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The ecosystem of the Mid-Atlantic Ridge at the sub-polar front and Charlie–Gibbs Fracture Zone; ECO-MAR project strategy and description of the sampling programme 2007–2010☆

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ABSTRACT

The ECOMAR project investigated photosynthetically-supported life on the North Mid-Atlantic Ridge (MAR) between the Azores and Iceland focussing on the Charlie–Gibbs Fracture Zone area in the vicinity of the sub-polar front where the North Atlantic Current crosses the MAR. Repeat visits were made to four stations at 2500 m depth on the flanks of the MAR in the years 2007–2010; a pair of northern stations at 54°N in cold water north of the sub-polar front and southern stations at 49°N in warmer water influenced by eddies from the North Atlantic Current. At each station an instrumented mooring was deployed with current meters and sediment traps (100 and 1000 m above the sea floor) to sample downward flux of particulate matter. The patterns of water flow, fronts, primary production and export flux in the region were studied by a combination of remote sensing and in situ measurements. Sonar, tow nets and profilers sampled pelagic fauna over the MAR. Swath bathymetry surveys across the ridge revealed sediment-covered flat terraces parallel to the axis of the MAR with intervening steep rocky slopes. Otter trawls, megacores, baited traps and a suite of tools carried by the R.O.V. *Isis* including push cores, grabs and a suction device collected benthic fauna. Video and photo surveys were also conducted using the SHRIMP towed vehicle and the R.O.V. *Isis*. Additional surveying and sampling by landers and R.O.V. focussed on the summit of a seamount (48°44′N, 28°10′W) on the western crest of the MAR between the two southern stations.

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1. Introduction

The Mid-Atlantic Ridge (MAR) was described by Murray and Hjort (1912) as dividing the ocean into eastern and western deep basins from Iceland to at least 53°S. During their voyage on board R.V. *Michael Sars* in 1910 they discovered abundant and diverse fish and invertebrate faunas on these mid-ocean shallow areas of the North Atlantic. Information on the geographical extent of the ridge emerged over subsequent decades. Tolstoy and Ewing (1949) produced continuous echograms traversing the MAR revealing topographical details. More comprehensive mapping during the 1950 and 1960s (Doel et al., 2006) showed that the MAR forms part of a continuous chain of ridges circumscribing the planet (Heezen, 1969). Biological research on mid ocean ridge systems was greatly stimulated by the discovery of chemosynthetically-supported life around hydrothermal vent sites, first in Pacific Ocean (Corliss and Ballard, 1977), subsequently on the MAR (Rona et al., 1986) and later at numerous locations around the global ocean ridge system (Van Dover, 2000; Baker et al., 2010). However, despite their wide-spread occurrence, vent fields are small in area and contribute a minor fraction of the total biological productivity on mid ocean ridges. Export from photosynthesis in the surface layers of the ocean provides the bulk of food resources to the benthos (Priede et al., 2013a). From 1973 in the North Atlantic, fishery fleets of several nations began to exploit

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resources of the MAR with deep-water long line and trawl fisheries that focused on roundnose grenadier (*Coryphaenoides rupestris*), alfonsino (*Beryx splendens*), orange roughy (*Hoplostethus atlanticus*), cardinal fish (*Epigonus telescopus*), tusk (*Brosme brosme*), 'giant' redfish (*Sebastes marinus*) and blue ling (*Molva dypterigia*) (ICES, 2012). Scientific surveys of these target species have been undertaken (Hareide and Garnes, 2001; Kukuev, 2004) and attention has been directed to studies of life on the summits of sea mounts (Rogers, 1994; Mironov et al. 2006) which may be impacted by trawling activity. Standard works describing patterns of deep-sea biodiversity in the North Atlantic Ocean for demersal fishes (Haedrich and Merrett, 1988) and benthic invertebrates (Allen and Sanders, 1996; Rex and Etter, 2010) have shown depth zonation of species on the slopes of the eastern and western margins of the Ocean but defined no ecological relationships along the MAR. Overall, information on the ecosystems of the MAR remains relatively sparse.

The Census of Marine Life project MAR-ECO (Patterns and Process of the Ecosystems of the North Mid-Atlantic) was organised to investigate photosynthetically-supported life on the segment of the MAR between Iceland and the Azores (Vecchione et al., 2010). As part of this project in 2004 the R.V. *GO Sars* undertook surveys at 38 superstations from 60°18′N to 41°22′N sampling fauna from the sea surface to the sea floor using a wide range of devices including sonars, trawls and remotely operated vehicles (ROVs) (Wenneck et al., 2008). The area around the Charlie–Gibbs Fracture Zone (CGFZ) was identified as the most important latitudinal transition zone in environment and biodiversity along the ridge (Vecchione et al., 2010). The present project, ECOMAR, was designed to investigate the CGFZ area (Fig. 1) which lies approximately mid-way between Iceland and Azores. Owing to its remoteness from landmasses this region is not routinely visited by research vessels. The R.V. *GO Sars* sampled at depths ranging from 607 to 3512 m and did not revisit any stations during the course of its voyage. For ECOMAR, four

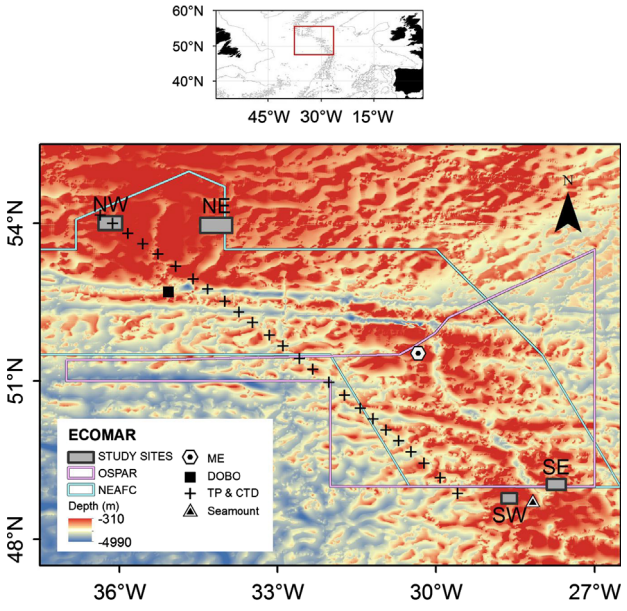

Fig. 1. Chart of the North Atlantic Ocean showing the location of the ECOMAR study area and four Superstations. The upper panel indicates the area shown the main map. Bathymetry is 30″ resolution data from GEBCO. Rectangles for each of the superstations NW, NE, SW and SE correspond to areas in Figs. 5–8 respectively. OSPAR—boundary of the Charlie–Gibbs South Marine Protected Area (OSPAR, 2010); NEAFC—boundary of the middle MAR area for protection of vulnerable marine ecosystems (Charlie–Gibbs Fracture Zone and Sub-Polar Frontal Region) (NEAFC, 2008); ME—location of moored echosounder (Godø et al., 2013); DOBO—Deep Ocean Benthic Observatory on the floor of the Charlie–Gibbs Fracture Zone North rift valley (Blanco et al., 2013); TP+CTD—positions of CTD casts along the track of the Topex-Poseidon satellite (Read et al., 2010); Seamount—seamount reference number 37378 catalogued by Yesson et al. (2011).

Table 1
List of ECOMAR cruises to the Mid-Atlantic Ridge with dates of departure from port and arrival.

Year	Vessel	Cruise no.	Dates	
			Start	End
2007	R.R.S. *James Cook*	JC011	13 July	18 August
2008	R.R.S. *Discovery*	D331 T	24 July	15 August
2009	R.R.S. *James Cook*	JC037	1 August	9 September
2010	R.R.S. *James Cook*	JC048	26 May	3 July

superstations were defined (two north of the CGFZ and two to the south), all had the same bottom depth (2500 m) and were revisited during voyages by the R.R.S. *James Cook* and the R.R.S. *Discovery* during the years 2007–2010 (Table 1) to replicate sampling, time-series investigations and flux studies.

Heezen and Tharp (1957) in their map of the bathymetry of the North Atlantic Ocean first indicated the discontinuous nature of the MAR with transverse fractures at intervals along the axis of the ridge. Their interpretation, whilst essentially correct, was impressionistic regarding the location of fracture zones. Global bathymetry aided by satellite (Smith and Sandwell, 1997) with 30″ resolution (GEBCO, 2013) showed the precise distribution of fracture zones and clearly identifies the CGFZ as the most important topographic feature in the Mid North Atlantic between the Azores and Iceland.

The CGFZ is the site of major transform faulting that has displaced the ridge axis 370 km westwards in the north with respect to the south. The term CGFZ strictly refers to a pair of rift valleys, Charlie–Gibbs North and Charlie–Gibbs South that cross the MAR between 52° and 53°N (Fig. 1). They are about 10 km wide, bottom depth over 4 km below sea surface, running almost exactly east–west, parallel to one another 35 km apart. The northern valley was first surveyed in 1966 and together with postulated subsidiary fracture zones was named "Charlie" after an ocean weather ship station in the area (Johnson, 1967). More extended surveys by the USNS *Josiah Willard Gibbs* in 1968 revealed the double nature of the fracture zone for which Fleming et al. (1970) proposed the name "Gibbs Fracture Zone" after the survey vessel. Peter R. Vogt of the U.S. Naval Oceanographic Office suggested the compromise dual name "Charlie–Gibbs" (Vogt and Johnson, 1975), which was rapidly adopted in subsequent publications (Shor et al., 1979). As part of the MAR-ECO project during 2003 the R.V. *Akademik Mstislav Keldysh* deployed the manned submersibles *Mir*-1 and *Mir*-2 in the axis (52°47′N) and the northern slopes (52°58′N) of Charlie–Gibbs North and surveyed plankton (Vinogradov, 2005), demersal nekton including fishes (Felley et al., 2008) and invertebrate megafauna (Gebruk and Krylova, 2013) at depths from 1740 to 4500 m.

The Charlie–Gibbs term is now also applied to much larger areas of the MAR, e.g. "Charlie–Gibbs Marine Protected area (CG-MPA)" between 49°00′N and 53°30′°N (OSPAR, 2010) and "Middle MAR Area (Charlie–Gibbs Fracture Zone and Sub-Polar Frontal Region)" between 49°00.00′N and 54°58.99′N (NEAFC, 2008). Within these management regimes on the MAR environmental conservation measures have been implemented (O'Leary et al., 2012) Fig.1.

In this area the North Atlantic Current (NAC) tends to be steered by topography (Bower and von Appen, 2008) so that a northern branch crosses the MAR near the CGFZ from west to east. The northern edge of the NAC defines the location of the sub-polar front (Fig. 2) between colder Sub Arctic Intermediate Water to the north and warmer North Atlantic Intermediate Water to the south (Søiland et al., 2008). Whilst surface flow is predominantly eastward, within the CGFZ there is an intermittent westward flow of cold deep bottom water originating from the Iceland–Scotland overflow from the Arctic (Saunders, 1994). The CGFZ is therefore

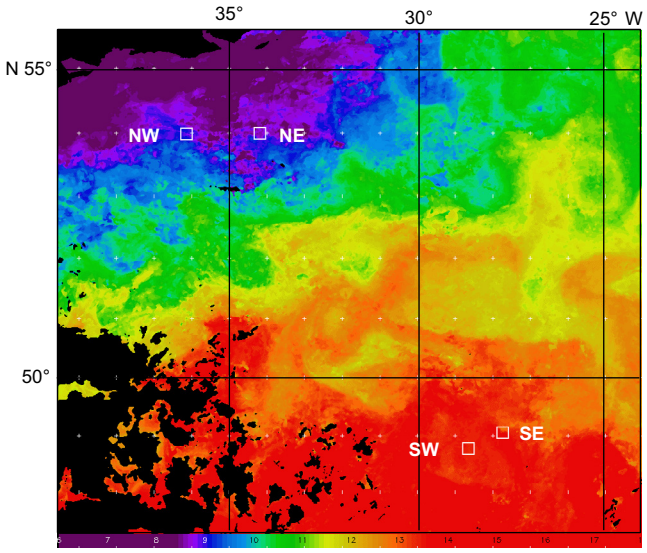

Fig. 2. Sea surface temperature (SST) image transmitted to the R.R.S. *James Cook* prior to cruise JC048, NOAA–AVHRR, 7 day median temperature 14–20 May 2010.

not simply a topographic discontinuity in the MAR but is an oceanographic transition zone between waters of different temperatures and flow regimes. Biogeographically the CGFZ is within the North Atlantic Drift Province (NADR) defined by Longhurst (1989) as lying between 43°30′N and 55°30′N with the Atlantic Arctic (ARCT) and Atlantic Sub Arctic (SARC) provinces to the north and North Atlantic Subtropical Gyre Province (NAST) to the south. UNESCO (2009) reviewed the biogeographic classification of the oceans and in the pelagic realm defined the area north of the CGFZ-sub-polar front as the Subarctic Atlantic Province with a sea surface temperature (SST) range of 2.06–14.00 °C and the area to the south as the North Atlantic Current Province with SST 7.49–25.52 °C. In the benthic realm UNESCO (2009) recognised the lower bathyal zone (800–3500 m depth) as consisting of three main physiographic categories: lower continental margins, seamounts together with oceanic island slopes, and mid-ocean ridges. Whilst the ocean margins are dominated by sedimentary deposits from continental run-off, UNESCO (2009) postulated that mid-ocean features are more likely to be free of sediment, offering large expanses of hard substrate for settlement of invertebrates and habitat for bathyal fishes. In the UNESCO (2009) classification of Lower Bathyal Provinces, the ECOMAR study area lies approximately on the boundary between the Northern North Atlantic Province and the North Atlantic Province. Superimposed on these benthic provinces are the hydrothermal vent provinces in which a MAR Azores Province is recognised but it is suggested there may be no extension northward towards to Iceland owing to deepening of the ridge crest and absence of venting activity (UNESCO, 2009).

The aims of ECOMAR were to evaluate mid-ocean biological productivity and biomass in comparison with the surrounding ocean, and to identify differences between north and south of the sub-polar front/CGFZ and differences between east and west of the ridge axis.

1.1. The effect of the Mid-Atlantic Ridge

Many arguments regarding the biology of the seamounts (Rowden et al., 2010; Clark et al., 2010) are also applicable to mid-ocean ridges which can be considered as complex aggregations of sea mounts.

1. The primary effect of the presence of a ridge compared to a hypothetical ocean with a continuous abyssal plain is simple elevation of the sea floor providing habitats for bathyal species that are otherwise confined to narrow preferred depth zones around the ocean margins (Rex and Etter, 2010; Priede et al.,2010). Remoteness of the MAR may also provide sufficient isolation for speciation and development of endemism (Wilson and Kaufman, 1987; Stocks and Hart, 2007). Elevation of the sea floor reduces the vertical distance over which export production is transported downwards, resulting in increased organic carbon reaching the sea floor thus sustaining a greater benthic biomass than would otherwise be possible on an abyssal plain (Wei et al., 2010; Duineveld et al., 2004). The crest of the ridge also may be sufficiently near the surface so that pelagic fauna executing night-time downward vertical migrations impinge on the slopes of the ridge delivering additional food to organisms living there. Some pelagic species may spontaneously congregate around slopes or features of the MAR thus importing biomass from the surrounding ocean. Genin (2004) identified five distinct behavioural and physical mechanisms by which sea bed topography creates biomass concentrations in overlying waters, upwelling, topographic blockage of descending zooplankton, counter-upwelling depth retention, counter-downwelling depth retention and enhanced horizontal flux. All of these may be applicable to parts of the MAR.
2. A secondary effect of presence of a ridge is that currents (Bower and von Appen, 2008), tides (Egbert and Ray, 2000) and internal waves (van Haren et al., 2005) dissipate energy on the ridge topography. This dissipation may have the effect of upwelling nutrients towards the surface thus stimulating primary production over the summit. Several studies have detected enhanced concentrations of phytoplankton above sea mounts (Mouriño et al., 2001). Iron leached from volcanic rocks of the Crozet islands enhanced primary production and organic carbon export to the adjacent deep sea areas of the southern Indian Ocean (Pollard et al., 2009; Wolff et al., 2011). Flow effects such as Taylor cones (Mohn et al., 2009) around topography may help retain and concentrate pelagic biomass that would otherwise be widely dispersed in the ocean.

1.2. The effect of the sub-polar front and CGFZ

1. The width of the two transverse valleys, Charlie–Gibbs North and Charlie–Gibbs South, plus the displacement of the axis of the MAR by 270 km may constitute a physical barrier preventing or reducing latitudinal dispersal of some bathyal fauna.
2. The presence of fronts and water circulation through the CGFZ may act as a barrier to movement of pelagic fauna, eggs and larvae between north and south (Woodson et al., 2012; McManus and Woodson, 2012).
3. Different water masses and oceanographic regimes to the north and south of the sub-polar front are likely to result in differences in timing, quality and amount of primary production. These differences in primary production will in turn entrain differences in export flux from the surface, leading to differences in biomass and species composition in the two regions.
4. The frontal region itself is likely to support distinctive patterns productivity (Taylor and Ferrari, 2011) that can influence biomass and biodiversity.

1.3. East–west differences across the axis of the MAR

1. The axis of the MAR may be a barrier to dispersal of organisms living on the flanks of the MAR at lower bathyal depths. Species differences might be expected between the east and west.

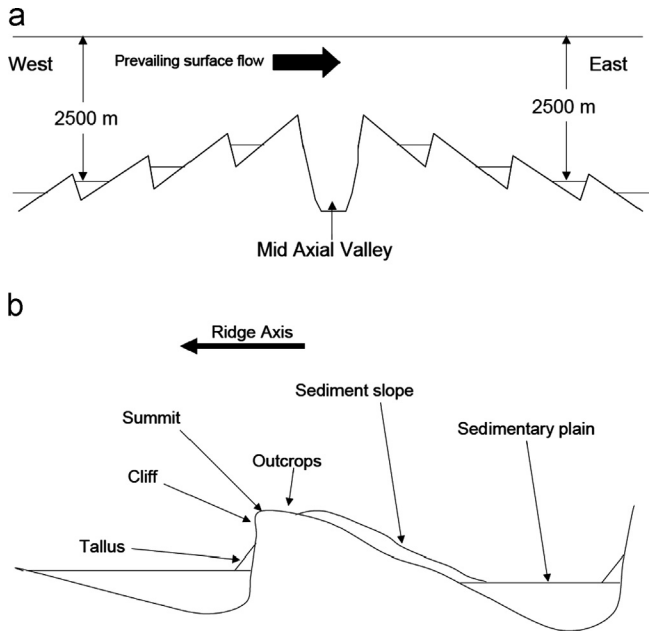

Fig. 3. Conceptual diagram of a cross section of the Mid-Atlantic Ridge. (a) The entire ridge showing the axial rift valley with the crest of the ridge and series of terraces on the flanks on either side. Between the ridges of the terraces there are flat sediment-filled basins. The ECOMAR superstations with moorings are located at 2500 m depth on either flank of the ridge. Prevailing surface flow is indicated from west to east. (b) Detail of terraced structure and habitat types. Bare rock only occurs near the summits of the terraces on steep faces with cliffs. The steep faces are oriented towards the ridge axis.

2. The North Atlantic basin has been colonised by fauna originating from the eastern and western ocean margins (Mironov et al., 2006) and in mid ocean there is likely a transition zone between eastern and western faunas, which may manifest itself on the MAR.
3. Although the MAR topographically shows east–west symmetry the hydrography is asymmetrical with predominant surface flow from west to east so that on the western side of the MAR flow impinges on the slopes and summits whereas in the east these features lie in the lee of the flow (Fig. 3). Such hydrographic asymmetry may create subtle differences in micro-habitats with a predominant dispersal of material, towards the east.

2. Materials and methods

2.1. Strategy. ECOMAR was organised in six work packages

1. **Water circulation.** Studies were based on a combination of remote sensing, ship-borne measurements, floats and moored instruments. Remote sensing utilised SST data from the AVHRR (advanced very high resolution radiometer) and satellite altimetry to derive sea surface height and surface geostrophic velocities. On board ship full depth CTD profiles with a lowered acoustic current profiler (LADCP) were conducted on transects across the MAR between the superstations and along a transect west of the MAR along the Topex/Poseidon/Jason-1 altimeter track to resolve regional flow patterns. Argo float data were downloaded from the project website (Read et al., 2010). Moorings at each of the ECOMAR superstations were equipped with an array of current meters and ADCPs providing continuous data over the periods indicated in Table 2.
2. **Remote sensing and primary production**. The distribution of thermal fronts over the MAR was investigated using composite front maps derived from microwave (AMSR-E, TMI, WindSAT) and infrared SST (AVHRR, MODIS) data. Primary production estimates were derived from a wavelength resolving model using mean monthly 9 km NASA SeaWiFS OC4v4 Chla and Pathfinder v2009 AVHRR SST data. Primary production was estimated using satellite remote sensing calibrated by ship borne incubations and in situ measurements at different depths throughout the photic zone using methods such as described by Tilstone et al. (2009). From these data, calculations were made of export flux to the sea floor.
3. **Pelagic biomass and biodiversity.** The distribution of pelagic zooplankton and nekton biomass down to 800 m depth was investigated using vertically-oriented, multi-frequency scientific echo sounders (Simmonds and MacLennan, 2005; Cutter et al., 2009; Cox et al., 2011) validated by net tows. A rectangular mid-water trawl (RMT) was used (Baker et al., 1973) with two opening and closing nets, mouth areas of 1 and 8 m^2 and mesh size of 330 μm and 4.5 mm, respectively. Vertical profiles of abundance of bioluminescent nekton and zooplankton were obtained with a low-light camera and impact screen mounted on the CTD rosette (Priede et al., 2006; Heger et al., 2008). These measurements extended down to the sea floor beyond the depth range of sonar and RMT. Pelagic gelatinous plankton were also observed using the R.O.V. *Isis* and sampled using the suction sampler and a "D" sampler that encloses a 6.5 l volume of water in a cylinder using hydraulically operated doors (Youngbluth, 1984). The abundance of pelagic fauna in the benthic boundary layer was also investigated by mounting a low light camera and particle-recording camera on the tool tray of the R.O.V. *Isis*.
4. **Export flux.** Two sediment traps were mounted on each of the four ECOMAR moorings at 100 m and 1000 m above the sea floor to quantify export flux from the surface for comparison with stations at similar latitudes in the North-east Atlantic (Lampitt et al., 2001, 2010) and globally (Honjo et al., 2008).
5. **Benthic biomass and biodiversity.** Benthic fauna were sampled and imaged using a suite of techniques described in detail by Priede et al. (2013b). Video and still image transects were conducted with the SHRIMP (Seafloor High Resolution Imaging Platform towed vehicle) operated at 2–3 m above the sea floor during cruise JC011in 2007. (Table 1). In 2010 on cruise JC048 systematic line transects, using the suite of cameras on board the R.O.V. *Isis*, provided quantitative estimates of fauna per unit area. This sea floor imaging also provided contextual information on habitat type such as substrate type and distribution of sessile fauna. Mobile fauna attracted to bait were imaged by digital camera on board PAL (Photo Acoustic Lander) using methods described by King et al. (2006) and Priede and Bagley (2000). Some studies were done using a low light camera on a bioluminescence lander to detect the presence of bioluminescent fauna attracted to bait (Priede et al., 2006; Heger et al., 2007). Demersal fishes and benthic invertebrate megafauna were collected using a 45 ft (13.7 m) semi-balloon otter trawl (OTSB, Marinovich Trawl Co., Biloxi, USA) fished on a single warp (Merrett et al., 1991). This gear is identical to that used for sampling fish (Gordon et al., 1996; Priede et al., 2010)

Table 2
Locations of the moorings at the four ECOMAR super-stations with first deployment dates (start) and final recovery dates (end) indicating approximately the duration of data collection by sediment traps and current meters.

Location	Latitude N	Longitude W	Start	End
SE	49°02.60′	27°43.48′	19 July 2007	23 June 2010
SW	48°46.80′	28°38.43′	26 July 2007	16 June 2010
NW	53°59.33′	36°07.39′	1 August 2007	2 June 2010
NE	54°00.05′	34°10.61′	9 August 2007	8 June 2010

and invertebrates (Howell et al., 2002; Billett et al., 2009) on the abyssal plains and continental rise and slopes of the NE Atlantic, thus providing directly comparable data. An acoustic transmitter on one of the trawl doors provided bottom contact information enabling the area of sea floor swept by the trawl to be determined, allowing results to be expressed quantitatively in terms of numbers and biomass per unit area. The soft-bottom macrofauna were sampled using a megacorer (Bowers and Connelly) equipped with 100 mm internal diameter core tubes. Smaller 59 mm internal diameter tubes on some deployments allowed sampling of meiofauna. This gear was deployed at a designated coring site at each of the ECOMAR superstations using a vertical Kevlar cable and provided quantitative information on abundance and biomass. Small mobile necrophagous fauna were captured using a baited amphipod trap mounted on a free-fall lander frame. Sessile and slow-moving megafauna were collected by the R.O.V. *Isis* using the manipulator claws, suction sampler and box corer. Push cores operated by the manipulator arms were used to obtain targeted samples of soft sediment for megafauna and meiofauna. The topography of the MAR (Fig. 2) determined the sampling method used. The megacorer and the bottom trawl were confined to flat sedimentary plains with absence of hard obstructions and an appropriate depth of soft sediment. The baited landers, PAL, amphipod trap and bioluminescence lander were deployed on flat areas, slopes, summits and outcrops but not on steep slopes and cliffs. The SHRIMP could be operated to obtain imagery over all terrains and indeed provided the first information on sediment cover and the nature of the flat plains and slopes of the flanks of the MAR. The R.O.V. *Isis* was capable of imaging and sampling over all bottom types. For working on vertical cliff faces the main cameras on the ROV were mounted facing horizontally. Sampling on unstable tallus sediment slopes was very difficult owing to triggering of frequent avalanches and turbidite flows, which clouded the view from the cameras.

6. **Population genetics.** This study determined population connectivity between the four ECOMAR superstations and other areas of the Atlantic Ocean. Samples were obtained from the trawls and baited traps as well as comparative material from other expeditions.

2.2. Cruises

A series of four cruises was undertaken in the summer months of 2007–2010 (Bagley, 2008; Priede, 2007, 2009, 2010) (Table 1). Taking advantage of the sonar and dynamic positioning capabilities of the recently commission research vessel R.R.S. *James* Cook during the first cruise (JC011), the study area was mapped using swath bathymetry and locations of the four ECOMAR superstations where the depth was 2500 m were identified. An instrumented mooring with current meters and sediments traps was deployed at each station. Biological sampling was undertaken at all stations and CTD (conductivity temperature depth) casts were conducted from the south-west to north-west stations across the frontal region following the track of the TOPEX-POSEIDON satellite orbit (Fig. 1) to gather data on the water masses and flow regimes over the MAR (Read et al., 2010). In 2008 the R.R.S. *Discovery* serviced the moorings, collecting sediment trap samples and current meter data but no other sampling or survey work was done. The 2009 cruise (JC037) undertook a full biological sampling programme at each of the four stations as well as servicing the moorings. The area around the CGFZ was also visited by the NOAA FSV *Henry B. Bigelow* during 12 June–17 July 2009 to sample pelagic fauna around the sub-polar front and to repeat-sample some of the R.V. G.O. *Sars* bottom trawl stations. Results of that work are reported by Cook et al. (2013) and Sweetman et al. (2013). On the final cruise by the R.R.S. *James Cook* in 2010 (JC048), the remotely operated vehicle (ROV) *Isis* conducted video surveys and sample collections at all stations. All the moorings were recovered during this final cruise resulting in almost 3 years of continuous environmental data from all of the stations.

2.3. Station locations

Despite reference to the Charlie–Gibbs Fracture Zone in the title of the project little sampling was conducted within the fracture zone valleys. A long-term platform, DOBO, deep ocean benthic observatory (Kemp et al., 2008), was deployed in 2007 on the floor of Charlie–Gibbs North at 3690 m depth (52°41.35′N, 35°04.17′W) near the location previously instrumented and reported by Saunders (1994) to be representative of average flow through the CGFZ (Priede, 2007). DOBO failed and was recovered in 2010 having accumulated an assemblage of fouling organisms which are reported by Blanco et al. (2013). In 2010 R.O.V. *Isis* made video transects and observations megafauna on the sea floor of Charlie–Gibbs North in the vicinity of the DOBO location.

Most effort in ECOMAR was directed at the four ECOMAR superstations. A depth of 2500 m was targeted for all four stations to ensure comparability in view of the well-known zonation of bottom-living species with depth (Rex and Etter, 2010; Howell et al., 2002). This depth is near the middle of the lower bathyal zone (800–3500 m) as defined by UNESCO (2009) and at a depth stratum that is representative of the largest area of the flanks of the MAR. This depth also gave sufficient distance between east and west to be able to resolve ecological differences between the two sides of the ridge which might not be apparent at stations closer together on the crest of the ridge. The moorings deployed at each station were designed two sediment traps, one at 1000 m above the sea floor (1500 m below surface) and a second trap 100 m above the sea floor. Finding the correct depth defined the exact locations of the stations. It was pre-determined that the northern stations should be at 54°N, 142 km north of the northern rift valley of the CGFZ and away from the influence of the sub-polar front. The southern stations had to avoid tracks of submarine cables traversing the MAR. Consequently ca. 49°N was chosen. This resulted in a distance of 430 nautical miles between the northern and southern stations, which can be travelled by a research vessel within 48 h avoiding excessive cruise durations.

Prior to 2007, the GEBCO charts had a resolution of 1′ (IOC, IHO, BODC, 2003). The best available bathymetry for the MAR had been compiled by Murton (2003) from which charts down to 0.25′ resolution could be accessed. This resolution resulted in a 297×463 m grid on planning charts but higher resolution was necessary to plan sampling and deployments of equipment on the sea floor. During the first cruise, JC011, surveys were conducted from the R.R.S. *James Cook* with the Kongsberg EM120 multibeam swath bathymetry system. Data were displayed in real-time using OLEX 3D chart system software, (Olex AS, Trondheim, Norway). The multibeam system produced a grid of soundings at 40–50 m intervals over a swath width of 7 km at 2500 m depth which were interpolated by OLEX onto 14×14 m grid displayed in real time on a chart plotter. The flanks of the MAR consisted of alternating flat sedimentary plains and sloping terraces. Suitable locations for the moorings at 2500 m depth were found on either side of the ridge axis as shown conceptually in Fig. 3. The positions of the southern stations were adjusted so that a straight line between them was perpendicular to the local axis of the MAR. The surveys also revealed a sea mount summit on the western crest of the MAR between the SE and SW stations (Fig. 1). The minimum depth recorded was 741 m at 48°43.2′N, 28°10.0′W. Some sampling was

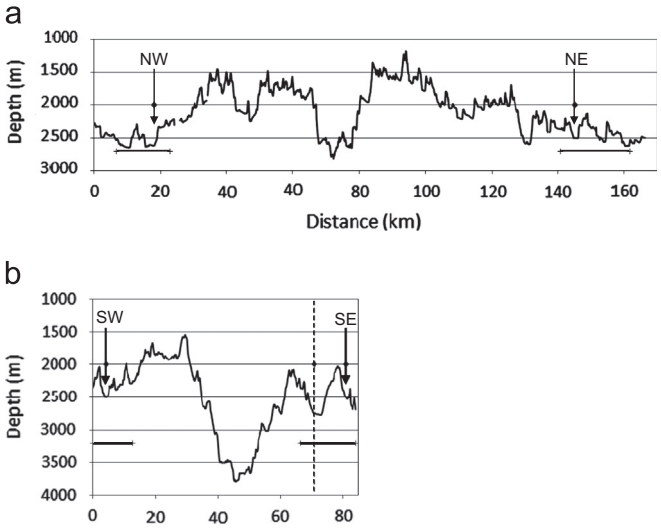

Fig. 4. Transects across the Mid-Atlantic ridge taken from swath bathymetry surveys by the R.R.S. *James Cook* in 2007 (Cruise JC011) sampled at 0.1′ longitude intervals. Horizontal bars—the areas covered by charts of the superstations (Figs. 5–8). Arrows—locations of the moorings placed at 2500 m depth at each of the superstations. (a) Northern transect at 54°N between 36°24′W and 33°51.3′W. The NW mooring is offset 1200 m south of the transect, the NE mooring is on the transect. (b) The southern transect between 48°45.696′N 28°41.348′W, 49°4.847′N 27°51.000′W (indicated by vertical dashed line) and 49°01.984′N 27°41.000′W.

also conducted at this location identified as number 37,378 in the global catalogue of seamounts (Yesson et al., 2011).

2.3.1. The northern stations

At latitude 54°N the MAR is approximately 980 km wide between the 3500 m depth contours on either side of ridge axis. The selected mooring locations (Table 2) are 127 km apart. The axial rift valley descends to a maximum depth 2814 m and the crest of the ridge is higher on the eastern side with a summit at 1179 m (Fig. 4a).

2.3.2. North-west superstation

The north-west mooring was deployed on the SE edge of a sedimentary plain (Fig. 5). A flat area to the north at around 2610 m depth was designated for trawling. To avoid rough ground, trawling had to be conducted in a “trawl box” along the middle of the plain in a North to South or South to North direction parallel to the MAR axis. This direction was generally perpendicular to the prevailing westerly winds and seas requiring use of the tracking capabilities of the R.R.S. *James Cook* dynamic-positioning system and thrusters to maintain the correct course for trawling. The position for coring was at 2620 m depth in the centre of the flat plain avoiding the trawl box. Baited landers were placed at depths close to 2500 m to the south and west of the mooring location but were spaced at least 1500 m apart to avoid mutual interference of odour plumes from adjacent stations. During cruise JC011 SHRIMP was deployed twice on transects across contrasting steep and flat terrain to observe the sea floor. During cruise JC048 five dives were conducted with R.O.V. *Isis* to the SW of the mooring location. The range of depths sampled at the NW station was from 2210 m on the summit of the terraces to 2620 m on deepest parts of the trawling areas.

2.3.3. The north-east superstation

The north-east mooring was located on a sedimentary plain at 54°N with the site chosen for coring in the centre 1130 m to the north (Fig. 6). A large expanse suitable for trawling was found 15 km towards the east with an average depth of 2440 m. SHRIMP

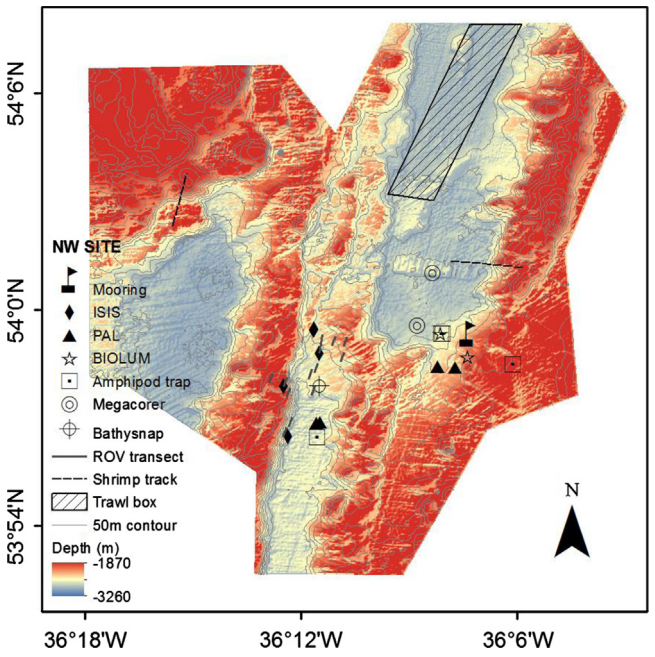

Fig. 5. The north-west superstation showing the mooring location and areas sampled. Bathymetry from multibeam swath surveys during cruise JC011 in 2007 processed by OLEX software and displayed using ArcGIS. Mooring—location of the sediment trap mooring on sea floor at 2500 m depth; ISIS—starting points of R.O.V. *Isis* dives during cruise JC048; PAL—locations of baited lander (Photo Acoustic Lander) for fish studies (Cousins et al., 2013-b); BIOLUM—locations of bioluminescence lander with high sensitivity camera (Craig, 2012); Amphipod trap—trap locations (Horton et al., 2013); Megacorer—Multi-corer location (Shields et al., in press); Bathysnap—long term time lapse camera location (Priede, 2007); ROV transect—500 m long video line transects of the sea floor during cruise JC048 (Bell et al., 2013; Jones et al., 2013). Shrimp track—sea floor video survey line by SHRIMP during cruise JC011 (Priede, 2007); Trawl box—flat area of sea floor within which bottom trawling was done for invertebrate megafauna (Alt et al., 2013) and fishes (Cousins et al., 2013-b).

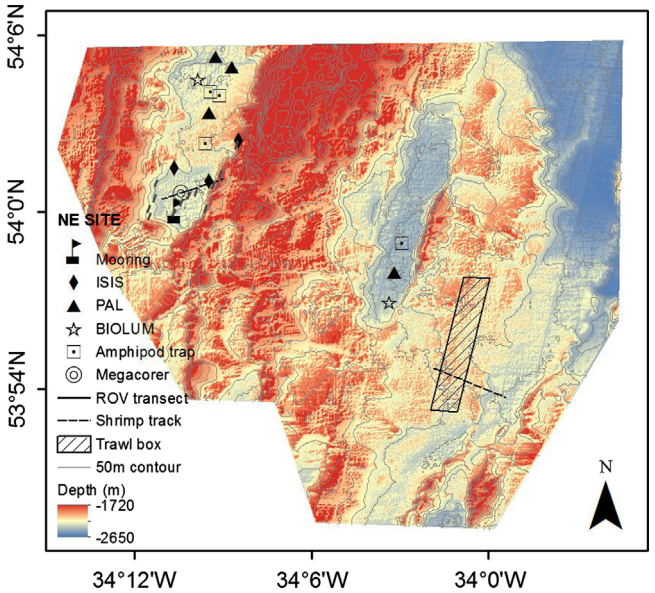

Fig. 6. The north-east superstation showing the mooring location and areas sampled. Key as for Fig. 5.

was used for surveys across the trawl area and steep terraces and the plain near the mooring site. Three R.O.V. *Isis* dives were located near the mooring location in areas of contrasting slopes. Baited

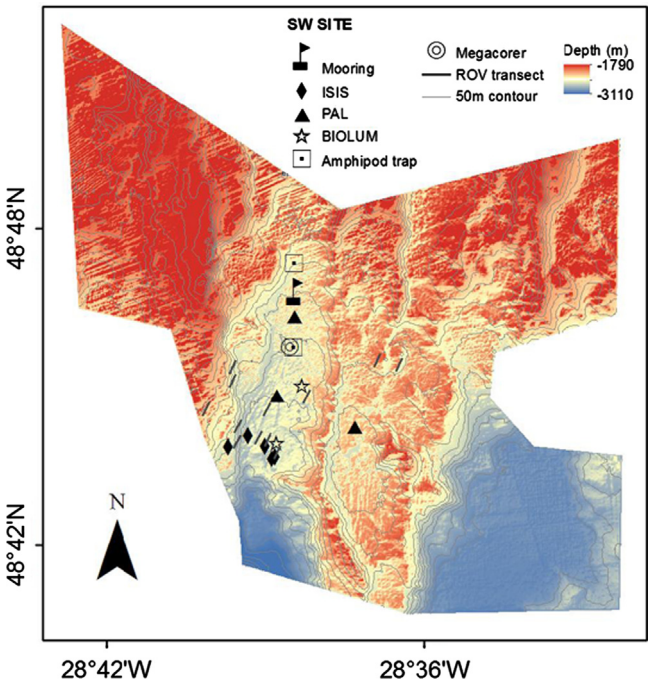

Fig. 7. The south-west superstation showing the mooring location and areas sampled. Key as for Fig. 5.

landers were deployed north of the mooring location and on a flat plain between the trawl and mooring area. The depths sampled ranged from 2235 m on the crests of the ridges down to 2555 m.

2.3.4. *The southern stations*

The MAR is much narrower in the south than the north. The width between the 3500 m depth contours is 128 km and the distance between the ECOMAR mooring locations was 73 km. The axial valley depth is 3793 m, increasing to over 4000 m nearby. The western crest of the ridge is 1547 m, higher than the east (Fig. 4b).

2.3.5. *The south-west superstation*

The SW mooring was deployed on flat ground towards the north of a sedimentary plain (Fig. 7). Sufficient flat ground at an appropriate depth for trawling was not found at the SW superstation. The megacorer was deployed on a sedimentary plain 2 km to the south of the mooring and baited lander deployments were located nearby. Six R.O.V. *Isis* dives were conducted to the south across the sedimentary plain and on the steep scarp slope to the west. The overall range of depths sampled in the SW was 2366–2628 m depth.

2.3.6. *The south-east superstation*

The SE mooring was located on an open slope east of the MAR with very little flat terrain in the near vicinity (Fig. 8). The trawling area and megacorer station were situated in a sedimentary basin 13 km nearer the MAR axis to the west at a depth of 2750 m. Most of the lander deployments were conducted around the mooring location closer to the target depth of 2500 m but with some exploration of shallower depths. SHRIMP was used for one transect across part of the trawling basin and sloping terrain to the west. The five R.O.V. *Isis* dives were distributed between flat substrate in the trawl box and steeper slopes near the mooring. The overall range of depths sampled in the SE was 2056–2762 m.

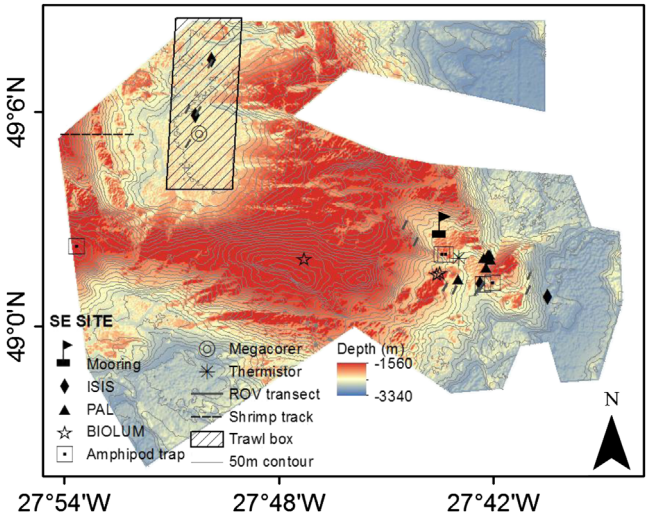

Fig. 8. The south-east superstation showing the mooring location and areas sampled. Key as for Fig. 5. Thermistor—thermistor chain mooring deployed during cruise JC037 (Priede, 2009)

3. Overview of results

In this introductory paper it is not appropriate nor possible to provide an exhaustive account of the ECOMAR project, the purpose here is to indicate how the sampling described above was utilised. Priede et al. (2013a) and Niedzielski et al. (2013) show that the MAR accounts for 44.7% lower bathyal area (800–3500 m depth) in the North Atlantic Ocean. The pattern of circulation over CGFZ section of the MAR and the path of the North Atlantic current are described by Read et al. (2010). Although the predominant surface current is west to east, data from the moorings shows the topography steers the near-bottom flow to follow the north–south orientation of the terraced structure of the flanks of the MAR so that benthic organisms experience tidal and residual flow parallel to the ridge axis (Priede at al. 2013a). Time-series integration of thermal front detection provided new information on the spatial and seasonal distribution of oceanic fronts in the North Atlantic. At the surface there was a complex pattern of fronts and whilst the northern stations were clearly in cooler waters north of the sub-polar front, the southern stations were within the frontal zone of complex circulation and the NAC (Miller et al., 2013). This approach has revealed that the influence of the MAR on deep circulation also guides the surface flows from branches of the NAC.

A conspicuous feature on the sea surface at the ECOMAR study area was the presence of sea birds and sea mammals. During cruise JC011 systematic counts were performed and submitted to the Trans North Atlantic Sightings Survey (TNASS, http://www.nammco.no/Nammco/Mainpage/Tnass). Over 300 northern fulmar (*Fulmarus glacialis*) were observed around the vessel on one occasion at the NW superstation (Priede, 2007). Edwards et al. (2013) tracked a nesting male that travelled from Scotland to the MAR, foraging along persistent fronts, returning to the nest within 15 days indicating potential for connectivity between nesting coastal birds and foraging in mid ocean regimes. Godø et al. (2013) analysed data from a moored inverted echosounder deployed on the MAR at 920 m depth during the voyage of R.V. *GO Sars* in 2004. They were able to track whales during feeding dives between the surface and the summit of the MAR.

Primary production on the MAR was clearly influenced by the pattern of fronts. There was some evidence of higher production over the shallower Reykjanes ridge section of the MAR south of

Iceland (Tilstone et al., 2013). Martinez-Vicente et al. (2012) examined the relationship of phytoplankton and bacteria to optical backscattering over MAR and detected three different pelagic plankton communities associated with the sub-polar front.

Mean export flux from the surface over the four ECOMAR superstations (Priede et al., 2013a) was not greater than that recorded over the Porcupine Abyssal Plain by Lampitt et al. (2010) suggesting there is no regional enhancement over the MAR. Analysis of the sediment trap data (Abell et al. 2013) supported this conclusion. The biodiversity and abundance of zooplankton, especially euphausiids over the MAR are described by Letessier et al. (2009, 2011, 2012). Sutton et al. (2013) list 56 species of mid-water fishes captured during ECOMAR cruises JC011 and JC037.

Numerous samples of benthic fauna from the CGFZ area were collected during the ECOMAR cruises (Gebruk et al., 2013; Priede et al., 2013b). Benthic foraminifera are described by (Gooday et al., 2013a, 2013b), glass sponges (Porifera, Hexactinellida) by Lopes and Tabachnick (2013) and Tabachnick and Menshenina (2013), mushroom soft corals (Octocorallia: Alcyonacea: Alcyoniidae) by Molodtsova (2013) and polychaetes by Kongsrud et al. (2013), Shields and Blanco-Perez (2013) and Shields et al. (2013). From the amphipod traps new species are described by Horton and Thurston (2011, 2013) together with novel information on population structure of *Abyssorchomone abyssorum* (Duffy et al., 2013) and genetic analysis of adaptive radiation of the Lysiannoidea (Corrigan et al., in press). Bottom trawl samples revealed 153 invertebrate megafauna taxa at the three stations that were sampled with significant differences in species composition and highest biodiversity at the SE superstation (Alt et al., 2013). From benthic trawl samples and ROV collections the asteroids are described by Dilman (2013) and holothurians by Rogacheva et al. (2013). Some holothurians were observed to lift off the bottom and swim, showing considerable ability to move by this means across the complex terrain of the MAR (Rogacheva et al., 2012).

Using the R.O.V. *Isis* the first Atlantic Ocean specimens of free-living deep sea torquaratorid acorn worms (Hemichordata, Enteropneusta) were retrieved and included a new genus and three new species (Osborn et al., 2012; Priede et al., 2012). There was a distinct latitudinal difference in distribution with the larger *Tergivelum cinnabarinum* numerically dominant at the northern stations and smaller wide-lipped species *Yoda purpurata* prevalent in the south (Jones et al., 2013). From ROV video transects Bell et al. (2013) analysed the diversity and occurrence of bioturbation traces or lebenspurren at each of the stations and documented significant reworking of the sediment by a variety of fauna. Using a low light camera on the R.O.V. *Isis*, Craig et al. (2011) observed naturally-occurring displays of bioluminescence from zooplankton impinging on stalked crinoids *Anachalypsicrinus nefertiti* on rocky outcrops suggesting that such locations might be visually conspicuous to deep sea fauna in an environment devoid of solar light.

Demersal fishes were sampled by trawl (26 species) (Cousins et al., 2013b), baited landers (19 species) (Cousins et al., 2013-a) and by ROV (six species) (Linley et al., 2013). The baited lander detected five species, mainly Chondrichthyes, that were not captured by the trawls. Biomass, abundance and biodiversity showed strong similarities to the NE Atlantic ocean margins of the Porcupine Seabight. Fish samples from ECOMAR, previous cruises to the MAR and elsewhere were used in genetics studies on the orange roughy (*H. atlanticus*) (White et al., 2009a, 2009c) the roundnose grenadier (*C. rupestris*) (White et al., 2009b, 2010b, 2010c), shortbeard grenadier (*Coryphanoides brevibarbis*) (White et al., 2009b, 2010a) blue hake (*Antimora rostrata*) (White et al., 2010b, 2011) and abyssal grenadier (*Coryphaenoides armatus*) (Ritchie et al., 2013). Generally there is a lack of structure in the populations indicating a high degree of connectivity across the Atlantic Ocean.

Reid et al. (2012) conducted stable isotope analysis of carbon, nitrogen and sulphur from 28 invertebrate species and 10 species of fishes collected from the northern and southern ECOMAR superstations in order to elucidate their trophic status. They identified two dominant trophic pathways with organic matter passing either through deposit feeders or predatory and scavenging deep-sea fishes and crustaceans. Detailed studies on four species of fishes *A. rostrata*, *C. armatus*, *Coryphaenoides brevibarbis* and the abyssal halosaur, *Halosauropsis macrochir* (Reid et al., 2012, 2013) show great variability in tissue isotopic signatures, possibly related to dietary shifts during growth. Analysis of fatty acids and stable isotopes in *C. armatus* suggested that physiological processes may also influence biomarker signatures (Mayor et al., 2013).

4. Conclusions

The MARECO (Bergstad et al., 2008) and ECOMAR sampling programmes have provided unprecedented detailed information on the biology of an important segment of the MAR. Despite topographical complexity, the sea floor is dominated by soft sediment coverage (Niedzielski et al., 2013) with bare rock only outcropping in the steepest areas or cliffs. The Northern MAR is an area of relatively slow spreading of the sea floor, ca. 25 mm yr^{-1} (Aumento et al., 1968) compared with rates over four times faster in spreading centres in the Pacific Ocean. Slow spreading and the depth of the ridge crest ($>$ 1000 m) well below the influence of surface currents may be conducive to sediment accumulation. The fauna found are typical of sedimentary bathyal continental slope and rise settings. By focussing on four stations at 2500 m depth ECOMAR provided a basis for comparison of MAR fauna in different biogeographic regions. It may be possible to conduct a similar study in future four sampling sites at 1500 m depth. Such a study higher up the flanks of the MAR featuring mid to upper slope fauna where biodiversity and biomass are likely to be higher may be an obvious next stage for research on this sector of the MAR.

Following the start of the ECOMAR programme the marine protected areas (MPAs) have been established on the MAR around the Charlie–Gibbs Fracture Zone by both OSPAR (Olso-Paris Convention) and the NEAFC (North-East Atlantic Fisheries Commission) (O'Leary et al., 2012). It is interesting to note that four ECOMAR superstations are near the northern and southern boundaries of the NEAFC area. The SW superstation and the seamount fall outside the southern boundary of both OSPAR and NEAFC MPAs.

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