentage of frames with visible fish were recorded for each species (Table 2).

3. Estimation of abundance

Abundances of *Coryphaenoides armatus* and *Antimora rostrata* were calculated using the methods outlined in Priede et al. (1990), which require estimates of velocity of the water flow (V_w) dispersing



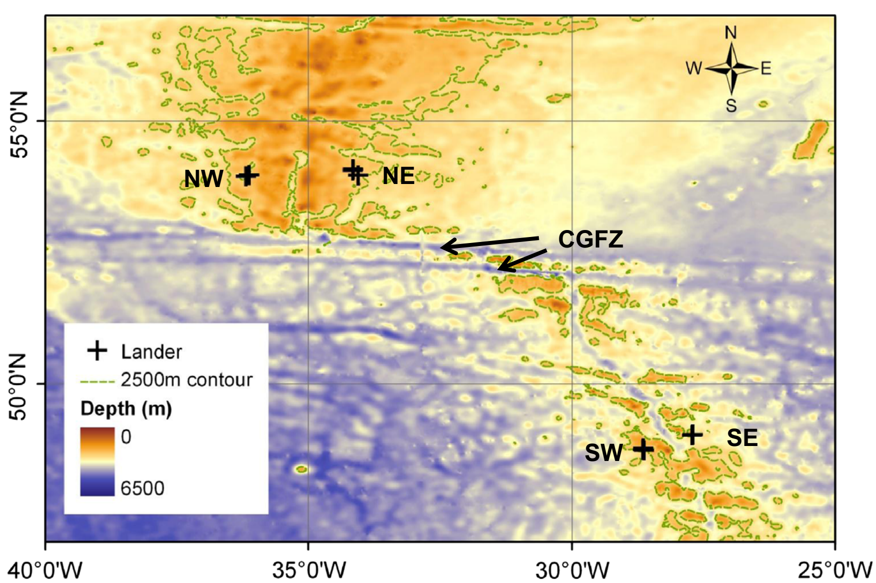


Fig. 1. Chart of the North Atlantic Ocean showing the Charlie-Gibbs Fracture Zone area of the Mid-Atlantic Ridge. Upper panel – the North Atlantic Ocean basin with study area indicated by the red rectangle. Lower panel – Detail of the Charlie-Gibbs Fracture Zone area with lander locations indicated at the NW, NE, SW and SE sites. CGFZ – arrows indicate the two main canyons of the fracture zone. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1
Photographic and Acoustic Lander (PAL) deployment summary for RRS *James Cook* cruises JC011, JC037 and JC048.

Cruise	Station #	Region	Latitude (N)	Longitude (W)	Deployment date	Touchdown time (GMT)	Depth (m)	Deployment duration (hh:mm)
JC011	11	SE	49°02.02′	27°42.15′	19/07/2007	21:28	2512	22:03
	22	SE	49°02.00′	27°42.11′	22/07/2007	13:00	2546	27:58
	73	NW	53°56.85′	36°11.59′	04/08/2007	17:20	2573	26:02
	83	NW	53°56.86′	36°11.47′	06/08/2007	22:03	2567	16:48
	97	NE	54°05.26′	34°09.24′	09/08/2007	13:44	2500	47:37
	115	NE	54°03.37′	34°09.47′	12/08/2007	18:48	2482	21:30
JC037	6	SE	49°01.87′	27°42.07′	07/08/2009	16:37	2456	69:42
	21	SE	49°02.24′	27°41.49′	11/08/2009	12:35	2546	139:14
	28	SE	49°01.32′	27°42.98′	18/08/2009	11:22	2504	09:06
	36	SW	48°44.24′	28°37.32′	20/08/2009	22.25	2505	20:17
	44	SW	48°44.84′	28°38.78′	22/08/2009	08:17	2601	27:08
	53	NW	53°58.38′	36°07.73′	25/08/2009	22:30	2559	34:17
	62	NW	53°58.40′	36°08.22′	28/08/2009	11:27	2513	45:33
	77	NE	53°57.97′	34°03.19′	31/08/2009	21:56	2535	46:13
	87	NE	54°03.37′	34°09.47′	02/09/2009	09:51	2479	23:00
JC048	9	NW	53°58.40′	36°08.22′	02/06/2010	07:23	2542	25:18
	21	NE	54°04.92′	34°08.69′	08/06/2010	12:47	2506	23:54
	31	SW	48°46.32′	28°38.44′	16/06/2010	11:08	2500	72:46
	47	SE	49°01.87′	27°42.09′	23/06/2010	14:12	2519	66:28

odour from the bait and swimming speed of fish approaching the bait (V_f). Swimming speeds (V_f) were taken from the nearest available studies in the NE Atlantic Ocean and were assumed to be 0.077 m s^{-1} for *C. armatus* (Henriques et al., 2002) and 0.213 m s^{-1} for *A. rostrata* (Collins et al. 1999). Water velocity (V_w) was taken as 0.05 m s^{-1} as in Henriques et al. (2002). Water velocity data from the ADCP could not be used to estimate near-bottom odour dispersal flow since the measurements were from 6 to 10 m above the sea floor.

3.1. Length measurements

Total lengths of fish were taken from images using ImageJ 1.42q, a Java-based public domain program developed at the USA National Institutes of Health, Bethesda, USA (available at http://rsb.info.nih.gov/ij/index.html). The software was calibrated using the within-image reference scale. Fish were only measured if the full length of the body was visible at the level of the reference cross or below and re-measuring of the same individual was avoided (King et al., 2006).

3.2. Statistical analyses

Similarity in scavenger assemblage structure was examined using PRIMER (v5.0; Clarke and Gorley, 2006). Untransformed N_{max} data were used to reveal spatial groupings without enhancing contributions of rare or absent species, and to keep stress values minimal (Clarke and Warwick, 1994, Clarke and Gorley, 2006). Group average cluster analysis was conducted on Bray–Curtis similarities (Bray and Curtis, 1957). Non-metric, multi-dimensional scaling (MDS) was applied to present clusters in 2 dimensions. ANOSIM analysis was used 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 regions, and also the dissimilarity between sampling regions.

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).

Univariate statistical analyses were performed in Minitab (v16.0). Arrival time data (t_{arr}) were used as indicators of species abundance. Preliminary examination showed that t_{arr} data for both *A. rostrata* and *C. armatus* did not fit the assumptions necessary for parametric tests, therefore Kruskal–Wallis tests were used for testing the equality of population medians. Post-hoc Dunn's tests were applied where differences were detected. In order to compares species assemblages between regions, total species richness (R), Shannon diversity index (H') and Pielou's eveness (J') were assessed. There data were found to fulfil the assumptions for parametric statistical analysis so differences in R, H' and J' between regions were tested using an ANOVA, with a Tukey's test used for post-hoc analysis. To determine if trawl and lander derived abundance estimates were correlated a Pearson correlation was used.

4. Results

4.1. Species observed

A total of 19 fish taxa were recorded 16 at the SE site, 13 in the SW, 14 in the NE and 14 in the NW (Figs. 2 and 3, Table 2). There were potentially five species of macrouridae but it the resolution of the images did not permit discrimination of species in particularly the smaller specimens so some identifications remain tentative. The species most often observed were *C. armatus*, *A. rostrata* and *Hydrolagus affinis*. *C. armatus* and *A. rostrata* were numerically dominant and observed over the highest percentage of frames (Table 2). *Bathyraja pallida* was only observed in the SE. *Amblyraja jenseni* was only observed at the NW station. *Spectrunculus grandis* was not observed in any of the NE deployments and occurred in a high percentage of frames at the southern stations and in higher numbers than *C. armatus*.

The species accumulation curves indicate that species richness in the north is slightly lower than in the south (Fig. 3) but there was no significant difference in mean species richness between regional sampling sites (F_3=2.22, P=0.128). However comparison of H' indices revealed significant differences between regions (F_3=4.35, P=0.02); post-hoc tests revealed higher diversity indices for both southern stations compared to the NE (Table 3). There were no significant differences revealed regionally for J' (F_3=2.26, P=0.123) (Table 3).

ANOSIM analysis revealed significant spatially explicit groupings based on region (Global R=0.329, P=0.005; Fig. 4). The SE

Table 2
Scavenging fish taxa attracted to deployed bait. Data for each taxon are, top- time of first arrival (min), centre- peak abundance at bait (N_{max}), bottom- proportion of images in which the taxon was visible (%). Taxa are arranged in taxonomic order.

Region	NW					NE					SW			S					
Cruise Station number Depth (m)	JC011 73 2573	JC011 83 2567	JC037 53 2559	JC037 62 2513	JC048 9 2542	JC011 97 2500	JC011 115 2482	JC037 77 2535	JC037 87 2479	JC048 21 2506	JC037 36 2505	JC037 44 2601	JC048 31 2500	JC011 11 2512	JC011 22 2546	JC037 6 2456	JC037 21 2546	JC037 28 2504	JC048 47 2519
Hydrolagus affinis	612 1 1.98		34 1 1.75	270 1 0.26	17 2 8.58	220 1 0.78		253 1 0.78	121 1 2.62	111 1 0.84	337 1 2.06	484 1 1.33	154 1 3.79	25 2 5.89	298 1 1.25	22 2 6.7		229 1 2.16	218 1 0.47
Shark *sp.*																			1358 1 0.24
Amblyraja jenseni		914 1 0.5		625 1 0.07															
Bathyraja pallida															136 1 1.49	445 1 0.06			
Bathyraja richardsoni		267 1 0.99	61 1 2.77	519 1 0.19	1053 1 0.26				564 1 0.45	24 1 1.33	337 1 0.58	454 1 0.06	123 2 1.03			80 1 0.78	5051 1 0.09		
Unidentifiable ray						1242 1 0.04												325 1 0.2	
Halosauropsis macrochir	1415 1 0.13						727 1 0.16				376 1 0.17		1537 1 0.04	654 1 0.15					
Notacanthus sp.						977 1 0.04												324 1 0.2	
Histiobranchus bathybius	458 1 0.58	324 1 1.68	57 2 0.44	636 1 0.04		74 1 0.19	42 1 0.08	171 1 0.7		296 1 0.35	407 1 0.17	255 1 1.7	59 1 0.17	397 1 0.30	24 1 0.54		56 1 0.73	320 1 1.57	82 1 0.37
Synaphobranchus kaupii	458 1 0.64	324 1 1.68				74 1 0.19	42 1 0.08			365 1 0.28	141 1 0.33	163 1 0.06	293 1 0.3	30 1 0.45	24 1 0.6		200 1 0.14	223 1 0.59	
Alepocephalus sp.				244 1 0.04							172 1 0.25								36 1 0.07
Bathysaurus ferox						922 1 0.11							837 1 0.09						
Coryphaenoides armatus	16 4 15.67	51 4 12.09	22 2 7.34	16 16 20.51	19 8 18.22	39 3 8.58	22 6 10.01	15 5 17.29	4 5 32.59	21 7 28.47	37 1 3.3	34 2 10.1	211 2 6.03	204 2 5.06	42 1 4.88	56 2 6.17	55 2 6.05	157 1 4.32	56 4 13.69
Coryphaenoides brevibarbis			1224 1 2.58	1490 1 0.33	240 1 0.59	780 1 0.45	136 1 1.49		314 1 0.3	412 1 0.14	34 1 0.41		71 1 0.9					458 1 0.2	471 1 0.07
Coryphaenoides mediterraneus/leptolepis			728 1 0.19			154 1 0.3	24 1 0.55		142 1 0.22	556 1 0.07	92 1 0.58	669 1 0.19	268 1 0.13	25 2 1.21	39 1 1.91		318 1 0.045	148 1 0.98	827 1 0.1
Juvenile macrourid	529 1 0.45	4 1 0.9	510 2 1.36			726 1 0.19	11 1 1.88	1074 1 0.08											
Antimora rostrata	4 5 23.48	4 3 19.52	5 5 10.02	4 8 9.44	17 8 19.74	18 9 13.63	4 8 8.44	8 5 16.05	4 5 30.27	12 4 29.52	3 8 30.53	4 5 30.56	2 7 23.56	4 9 20.17	4 4 16.02	4 6 17.8	7 2 2.93	4 6 24.36	2 3 8.23
Spectrunculus crassa			179 1 0.63	442 2 0.74	890 1 0.07			1042 1 0.08					752 1 0.56	133 1 0.98	464 1 0.18	822 1 0.17	36 2 2.24	110 1 1.18	31 1 0.37
Spectrunculus grandis	573 1 1.28	617 1 0.3	296 1 0.24	139 4 4.35	132 1 2.38						55 4 31.77	58 3 32.95	109 5 32.64	55 2 12.08	166 3 16.02	60 7 74	72 3 24.64	89 3 24.17	94 1 13.59

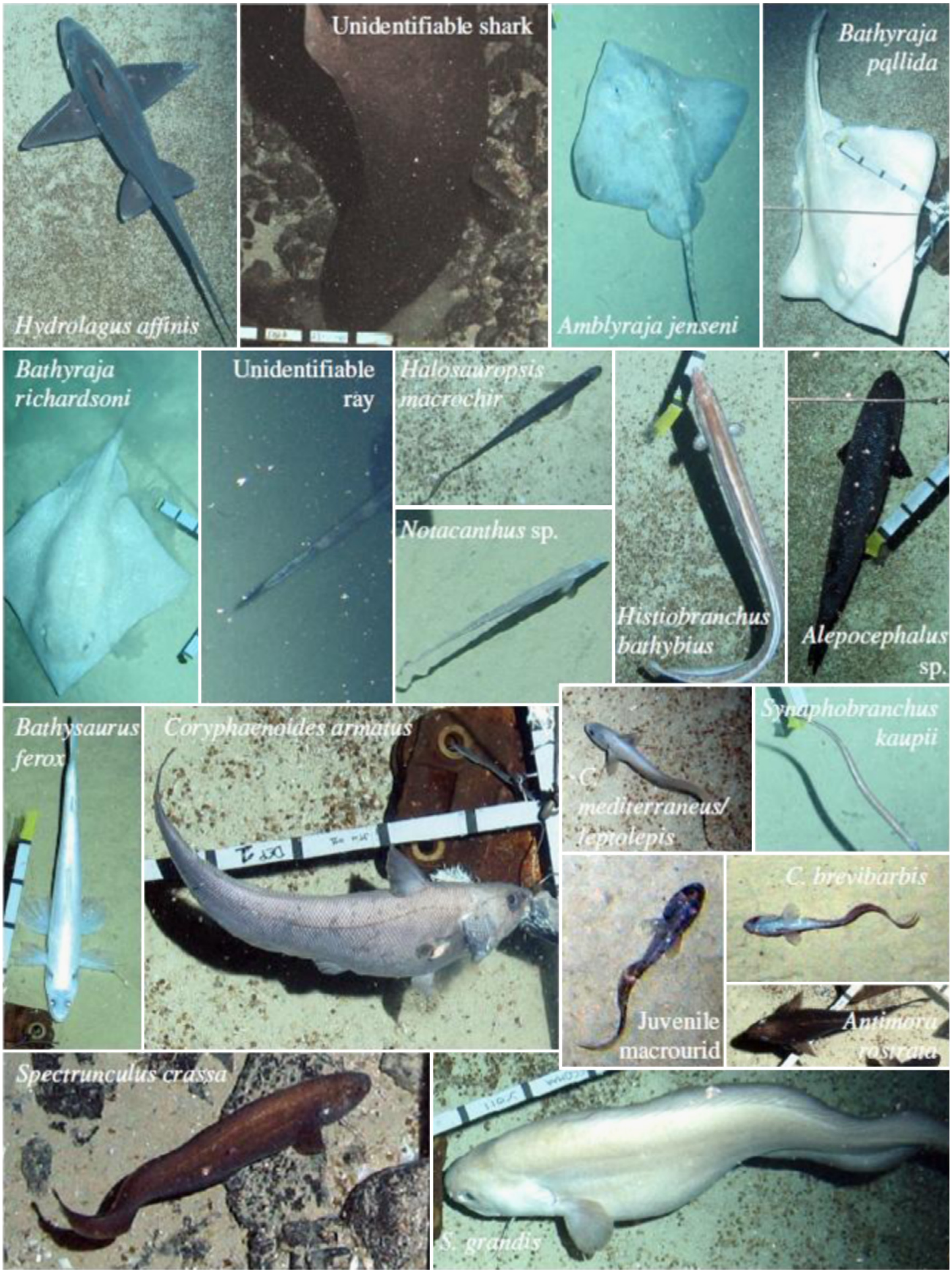


Fig. 2. Images of scavenging fishes observed attracted to bait deployed at around 2500 m depth on Mid-Atlantic Ridge.

site was significantly different from both the NW and NE sites. The SW site was significantly spatially separated from the NE site but not the NW site. There was no difference between the northern sites (Table 4). SIMPER analysis showed that *A. rostrata* and *C. armatus* consistently contribute to the within-group similarity for all regions. *S. grandis* also contributed to within-group similarity for the SE, NW and SW, but not for the NE where it was absent (Table 5). *S. grandis* was identified as most important in discrimination between regional groups by virtue of high dissimilarity/standard deviation values, however this was not consistent between all regional pairwise comparisons. Species with dissimilarity/standard deviation ratios >1.5 are those that discriminate between groups (Table 6).

4.2. Fish arrival times, numbers and abundance estimation

No significant differences were found between time of arrival of the first fish (t_{arr}) for *A. rostrata* and *C. armatus* based on cruise,

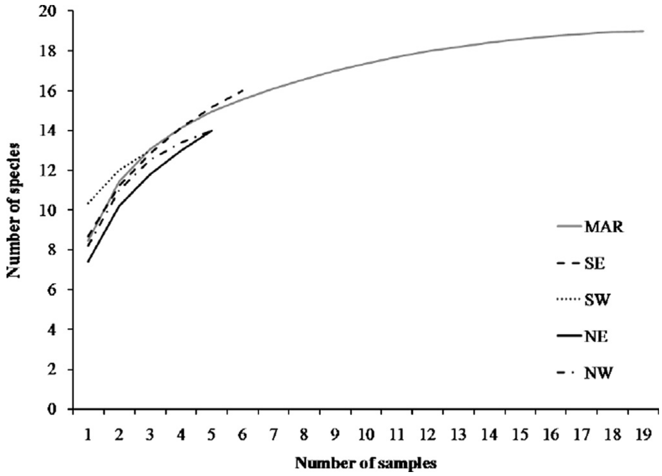


Fig. 3. Cumulative demersal fish species richness with increasing number of baited lander deployments deployments. MAR – all data combined. NW, NE, SW, and SE – data from the respective sites shown in Fig. 1. Number of samples = number of baited lander deployments.

Table 3
Mean species richness (R), Shannon diversity indices (H') and Pielou's (J') evenness for sampling regions. Standard deviation is shown in parentheses.

Region	N	R	H′	J′
NW	5	8.40 (±1.52)	1.78 (±0.22)	0.87 (±0.08)
NE	5	7.40 (±1.67)	1.61 (±0.16)	0.88 (±0.03)
SW	3	10.33 (±2.08)	2.00 (±0.15)	0.89 (±0.03)
SE	6	9.00 (±1.41)	1.95 (±0.18)	0.89 (±0.05)

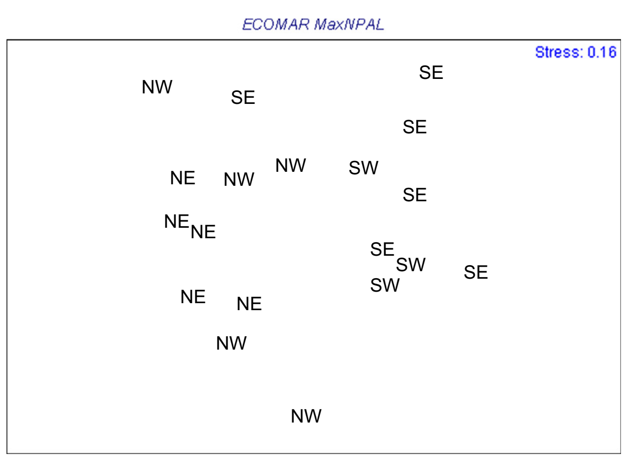


Fig. 4. Comparison of scavenging demersal fish species composition at the four study sites on the Mid-Atlantic Ridge, NW, NE, SW and SE. Bray–Curtis similarity analysis MDS plots of individual species based on untransformed N_{max} data (maximum numbers of individuals of each species seen at the baits). Each symbol represents a single lander deployment. Note the separation between northern (NW, NE) and southern (SW, SE) samples.

Table 4
ANOSIM pairwise comparisons of demersal scavenging fish community similarities between different sampling regions (untransformed N_{max} data).

Region pair	R statistic	P value
NW, NE	0.144	0.151
NW, SW	0.215	0.214
NE, SW	0.867	0.018
SE, NW	0.0345	0.019
SE, NE	0.671	0.004
SE, SW	−0.235	0.881

Table 5
SIMPER analysis results showing the species contributing to the within-group similarity of scavenging assemblages at the MAR regional sites. Only species contributing to >90% of the cumulative similarities are listed.

Region	Untransformed abundance data		
	Spp.	Av. N_{max}	Contribution %
SE	*Antimora rostrata*	5.00	31.88[a]
	Spectrunculus grandis	3.17	19.72[a]
	Coryphaenoides armatus	2.00	13.27[a]
	Spectrunculus crassa	1.17	9.54[a]
	C. mediterraneus/leptolepis	1.00	6.61
	Histiobranchus bathybius	0.83	6.61
	Hydrolagus affinis	1.17	6.58
NW	*A. rostrata*	5.80	37.60[a]
	C. armatus	6.80	30.14[a]
	S. grandis	1.60	8.81[a]
	H. bathybius	1.00	5.46
	Bathyraja richardsoni	0.80	4.94
	H. affinis	1.00	4.71
NE	*A. rostrata*	6.20	40.68[a]
	C. armatus	5.20	36.42[a]
	H. affinis	0.80	5.19
	C. mediterraneus/leptolepis	0.80	4.81
	C. brevibarbis	0.80	4.81
SW	*A. rostrata*	6.67	35.35[a]
	S. grandis	4.00	20.84[a]
	C. armatus	1.67	8.47[a]
	Synaphobranchus kaupii	1.00	6.33[a]
	H. affinis	1.00	6.33[a]
	C. mediterraneus/leptolepis	1.00	6.33[a]
	H. bathybius	1.00	6.33[a]
	B. richardsoni	1.33	6.33[a]

[a] Indicates species with dissimilarity/S.D. > 1.5. These are species that typify the group.

Table 6
Percentage contribution of species to dissimilarities between scavenging assemblages from different regions of the MAR (untransformed N_{max} data). Only species contributing > 90% of the cumulative dissimilarities are listed.

Species	NW vs. NE	NW vs. SW	NE vs. SW	SE vs. SW	SE vs. NW	SE vs. NE
C. armatus	26.60	27.82	24.11[a]	7.22	25.73	21.31[a]
A. rostrata	16.68	12.91	12.87	24.56[a]	15.81[a]	17.28
S. grandis	11.03[a]	16.86[a]	26.67[a]	15.87	13.09	20.29[a]
Juvenile macrourid	5.36	5.74	3.99		5.66	3.82
C. mediterraneus/ leptolepis	5.22	5.11[a]		2.74	5.38	2.94
S. crassa	5.13	4.19	2.63	8.10	4.72	6.33[a]
H. bathybius	4.18	5.51[a]	3.99	4.30	3.10	1.98
H. affinis	4.14	2.78		4.43	4.51	3.93
B. richardsoni	4.31	3.37	6.02	8.75[a]	3.74	3.08
C. brevibarbis	3.77	3.15	2.94	4.92	3.23	3.88
S. kaupii	2.62	5.03	5.46[a]	2.98	3.77	3.95
Amblyraja jenseni	3.00				2.42	
B. pallida				3.03		2.17
Halosauropsis macrochir		3.68	3.90	5.30		
Alepocephalus spp.				3.50		
Bathysaurus ferox			2.52			

* Indicates species with dissimilarity/S.D. > 1.5. i.e. species that provide discrimination between groups.

therefore data were pooled and tested for differences between sampling regions. No significant differences were detected in t_{arr} for *A. rostrata* between sampling regions ($P > 0.05$), however, t_{arr} was significantly longer at northern sites (8.0 ± 5.6 min) than at the southern sites (3.6 ± 1.5 min) ($H_3 = 5.48$, $P = 0.02$) (Table 7). For *C. armatus*, t_{arr} for both the NE and NW sites were found to be significantly longer than in the SE ($H_3 = 11.22$, $P < 0.05$, Dunn's test

Table 7
Antimora rostrata abundance estimates calculated from first arrival times t_{arr} using the model outlined by Priede et al. (1990); swimming velocity (V_f) was assumed to be 0.213 m s^{-1} (Collins et al., 1999) and water velocity (V_w) 0.05 m s^{-1}.

Region	Cruise	Deployment	N_{max}	Time of first arrival (min)	Theoretical abundance (fish km^{-2})
NW	JC011	73	5	4	3529
	JC011	83	3	4	3529
	JC037	53	5	5	2259
	JC037	62	8	4	3529
	JC048	9	8	17	195
		Mean		**6.8 (±5.7)**	**2608**
NE	JC011	97	9	18	174
	JC011	115	8	4	3529
	JC037	77	5	8	882
	JC037	87	5	4	3529
	JC048	21	4	12	392
		Mean		**9.2 (±5.9)**	**1701**
	Northern stations mean			**8.0 (±5.6)**	**2154**
SW	JC037	36	8	3	6274
	JC037	44	5	4	3529
	JC048	31	7	2	14117
		Mean		**3 (±1.0)**	**7973**
SE	JC011	11	9	4	3529
	JC011	22	4	4	3529
	JC037	6	6	4	3529
	JC037	21	2	7	1152
	JC037	28	6	4	3529
	JC048	47	3	2	14117
		Mean		**4.2 (±1.6)**	**4897**
	Southern stations mean			**3.8 (±1.5)**	**5923**

results; SE vs. NE, $Z=2.89$, $P<0.01$, SE vs. NW, $Z=2.60$, $P<0.01$). When data were pooled t_{arr}, was found to be significantly shorter in the north (23.0 ± 13.3 min) than in the south (94.7 ± 66.1 min), ($H_1=10.69$, $P=<0.001$). These results imply that population density of *A. rostrata* is significantly higher in the south than the north and conversely *C. armatus* occurs in higher density in the north. The abundance estimates (fish km^{-2}) calculated from t_{arr} data confirm this inference with population density of *A. rostrata* 2.7 times higher in the south than the north and *C. armatus* 7 times more abundant in the north than the south (Table 8)

Lander derived estimates of abundance for *A. rostrata* were on average 9 times higher than trawl estimates whereas for *C. armatus* the mean lander estimates were 1.2 times higher than trawl estimates (Table 9) There was no correlation between with trawl derived abundance estimates for *A. rostrata* (t_{arr} vs. trawl abundance, Pearson correlation $=-0.128$, $P=>0.05$, abundance estimate vs. trawl abundance, Pearson correlation $=-0.162$, $P=>0.05$) and *C. armatus* (t_{arr} vs. trawl abundance, Pearson correlation $=0.912$, $P=>0.05$, abundance estimate vs. trawl abundance, Pearson correlation $=-0.893$, $P=>0.05$). Whilst the lander data showed clear differences in population densities between north and south this was not apparent in the trawl data.

4.3. *A. rostrata* and *C. armatus* lengths

Regional differences were detected between *A. rostrata* lengths ($H_3=27.40$, $P=<0.01$); fish were found to be longer in the NE compared to the SW, the fish from the NW were larger than the SW, and fish in the SE were also larger than in the SW. When data were pooled as either northern or southern *A. rostrata* were also found to be significantly longer in the north compared with the southern stations ($H_3=13.94$, $P=<0.01$). *C. armatus* lengths were also found to be significantly different between regions ($H_3=28.23$, $P=<0.01$) with pairwise comparisons revealing that lengths are greater in the NW compared to the SE and SW, and the NE vs. SE stations. Again when data were pooled into either northern or southern *C. armatus* were found to be larger in the north ($H_3=24.80$, $P=<0.01$). Length frequency data from the PAL and trawls for both *A. rostrata* and *C. armatus* showed a unimodal distribution and generally fish of the same length range were observed at the lander as were sampled in the trawls (Fig. 5), however some larger specimens of *A. rostrata* (700–850 mm TL)

Table 8
Coryphaenoides armatus abundance estimates calculated from first arrival times t_{arr} using the model outlined by Priede et al. (1990); swimming velocity (V_f) was assumed to be 0.077 m s^{-1} (Henriques et al., 2002) and water velocity (V_w) 0.05 m s^{-1}.

Region	Cruise	Deployment	N_{max}	Time of first arrival (min)	Theoretical abundance (fish km^{-2})
NW	JC011	73	4	16	394
	JC011	83	4	51	39
	JC037	53	2	22	208
	JC037	62	16	16	394
	JC048	9	8	19	279
		Mean		**24.8 (±14.9)**	**263**
NE	JC011	97	3	39	66
	JC011	115	6	22	208
	JC037	77	5	15	448
	JC037	87	5	4	6297[a]
	JC048	21	7	21	228
		Mean		**20.2 (±12.7)**	**238**
	Northern stations mean			**23 (±13.3)**	**252**
SW	JC037	36	1	37	74
	JC037	44	2	34	87
	JC048	31	2	211	2
		Mean		**94.0 (±101.3)**	**54**
SE	JC011	11	2	204	2
	JC011	22	1	42	57
	JC037	6	2	56	32
	JC037	21	2	55	33
	JC037	28	1	157	4
	JC048	47	4	56	32
		Mean		**95.0 (±68.1)**	**27**
	Southern stations mean			**94.7 (±66.1)**	**36**

[a] High abundance from very short arrival time excluded from calculation of the mean.

Table 9
Comparison of baited lander and trawl derived abundance estimates for *Antimora rostrata* and *Coryphaenoides armatus* and the NW, NE and SE sites on the MAR (no trawl data are available from the SW site. *N* is the sample size, number of trawls or number of lander deployments.

	Trawl		Lander	
	N	(fish km^{-2})	*N*	(fish km^{-2})
Antimora rostrata				
NW	4	546 (±325)	5	2608
NE	3	188 (±39)	5	1701
SE	5	246 (±155)	6	4898
Coryphaenoides armatus				
NW	4	106 (±66)	5	263
NE	3	140 (±104)	5	238
SE	5	383 (±319)	6	27

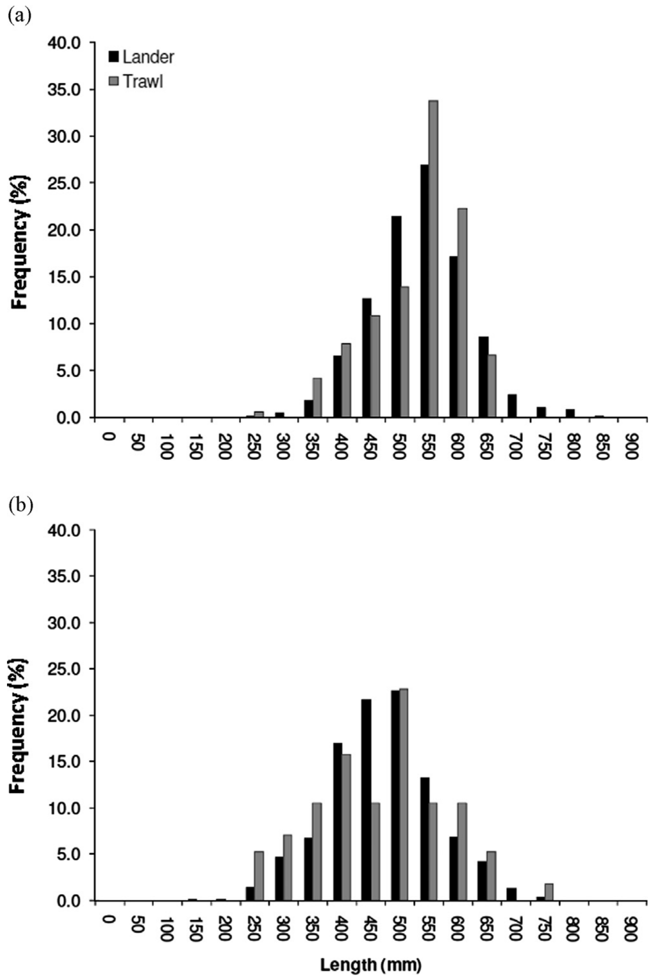


Fig. 5. Comparison of length frequencies of fish captured in trawls (from Cousins et al., 2013) and attracted to bait. (a) *Antimora rostrata* and (b) *Coryphaenoides armatus*.

were observed at the lander and were not caught as trawl specimens (Fig. 5a).

5. Discussion

Active scavenging fishes were photographed at all stations and we conclude there is no evidence that the crest of the ridge is a barrier to movement of bathydemersal fishes between the eastern and western flanks of the MAR. There was no significant difference in species composition either side of the MAR and population densities of *A. rostrata* and *C. armatus* were similar. Previous studies on the MAR have also found that longitude is not a significant variable structuring fish assemblages (King et al., 2006; Bergstad et al., 2008). In addition to the canyons of the CGFZ there are numerous fractures in the structure of the ridge that can act as channels for exchange, indeed King et al. (2006) found abyssal species in the confines of the MAR axial valley at 3420 m depth. In the previous studies samples had been taken at a various depths whereas here replicate sampling at identical depths either side of the axis MAR would have been more likely to resolve any longitudinal differences.

MDS analysis revealed a separation of fish assemblages between latitude 53°N, north of the CGFZ and 49°N to the south of the CGFZ. Data from trawls at the same depth range conducted in tandem with this study also reveal a north-south divide albeit with no trawls from the SW (Cousins et al., 2013). The SW and NW sites were not significantly spatially separate, but this is likely due to fewer SW deployments, and that many species in this region contribute to the within group similarity. *A. rostrata* and *C. armatus* were numerically dominant species in the present study, the trawl sampling (Cousins et al., 2013) and in previous baited lander studies on the MAR (King et al. (2006). A total of 19 taxa were recorded during this study compared with 22 from King et al. (2006) which sampled a wider range of depths and geographical area. King et al. (2006) observed nine fish taxa at approximately 2500 m on the MAR, all of which were observed in this study. The longer duration and higher number of deployments at this depth has revealed more species in the present study. Higher taxonomic resolution for the ray species was also achieved during this study, which accounts for some of the enhanced diversity compared with King et al. (2006). However images from King et al. (2006) were re-examined and the *Bathyraja* sp. identified as *A. jenseni*, *B. pallida* and *Bathyraja richardsoni* increasing the species count from eight to 11 at ca. 2500 m, which is still half of that observed in this study. *B. pallida* was observed further north in King et al. (2006) at 51 and 53°N compared with 49°N in this study. All species that were observed within PAL images are listed by Haedrich and Merrett (1988) except for *B. pallida*. *S. grandis* was not observed in the NE during this study, and also was not observed to the east of the northern axial valley in King et al. (2006), however they were observed to the east in the south (deployment 5, King et al., 2006). *S. grandis* were captured in the NE in trawls (Cousins et al., 2013).

Trawl sampling on the MAR at 2500 m depth collected 35 species using a Campelen trawl (Bergstad et al., 2008) and 26 species using a semi-balloon otter trawl (OTSB) (Cousins et al., 2013). Species that were represented in the lander images but not in the OTSB catches were *H. affinis*, Shark sp., *A. jenseni*, *B. pallida* and *Notacanthus* sp. The OTSB used by Cousins et al. (2013) is known not to catch large, more mobile predators such as sharks and rays (Merrett et al., 1991; Gordon and Bergstad, 1992) but did catch a notacanthid species; *Polyacanthonotus challengeri*.

Previous baited camera and trawling studies in the Porcupine Seabight, northeastern Atlantic at 2500 m depth (Priede et al., 2010) show that ca. 30% of the species caught within trawls are attracted to baits. Within this study the scavengers comprise approximately 65% of the OTSB trawled species from Cousins et al. (2013) (after removing the five species not seen in trawls) and 40% of the more comprehensive Campelen trawled species list from Bergstad et al. (2008). It therefore appears that at this particular depth on the MAR that scavenging species represent a higher fraction of the ichthyofauna than on the continental margin of the northeastern Atlantic. Fossen et al. (2008) using baited longlines sampled at least 40 species of fish between 400 and 4300 m on the MAR across three transects, however, only 20 species were recorded from 2500 m ($\pm$250 m) (Dyb and Bergstad, 2004). The species observed at longlines and baited cameras differ slightly owing to gear type, soak times, amount of bait (and therefore size of odour plume). In addition target species must actively consume the bait to be hooked by long-lines whereas they can be captured by camera by just entering into the vicinity of the bait (King and Priede, 2008).

Differences in H' were observed with elevated index values at both southern stations compared to the NE site, indicating that there is higher number of species in the south which are more equally distributed in terms of their N_{max}, compared to the NE station. Conversely, there was no difference observed in H' between the NW and either southern station, and there were no differences detected in total species richness or evenness between the northern and southern regions. Bergstad et al. (2008) also found higher diversity in the south on the MAR compared with more northerly stations, but over a much greater geographic distance than in this study. Bergstad et al. (2008) also showed more defined latitudinal differences between fish assemblages from shallower lower slope areas (1500–2250 m) than at greater depths. Greater diversity at the SE site was noted in Cousins et al. (2013) compared with the NE but not with the NW, however the NE was subject to reduced sampling effort compared to the SE and NW so the trend is not clear. For species attracted to bait, King et al. (2006) found no clear latitudinal divide in diversity, with mean species richness per deployment of 5.0 at 43°N, 3.3 at 51°30′ N and 5.8 at 53°N.

Abundance estimates of *C. armatus* range from 11–247 fish km^{-2} (regional means), with significantly lower t_{arr} and therefore higher abundance estimates in the north. Elevated estimated abundances of *C. armatus* have previously been linked with presumed higher surface productivity (e.g. King et al., 2006, King and Priede, 2008). This concept is further supported by the observation that the mean size of *C. armatus* was larger at the northern stations. However, Abell et al. (2013) found organic carbon export flux in sediment traps at 2400 m depth at the four stations to be very similar; NE 1.2 g m^{-2} yr^{-1}, NW 0.8 g m^{-2} yr^{-1}, SE 1.1 g m^{-2} yr^{-1}, SW 1.1 g m^{-2} yr^{-1}. Surface productivity estimates are also within similar ranges for each site; SE, 208.8 g C m^{-2} yr^{-1}, SW, 200.4 g C m^{-2} yr^{-1}, NW, 233.5 g C m^{-2} yr^{-1}, and NE, 187.8 g C m^{-2} yr^{-1} (Tilstone, Pers. Comm.). Thus a simple explanation that higher abundance and size of *C. armatus* in the north is linked to higher export flux of organic matter from the surface is not sustainable.

A. rostrata showed the opposite trend to *C. armatus*, with significantly longer t_{arr} in the north indicating lower abundance in the north. Reid et al. (2012) show that *A. rostrata* and *C. armatus* on the MAR have different tissue stable isotope compositions of carbon, nitrogen and sulphur despite similar foraging strategies (Reid et al., 2012). These differences in stable isotope ratios may be indicative of a higher proportion of benthic organisms in the diet of *C. armatus* (Stowasser et al., 2009) which may influence the north-south differences observed in these two species.

We found no correlation between trawl and baited lander-derived estimates of abundance. In a study on the Californian slope at depths from 105 to 3144 m in the NE Pacific Ocean Yeh and Drazen (2011) also found no correlation between baited camera and trawl estimates of species abundance. Although Priede and Merrett (1996) found a significant correlation ($P<0.001$) between trawl and baited lander data for *C. armatus* with estimates ranging from 2 to 1000 fish km^{-2} it is evident that caution is required when applied to smaller differences between sampling sites. The overall mean abundance estimates from trawl (210 km^{-2}) and lander (256 km^{-2}) for *C. armatus* in the present study differ by just 20%. Farnsworth et al. (2007) show that estimation of scavenger abundance from arrival times depends on numerous assumptions regarding fish behaviour and the dynamics of odour plumes it is clear that caution must be applied when suing the technique for species other for *C. armatus* in which it was originally validated. Nevertheless the differences in arrival times between north and south are significant and differences in species abundance may be part of the explanation.

In terms of length differences it is interesting to note that for both *A. rostrata* and *C. armatus* larger fish were observed at the northern study sites. No previous latitudinal differences in size have been noted for *C. armatus* or *A. rostrata*, only a general bigger-deeper trend with depth (Collins et al., 2005; Fossen et al., 2008) and some differences between Greenland and the MAR for *A. rostrata* (Fossen et al., 2008). Possible explanations for the observations of larger specimens at northern sites are speculative, but could be driven by differences in sex distribution as females in both species are larger (Collins et al., 2005; Fossen et al., 2008), or a difference in the trophic regime between the areas north and south of the CGFZ, as suggested by Reid et al. (2012). The latitudinal size difference observed in *C. armatus* is not due to the sampling of different populations as Ritchie et al. (2013) found a lack of genetic structure in *C. armatus* populations along the MAR. There were also no differences found in size selectivity for either *A. rostrata* or *C. armatus* between gear type. Conversely, Fossen et al. (2008) found that length frequency varied between gear type, and that generally smaller fish were caught in trawls compared to longlines, but they also found a unimodal distribution of length frequency in both gear types used. Priede and Merrett (1996) found the opposite trend, that smaller fish were photographed at bait than were sampled within trawls.

6. Conclusions

The current study reveals a diverse scavenging fish assemblage present on the MAR through a series of lander deployments over three sampling seasons. Scavenging assemblages were found to segregate based on whether they were north or south of the CGFZ. No unexpected species were observed and 11 species were observed across all sites. There was no evidence of differences between the eastern and western flanks of the MAR. Species observed within lander images make up a higher proportion of species captured by trawls from the same region when compared with data from the northeastern Atlantic ocean margin. The CGFZ appears to be a highly permeable barrier to movements of bathydemersal fishes with strong evidence of continuity in populations between north and south (Ritchie et al., 2013) and the same species occurring in both regions. However differences are detectable, reflecting contrasting hydrographic and potential differences in trophic regimes across this latitudinal transition zone. The baited lander method has the advantage of providing non-invasive sampling of a large proportion of the fish species present in the complex topography of the MAR.

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