Regional Environmental Assessment of the Northern Mid-Atlantic Ridge

Technical Study No. 29

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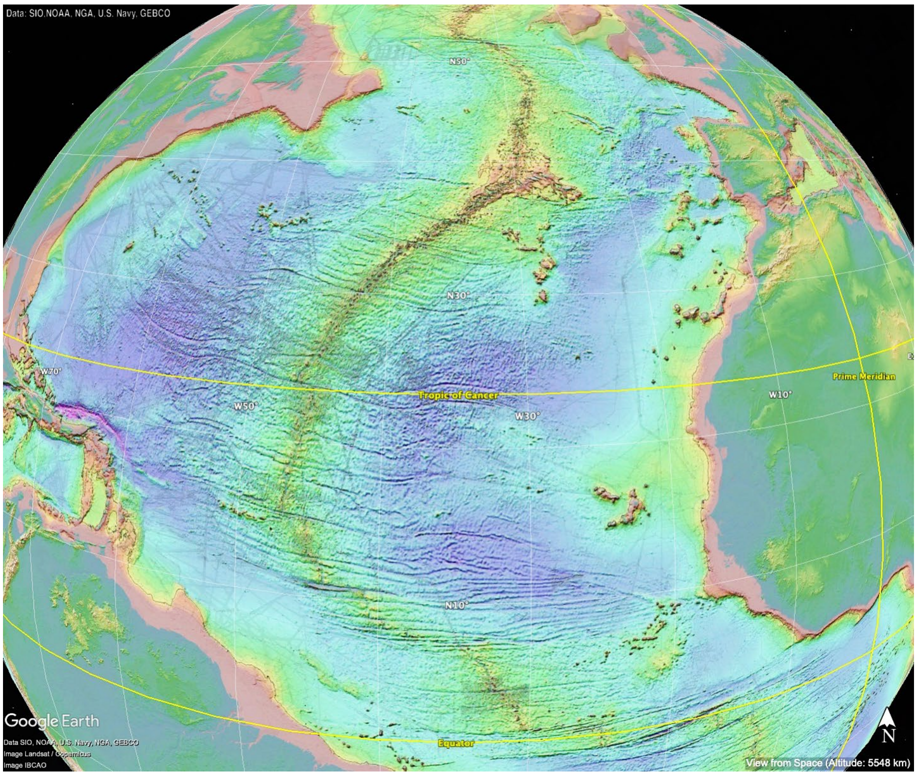
Regional Environmental Assessment of the Northern Mid-Atlantic Ridge



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1. Abbreviations

The Area	The seabed and ocean floor and subsoil thereof, beyond the limits of national jurisdiction
AABW	Antarctic Bottom Water
ABNJ	Areas Beyond National Jurisdiction
AMOC	Atlantic Meridional Overturning Circulation
AMV	Atlantic Multidecadal Variability
AUV	Autonomous Underwater Vehicle
BBL	Benthic Boundary Layer
CGFZ	Charlie-Gibbs Fracture Zone
COML	Census or Marine Life
ECOMAR	Ecosystems of the Mid-Atlantic Ridge at the Sub-Polar Front and Charlie-Gibbs Fracture Zone
ECS	Extended Continental Shelf
EEZ	Exclusive Economic Zone
EIA	Environmental Impact Assessment
EMP	Environmental Management Plan
GMPJO	Geometric Mean of the Proportion of Joint Occurrences
GOODS	Global Open Oceans and Deep Seabed biogeographic classification
ICCAT	International Commission for the Conservation of Atlantic Tunas
ISA	International Seabed Authority
ISOW	Iceland-Scotland Overflow Water
ITCZ	Intertropical Convergence Zone
IUCN	International Union for Conservation of Nature
JOGMEC	Japan Oil, Gas and Metals National Corporation
LTC	Legal and Technical Commission of the ISA
MAR	Mid-Atlantic Ridge
MAR-ECO	Patterns and processes of the ecosystems of the northern mid-Atlantic METI Japanese Ministry of Economy, Trade and Industry
MiCO	Migratory Connectivity in the Ocean project
MOMAR	Monitoring the Mid-Atlantic Ridge project
Mt	Million tons
NAC	North Atlantic Current
NADW	North Atlantic Deep Water
NAO	North Atlantic Oscillation
NBC	North Brazil Current
NEC	North Equatorial Current

NECC	North Equatorial Counter Current
nMAR	That part of the MAR that lies in the North Atlantic
nSEC	Northern branch of the South Equatorial Current
NOAA	National Oceanic and Atmospheric Administration
ODP	Ocean Drilling Programme
PMS	Polymetallic sulphides
RALS	Riser and Lift System
REMP	Regional Environmental Management Plan
ROV	Remotely Operated Vehicle
SEA	Strategic Environmental Assessment
SEC	South Equatorial Current
SponGES	Deep-sea sponge grounds ecosystems of the North Atlantic project
TAG	Trans-Atlantic Geotraverse hydrothermal field
UNCLOS	1982 United Nations Convention on the Law of the Sea
VME	Vulnerable Marine Ecosystem
VTS	Vertical Transport System
WOCE	World Ocean Circulation Experiment

2. Document purpose and scope

This document represents a compilation of background information to support the ISA secretariat in facilitating the development of a Regional Environmental Management Plan (REMP) by the International Seabed Authority (ISA) for the Area in the North Atlantic Ocean with a focus on polymetallic sulphides (PMS) deposits. REMPs are a key component of the ISA's strategy to ensure effective protection for the marine environment from harmful effects of deep-sea mining (ISA, 2019a). The ISA is mandated, in accordance with article 145 of UNCLOS, and with respect to activities in the Area, to take the measures necessary to ensure effective protection for the marine environment from harmful effects that may arise from those activities, and to adopt appropriate rules, regulations and procedures for, *inter alia*, the prevention, reduction and control of pollution and other hazards to the marine environment, the protection and conservation of the natural resources of the Area and the prevention of damage to the flora and fauna of the marine environment. Regional Environmental Management Plans therefore form part of the Authority's policy framework for environmental management. Approaches for facilitating development of such plans were presented to the ISA Council in February 2019 (ISA, 2019b). The Mid-Atlantic Ridge (MAR) in the North Atlantic Ocean has been identified on a preliminary basis as a priority area for development of REMPs for polymetallic sulphide deposits (ISA, 2019c).

Polymetallic sulphides are one of the three seabed mineral resources for which the ISA has awarded contracts for exploration – the others being manganese nodules and cobalt crusts. Polymetallic sulphides have analogous deposits on land and can contain economic proportions of metals such as copper, zinc, lead, gold and silver. It is important to note that deep-sea mining is still in an exploration phase and that no actual mining has yet taken place. There are therefore few precedents for developing REMPs. The only other Environmental Management Plan (EMP) developed by the ISA is for the Clarion-Clipperton Zone in the Pacific Ocean where exploration of manganese nodules is taking place (ISA, 2012). Polymetallic sulphides are a very different resource to manganese nodules, with different mining practices and they are located in very different environmental settings. It is therefore necessary to adapt area-based management approaches and other management measures taking into account the specific characteristics of polymetallic sulphide mining in the Atlantic, which will be different from the ones developed for nodule mining in the Pacific.

The MAR is host to a variety of ecosystems controlled by multiple factors such as water depth, food supply, seabed substrate and water mass characteristics. At certain locations along the MAR axis the high heat flows associated with plate tectonics drive the expulsion of hydrothermal fluids, which creates an additional seafloor habitat that sustains hydrothermal vent communities of organisms. The linear nature of mid-ocean ridges and intermittent occurrence of hydrothermally active areas along ridges pose challenges to these specialised communities, whose populations need to be able to interconnect from one hydrothermal vent site to another. In addition, areas with low levels of hydrothermal venting together with inactive vent sites are poorly characterised but may also support diverse and complex seafloor communities. Elsewhere along the MAR axis rocky substrates are common, and can support habitat-forming species, such as corals and sponges, that in turn host larger complex biological communities. This corridor of rocky habitats a few tens of kilometres wide along the ridge axis is the focus for exploration for minerals along the MAR.

This document provides an aggregation and synthesis of existing information relating to the northern MAR, including geomorphology, physical characteristics, geology and biological communities, as well a description of the current mining areas, mining process and ecosystem features (regional biodiversity, temporal variability, trophic relationships, ecosystem functioning, connectivity, resilience and recovery). This information will form the basis to conduct a regional environmental assessment, addressing knowledge gaps, to support the application of area-based management approaches and addressing cumulative impacts, which will inform the identification of elements for inclusion in the regional environmental plan for the MAR. This document should be of value beyond the development of the REMP where it can be used to set the regional framework for contractor's Environmental Impact Assessments (EIA's) and for subsequent re-evaluations of the REMP. As such it should be regarded as a living document that will be updated from time to time as new information becomes available.

2.1 References

International Seabed Authority. (2012) Decision of the Council relating to an environmental management plan for the Clarion-Clipperton Zone. ISBA /18/C/22.

International Seabed Authority. (2019a) Decision of the Assembly of the International Seabed Authority relating to the implementation of the strategic plan for the Authority for the period 2019–2023. ISBA /25/A/15.

International Seabed Authority. (2019b) Implementation of the Authority's strategy for the development of regional environmental management plans for the Area. ISBA /25/C/13.

International Seabed Authority. (2019c) Preliminary strategy for the development of regional environmental management plans for the Area. ISBA /24/C/3.

3. Area of consideration

In order to provide regional context for the REMP development it is necessary to understand physical processes and ecosystem distributions at full basin scale rather than simply along the Mid-Atlantic Ridge and within the Area. Thus, we have taken a wide remit looking at processes and ecosystems that occur across the North Atlantic from Iceland to the equator. The information compiled in this document extends from the southern boundary of the Icelandic extended continental shelf claim on the Mid-Atlantic Ridge (MAR) to the equator, exclusive of the Portuguese extended continental shelf (ECS) claim north and south of the Azores and the Brazilian Exclusive Economic Zone (EEZ) around the islands of St Peter and St Paul (Figure 3.1). Data covering the overlying water column is also included. The data sets we have compiled are from public sources, consisting of published scientific papers, biogeographic databases and online libraries. The specific geographic scope to be covered by the REMP will be considered through ISA processes.

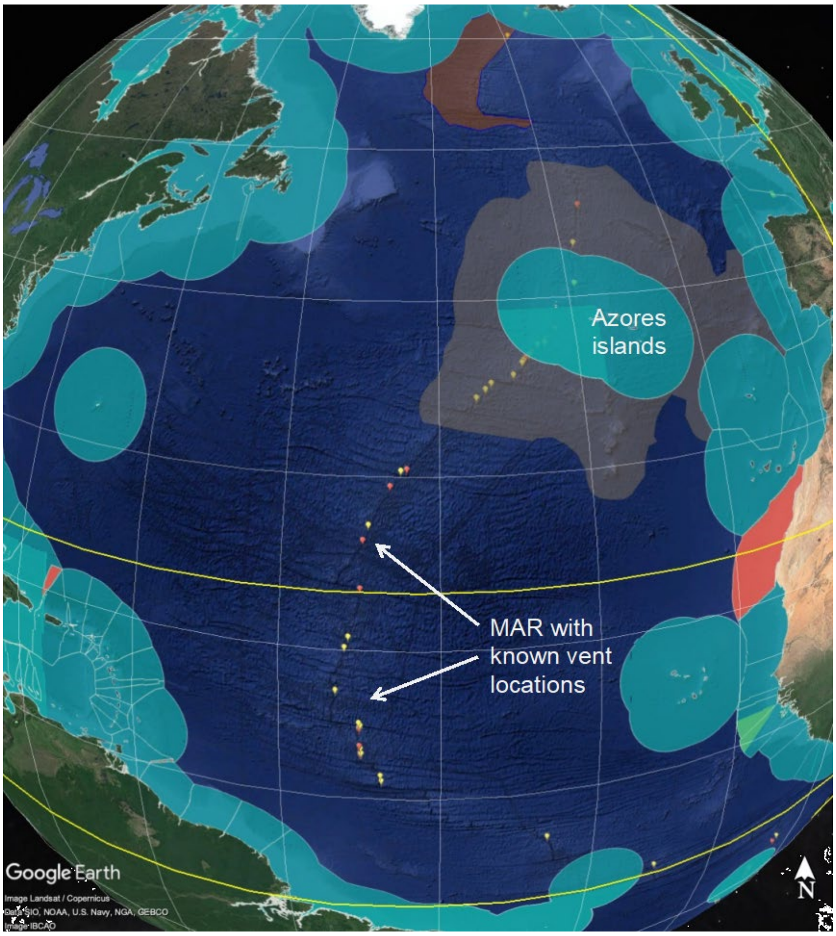

Figure 3.1. The geographic coverage of the background information to inform the development of the REMP for this region extends along the Mid-Atlantic Ridge from the southern boundary of the Icelandic extended continental shelf (ECS) claim (brown shading) to the equator, exclusive of the Portuguese extended continental shelf (ECS) claim north and south of the Azores (grey shading) and the Brazilian Exclusive Economic Zone (EEZ) around the islands of St Peter and St Paul. Boundaries on this map should not be taken as confirmed and the reader is directed to the disclaimers associated with the data sources. Data compiled from Google Maps with maritime boundaries from the Flanders marine Institute (www.marineregions.orghttps://doi.org/10.14284/312).

4. Geological Overview of the Mid-Atlantic Ridge of the North Atlantic

4.1 Description of the Mid-Atlantic Ridge

The Mid-Atlantic Ridge is an elevated area of seafloor that runs roughly north-south through the middle of the Atlantic Ocean (Figure 4.1). It is elevated because of convection cells within the mantle that bring hot mantle material towards the surface thus doming the crust. These convection cells diverge along the ridge axis pulling the crust apart with new lava flows and intrusive dykes creating new crust. This is the lithospheric plate boundary between the Eurasian and African plates to the east and the American and South American plates to the west. The MAR is a slow spreading plate boundary where the plates move apart at a rate of 20-30 mm/yr (see summary in Beaulieu et al, 2015). As the plates move away from the axis of the MAR and cool, their elevation decreases so that the deepest parts of the North Atlantic lie between the ridge and the continental margins to either side.

The ridge axis is broken into numerous segments by fracture zones that are formed by transform faults, and which can offset the ridge by hundreds of metres to hundreds of kilometres. The largest fracture zone in the Atlantic Ocean, located just south of the equator, is the Romanche Fracture Zone, which offsets the ridge axis by 900 km. Fracture zones appear as narrow, steep-sided valleys which can be as deep as 7761 m water depth in the case of the Romanche Fracture Zone. The Charlie Gibbs Fracture Zone is another large feature located between Iceland and the Azores, which creates an offset of 350 km (Figure 4.1) and is over 4500 m deep at its deepest location. The Vema Fracture Zone located at 10° 46' N is a narrow ~5000 m deep valley that offsets the MAR by 320 km (Kastens et al., 1999).

A number of different methods have been used to provide seafloor bathymetry maps each with varying degrees of coverage, resolution, and topographic uncertainty. Satellite based methods such as gravimetry and radar altimetry combined with often infrequent shipborne measurements can give large-scale structural estimates of whole oceans but with relatively low resolution. Ship mounted systems greatly improve the resolution especially multibeam echosounders, which provide broad swaths of data that can be compiled into aerial maps. However, in the deep sea there is a large acoustic footprint that results in relatively low resolution. To date relatively few areas have been mapped by swath bathymetry. Publicly available multibeam bathymetry data is available on the NOAA Bathymetric Data Viewer website (https://maps.ngdc.noaa.gov/viewers/bathymetry/) and an example of the data coverage is shown in Figure 4.2. The nMAR is one area where such data has been collected over many years of scientific investigation but there are large sections of the ridge axis that have no swath bathymetry and other areas where it varies from a few kilometres to a few tens of kilometres coverage either side of the ridge axis. This means that large areas of the ridge axis are poorly surveyed.

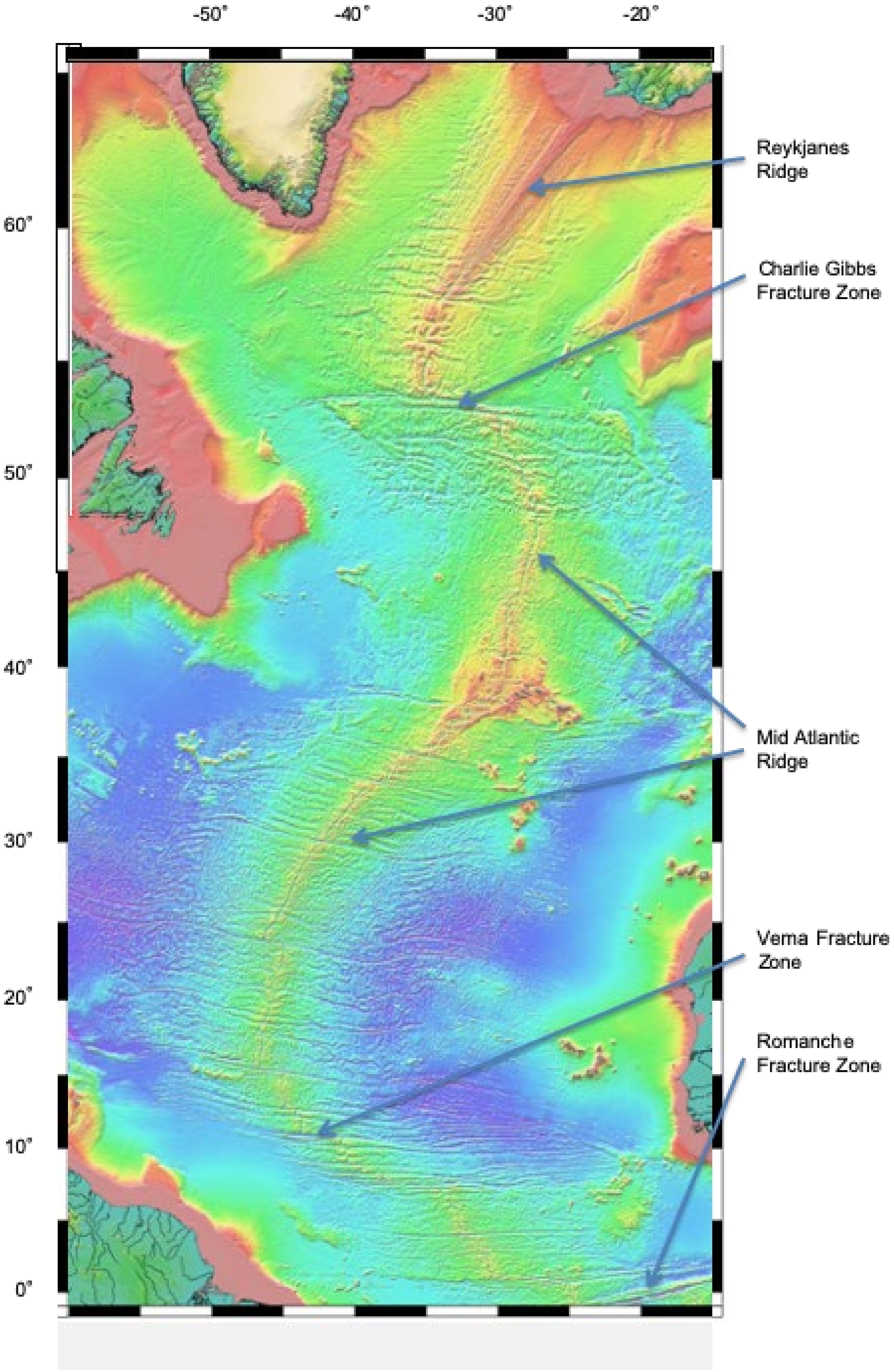

Figure 4.1 Bathymetry of the North Atlantic. Data grids and images are available at [http://topex.ucsd.edu/WWW html/srtm30 plus.html](http://topex.ucsd.edu/WWW_html/srtm30_plus.html). Reference: Becker et al., 2019)

The highest resolution data is obtained from multibeam echosounders operated close to the seabed either in remotely operated or autonomous vehicles. Such deep-towed surveys are expensive and cover very small areas but can produce images with great clarity (see for example Figure 4.3).

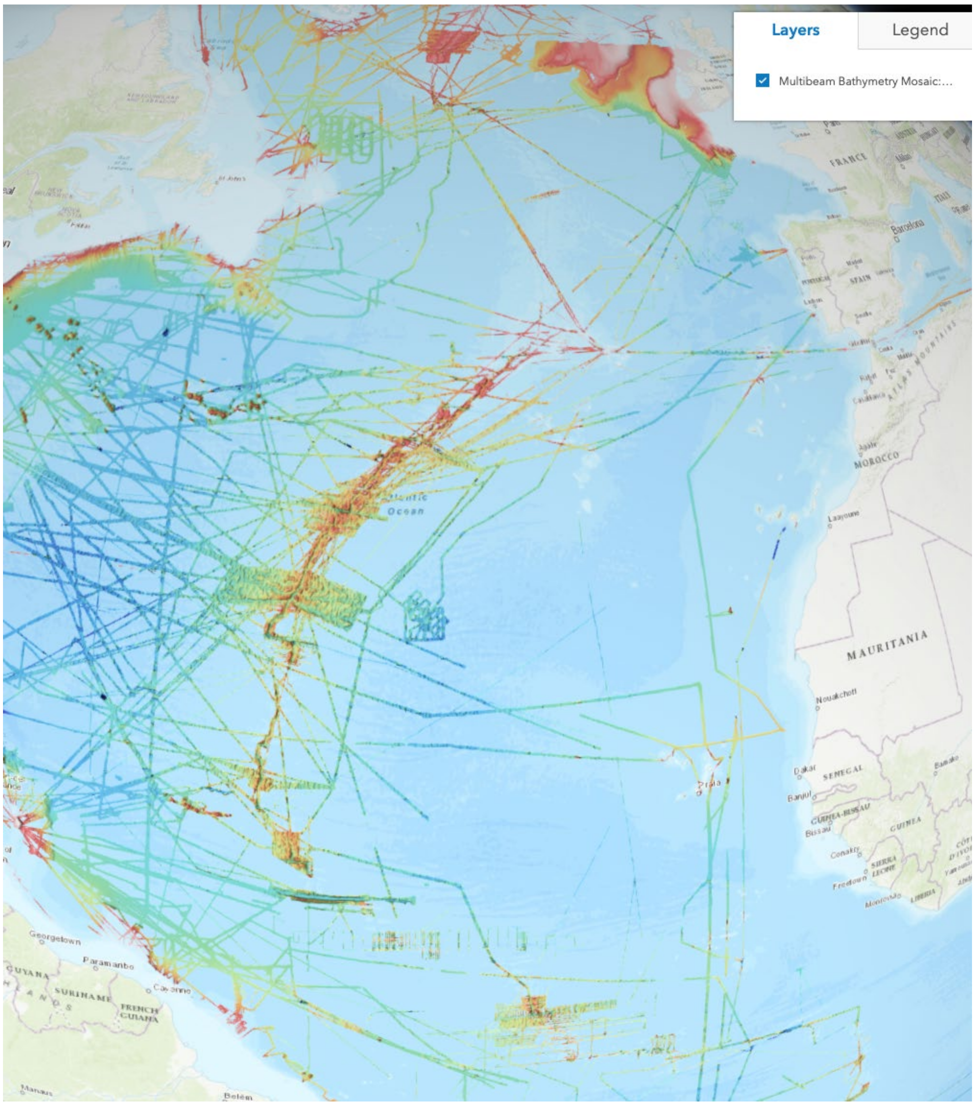

Figure 4.2. Colour shaded relief visualization of gridded multibeam bathymetric data from surveys archived at NOAA's National Centers for Environmental Information (NCEI). https://noaa.maps.arcgis.com/home/item.html?id=6b16e66ffd3740b5820875ad0af25042 accessed 22 August 2019

High-resolution bathymetry shows that the MAR comprises a middle (or axial valley) often with steep sides (Figures 4.3) through which runs the plate boundary. Outside of the middle valley there may be a series of ridges running parallel to the middle valley formed by faults in the crust. A recent paper by Klischies et al. (2019) shows one of the first detailed geological maps of a broader part of the ridge axis (Figure 4.4). Here a distinct set of ridges and valleys can be seen paralleling the ridge axis. The increasing build-up of sediment is apparent in the valleys as the crust becomes older away from the ridge axis. This sediment is formed from settling skeletons of plankton and wind-blown dust and progresses with time eventually smoothing off the topography and forming layers that may eventually reach a few kilometres in thickness (Figure 4.5). This means that the seabed of the ridge axis, including a strip a few kilometres to tens of kilometres to each side, is predominantly rocky, whilst beyond this the seabed is predominantly sedimented. The rate at which the rocks become sediment covered depends on the rate of sediment supply and the speed of plate movement. Sediment supply is controlled by the productivity of the surface ocean, input of wind-blown material and any dissolution of carbonate and/or silica at the seabed (Olson et al., 2016). Figure 4.6 shows higher rates of sediment supply around and north of the Azores compared to the ridge south of the Azores and Table 4.1 indicates slightly higher spreading rates to the south. Thus, the total area of the MAR covered by sediment is likely to be less south of the Azores to the equator.

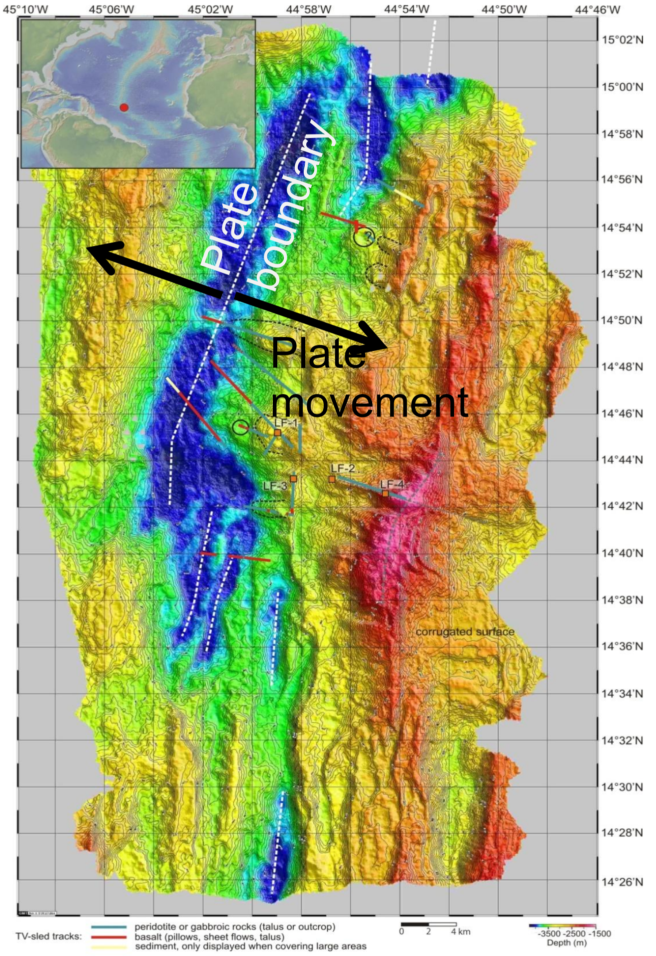

Figure 4.3 Detailed bathymetry of part of the Mid-Atlantic Ridge showing axial valley (marked by dashed white lines) and a series of ridges and troughs running parallel to the valley. Modified from Augustin, 2007.

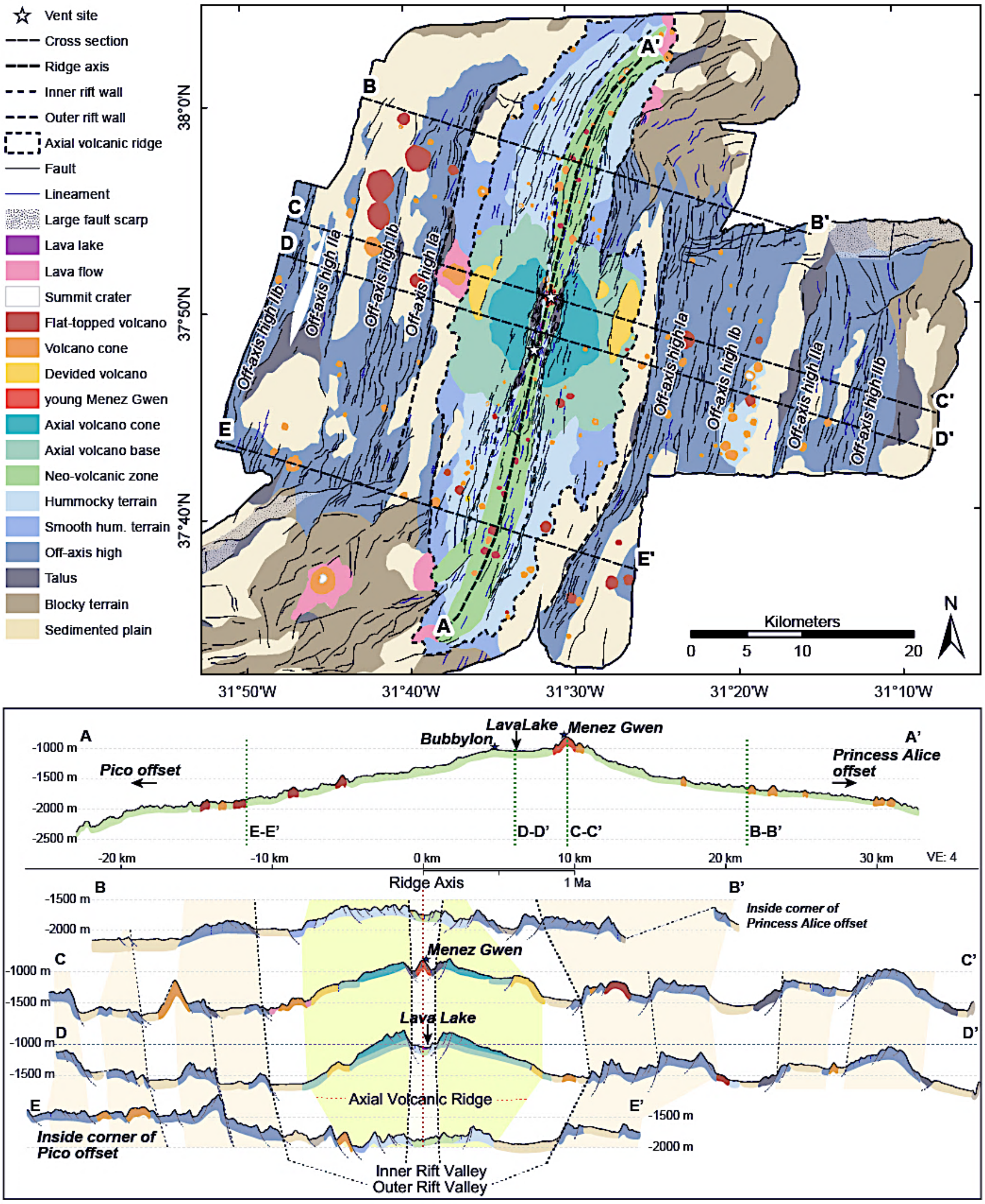

Figure 4.4 A) Geologic map with profile lines corresponding to the cross sections presented in B. B) Cross sections (vertical exaggeration of 4) through the Menez Gwen segment: A-A' along axis cross section Other cross sections axis-perpendicular from west (left) to east (right), and north (B-B') to south (E-E'). Colours refer to the mapped terrain units in A. Dashed lines connect major fault zones (black) and the ridge axis (red), which is considered to reflect crust of zero age. Shading highlights relatively elevated areas of off-axis high terrain interpreted to reflect periods of increased magmatic activity. (Figure courtesy of M. Klischies, GEOMAR).

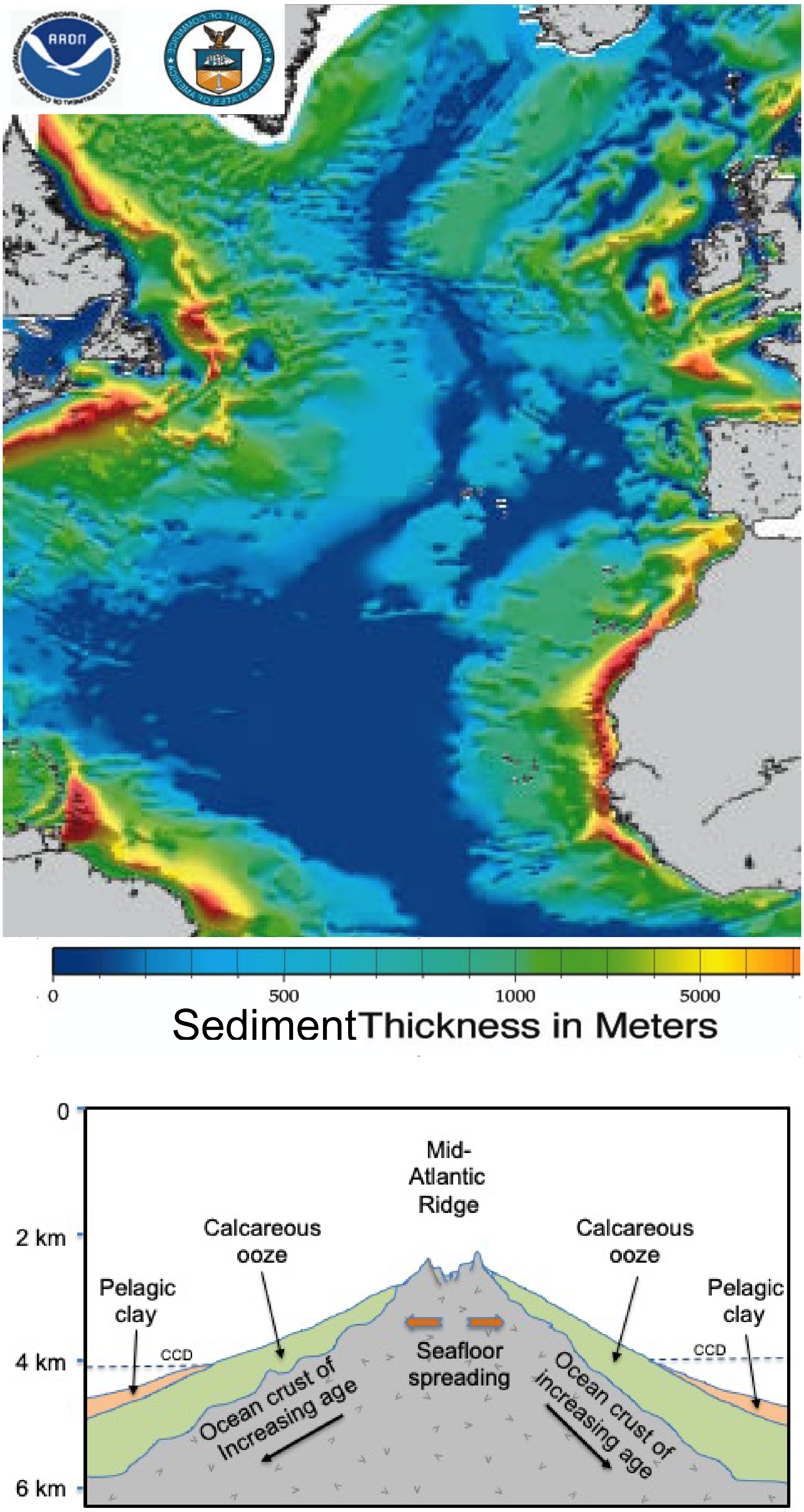

Figure 4.5. A) ***Upper panel****. Sediment thickness in the Atlantic Ocean. From NOAA Total Sediment thickness of the World's oceans and marginal seas* https://ngdc.noaa.gov/mgg/sedthick/ *B)* ***Lower panel.*** *Cross section of the MAR showing increasing age of crust away from ridge axis and gradual sediment build up away from the ridge axis.*

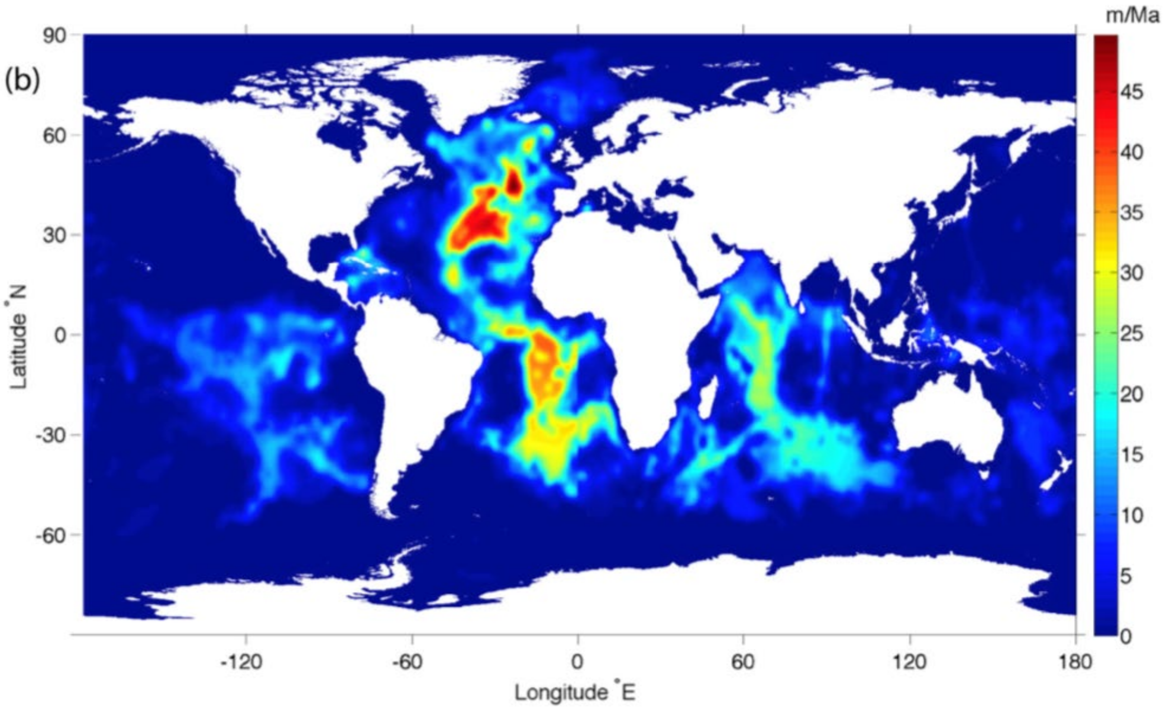

Figure 4.6 Present-day global ocean sediment accumulation rates. Reproduced from Olson et al (2016).

Niedzielski et al. (2013) carried out detailed surveys of sediment cover on the ECOMAR study area of the MAR (Figure 4.7) and found that most areas were sediment covered. Rocky substrates were common in the immediate vicinity of ridge axis but away from this the area was largely sedimented with extensive sediment ponds developing further away from the ridge axis. Similarly, Priede et al. (2013) stated that "*Hard substrata in the form of rocky outcrops and cliff faces harbour a diverse assemblage of sessile fauna dominated by corals, sponges and crinoids, but the area is small*". Even some steep slopes were sedimented, although elevated outcrops that were swept clear of sediments by currents retained hard substrates. In the area of the MAR studied by Niedzielski, which extended 50-100 km either side of the ridge axis, only 5.6% had slopes steeper than 30° and 70% of these steep slopes had hard substrates. Thus Niedzielski et al. (2013) concluded that the MAR (defined by them as between water depths of 800 and 3500 m and extending a maximum of 400 km either side of the ridge axis – see Figure 4.7) had 90% sediment cover. This has important implications for biodiversity because there are significant differences between the faunas of hard substrates and sedimented substrates. For example, Morris et al. (2012) found 10 times more corals on rocky substrates than sedimented ones at 45°N on the MAR. Gebruk & Krylova (2013) also mention that hard substrates provide more heterogeneous habitats that increase diversity in the MAR – also because hard substrate fauna provide substrate for other organisms (See the Biology Chapters 8 & 10 for more detail).

The topography of the MAR with its longitudinal valleys and ridges and multiple fracture zones and sills causes constrictions in the circulation of bottom waters and acceleration in flow velocity that enhances turbulent mixing (St Laurent & Thurnherr 2007) and can also have an effect on habitat variability (Priede et al. 2013).

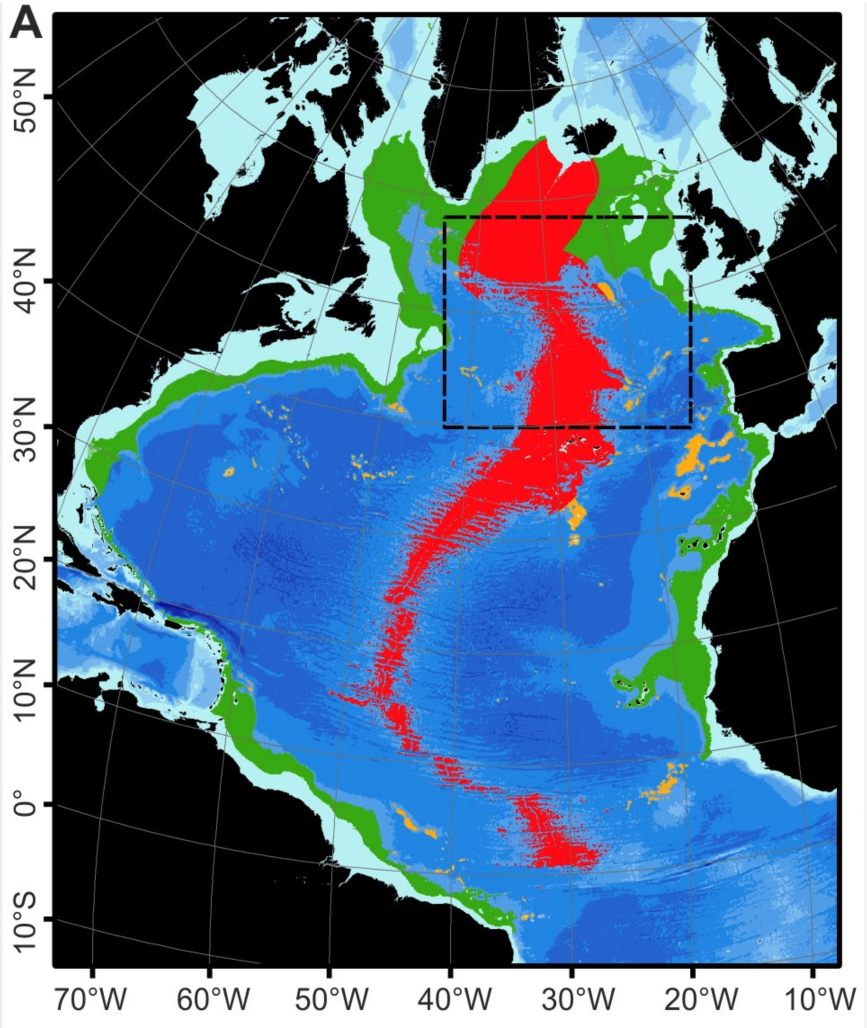

Figure 4.7. The North Atlantic basin showing the lower bathyal zones (depths 800–3500 m) on the MAR (red), continental margins (green) and non- contiguous seamounts (orange). The box represents the ECOMAR study area. Reproduced from Priede et al., (2013).

4.2 Seamounts

Seamounts are important features of the Atlantic seafloor since they are elevated above the local topography and often provide habitat for locally increased numbers of species and frequently have increased biomass. They occur commonly along the MAR and its flanks (Clark, et al., 2011; Yesson, et al., 2011). Seamounts may have steep sides where sediment does not collect, or they may be subject to swift currents that sweep away sediments leaving rocky substrates. These hard surfaces provide anchorage points for sessile filter-feeding animals and some of these, such as corals and sponges, provide structural habitat for many other species (Nalesso et al., 1995). In a study off New Zealand Rowden et al. (2010) showed that biomass was four times greater on seamounts than on adjacent continental margin slopes at equivalent depths due to high densities of stony corals. The flanks of the seamounts occupy a broad depth range with different species occupying different depth ranges and thus many different species can be found on single seamounts (Clark et al., 2010). The pelagic environment associated with some shallower seamounts is well known for hosting large aggregations of surface fish, sharks, seabirds, and marine mammals (Clark, 2013). Significant questions remain about seamount faunas such as how many species are endemic to particular seamounts or chains of seamounts, but they are likely to act as stepping stones in the connectivity of benthic organisms.

For these reasons, seamounts are regarded as important features for conservation (Clark et al., 2011; Yesson et al., 2011). Seamounts are defined as geological features with an elevation of more than 1000 metres above the ocean floor; features with elevations between 500 – 1000 m are known as knolls. Seamounts may provide a range of habitats including hard (rocky) and soft (mud and sand) substrate and these may be present over the range of depths represented by the seamount. Their summits will occur at wide range water depths and may come close to the ocean surface in some cases. This means that seamounts may extend into different biogeographic zones and in some cases may lie partly in oxygen minimum zones. Seamounts are also subject to varying levels of organic carbon flux that can influence faunal distributions, and were classified into those receiving high, medium and low fluxes by Clark et al. (2011). Seamounts may be isolated, part of a cluster or form part of a chain such as along the MAR axis. Clark et al. (2011) defined a proximity index in which seamounts are regarded as being close if they lie within 100 km of their nearest neighbour and distant if they lie further away than this.

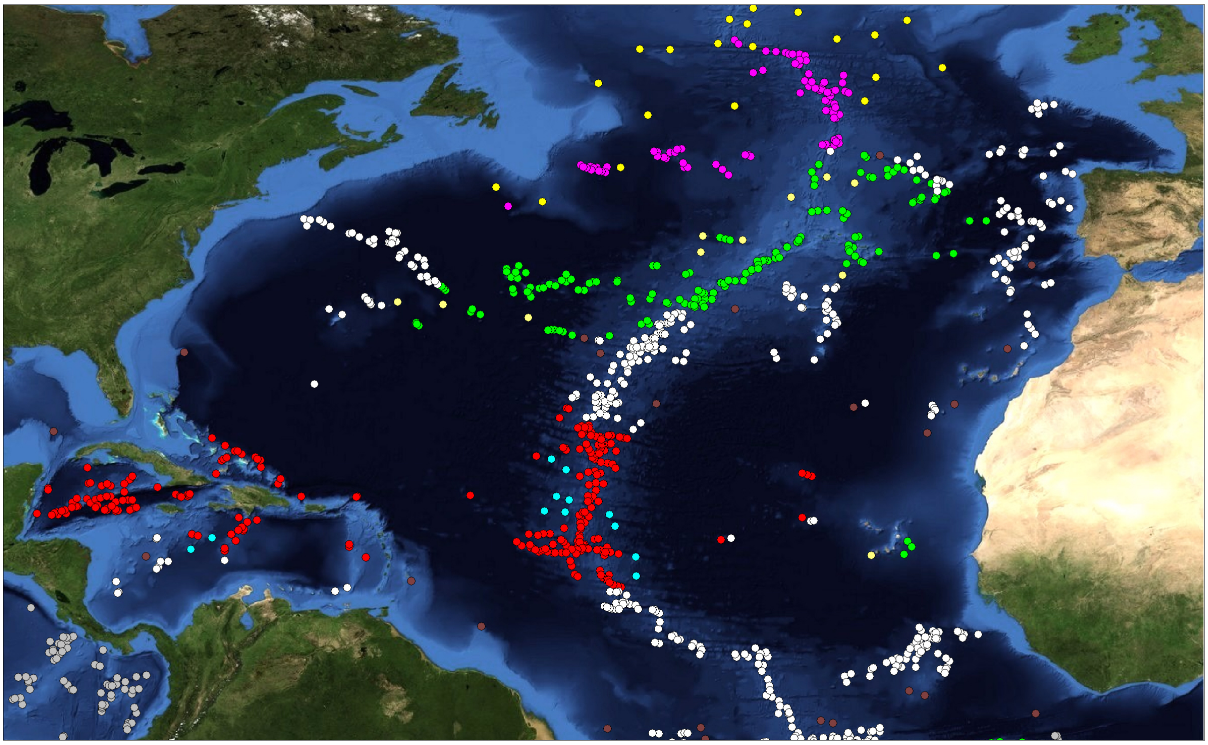

Figure 4.8 Distribution of major seamounts in the North Atlantic within the GOODS Lower Bathyal Province according to Clark et al. (2011). Image courtesy M. Clark, NIWA.

Clark et al (2011) identified 1197 seamounts with elevations greater than 1500 m in the North Atlantic and grouped these into 19 classes (Fig. 4.8). They regarded the primary distinguishing feature for these classes to be organic matter flux and their proximity index. Seamounts of the New England chain (white) are similar to those of the central region of the Mid-Atlantic Ridge (white and green), being characterised by lower bathyal depths, medium organic matter flux, and close proximity. The distinct band of red coloured seamounts in the Caribbean and on the MAR in Figure 4.8 are characterised by low organic matter flux.

Yesson et al. (2011) identified over 1400 seamounts within the North Atlantic and listed an additional 7537 knolls that they claim could provide equally important habitat. One feature which is apparent in the datasets of both Clarks et al. (2011) and Yesson et al (2011) is the concentration of seamounts along the ridge axis. This is due to the elevation of the ridge axis relative to the deep basins to each side of it and the older age of the basins which has provided more time for them to fill with sediments burying some of the seamounts.

4.3 Hydrothermal vents and formation of ore bodies

Along the ridge axis oceanic crustal heat flow drives convective seawater circulation into and through the crust, eventually to be expelled through conduits and chimneys, which form hydrothermal vents. Heated seawater is modified into an ore-forming fluid as it passes through the oceanic crust reacting with rocks and leaching metals and sulphur. At the seafloor, cooling, changing pH, and seawater mixing triggers precipitation of sulphide and gangue minerals from the fluid, most being dispersed by the hydrothermal plume. Cu-rich minerals soluble at high-temperatures are deposited close to the vent whereas Zn and Pb sulphide minerals soluble at lower temperatures are deposited farther away. If conditions are favourable, polymetallic massive sulphide deposits are formed at or below the seafloor and are composed predominantly by iron sulphides (pyrite and/or pyrrhotite), sphalerite, chalcopyrite, and/or galena as the main sulphide phases The chimneys are unstable and, over time, collapse to create mounds (Figure 4.9) that in some cases may also have minerals of economic interest. Comprehensive reviews on the genesis of polymetallic massive sulphide deposits and hydrothermal processes are found in Hannington (2014) and German and Seyfried (2014).

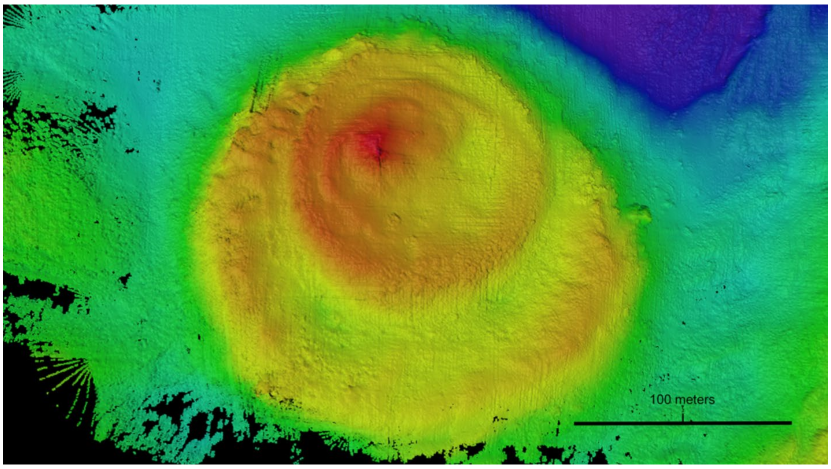

Figure 4.9 High-resolution ROV Jason SM2000 bathymetry map of the TAG active mound. Note the circularity of the feature, and the two discrete platforms with the cone and black smoker complex located on the top of the mound. Reproduced from Humphris et al., 2015.

The TAG active mound shown in Figure 4.9 is one of the largest and best-studied hydrothermal areas. It is situated 2.4 km east of the plate boundary in 3600 m water depth. It is about 200 m in diameter with a maximum elevation of 50-60 m (Humphris and Kleinrock, 1996). It has been intermittently active over the last 50,000 years (Lalou et al., 1998) and is currently in an active mode with vent sites at its summit that emit fluids at around 360°C. The TAG mound was drilled by the Ocean Drilling Programme (ODP) Leg 158 in 1994 (Humphris et al.,1995) with seventeen holes being drilled at five locations. The maximum depth of the drilling was 125 metres. The drilling results have enabled the subsurface structure of the mound to be determined (Humphris et al., 2015) as shown in Figure 4.10. It consists of a stockwork zone (denoted as silicified wallrock breccia and chloritized basalt breccia in Figure 4.10) that connects to a sulphide lens above (pyrite intervals in Figure 4.10).

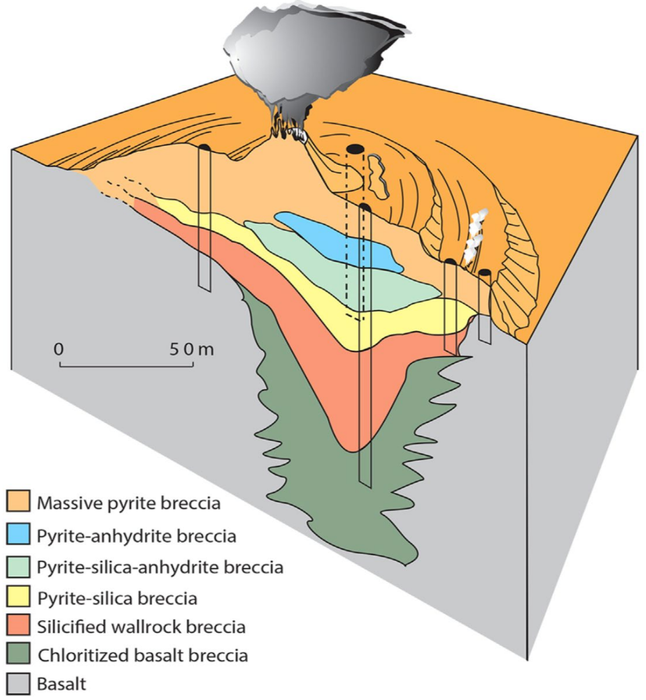

Figure 4.10 The subsurface stratigraphy of the TAG active mound determined by drilling during ODP Leg 158. The entire section is dominated by breccias composed of mixtures of clasts of different lithologies reflecting the episodicity of venting, entrainment of seawater into and beneath the mound, collapse and breakdown of structures during inactive periods, and recrystallization and cementation of old material during recurring periods of activity. (Reproduced from Humphris et al., 2015)

Vent sites often occur in clusters known as vent fields (Figure 4.11) which can cover areas of several square km. The TAG vent field is about 4 km N-S by 2 km E-W, whilst the Semenov Field is linear and nearly 6 km long (Cherkashov et al., 2017). Vent fields may contain both active and inactive vent sites. Some fields comprise a single site or location for ore deposits e.g. Krasnov, Peterburgskoe, Zenith-Victoria and Puy des Folles (Cherkashov et al., 2010). Other fields are comprised of a number of individual sites e.g. Ashadze, and Logatchev in Table 4.1. In some cases, some of the individual sites are hydrothermally active whilst others within the same field are inactive. This is the case with the TAG mound, which is part of the TAG vent field that includes a series of inactive vent sites (Murton et al, 2019).

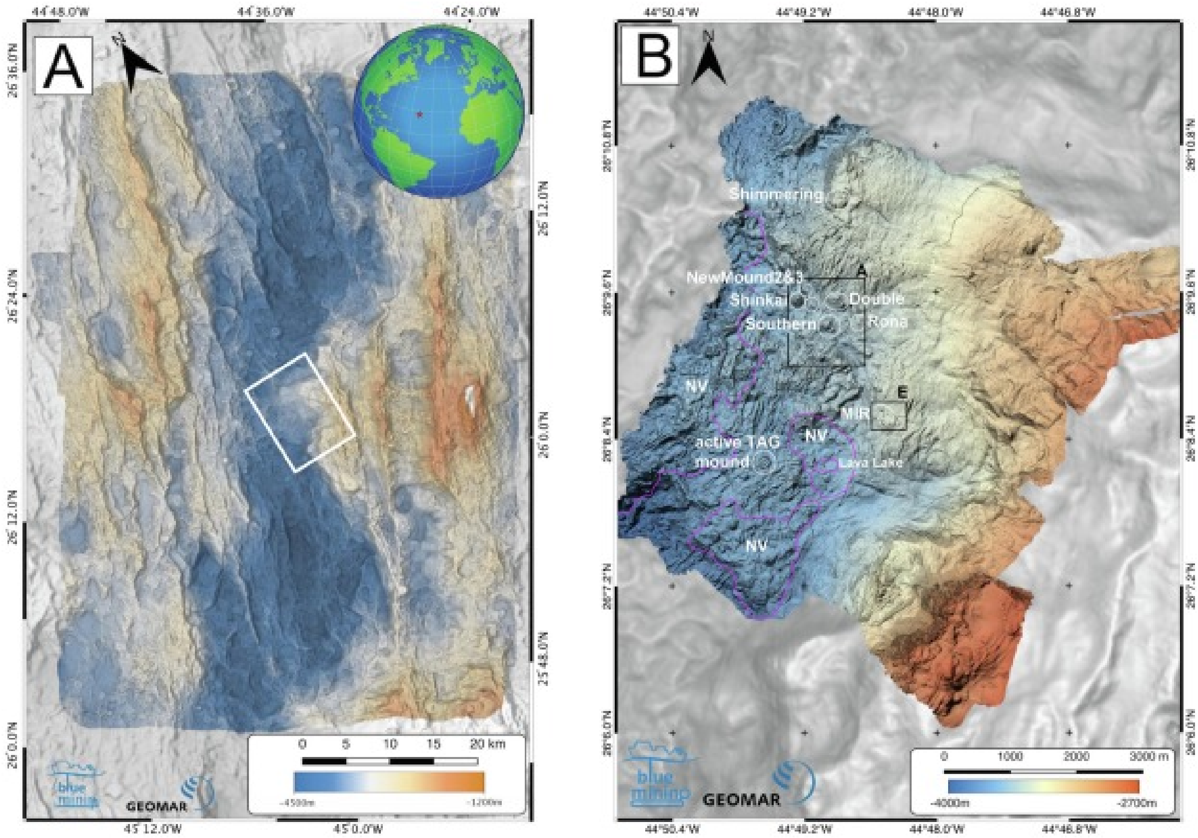

Figure 4.11 The TAG vent field, North Atlantic, showing its relationship to the MAR (left panel). In the right panel the active mound and a number of inactive mounds are indicated. For detailed description see Murton et al. (2019). Reproduced from Murton et al. (2019).

It is important to note that deposits of polymetallic massive sulphides on ocean ridges are formed through hydrothermal activity, expressed at the seafloor surface as venting, and that these occur intermittently along the ridge axis. Vents are formed in a range of locations relative to the spreading plates (Fouquet et al., 2010). Some vents form at the plate boundary in the axial valley where they are associated with volcanism and basaltic rocks and these are known as having a predominant magmatic setting. This type may also occur on top of the axial valley walls where their location is controlled by faults (Figure 4.12 lower panel). Other vents form away from the plate boundary in locations where mantle rocks are exposed at the seabed due to the removal of the crust by detachment faults. These are termed predominantly tectonic setting vents. Tectonically controlled vents lie to one side of the rift valley due to asymmetric spreading of the plates and are not directly associated with volcanic activity (Figure 4.12) but are sustained by fluid flow through the upper crust that is driven by hot subsurface intrusions and/or exothermic reactions. Detachment faults displace the vents away from the ridge axis by as much as 12 km for the Logatchev 2 vent (see Figure 4.12).

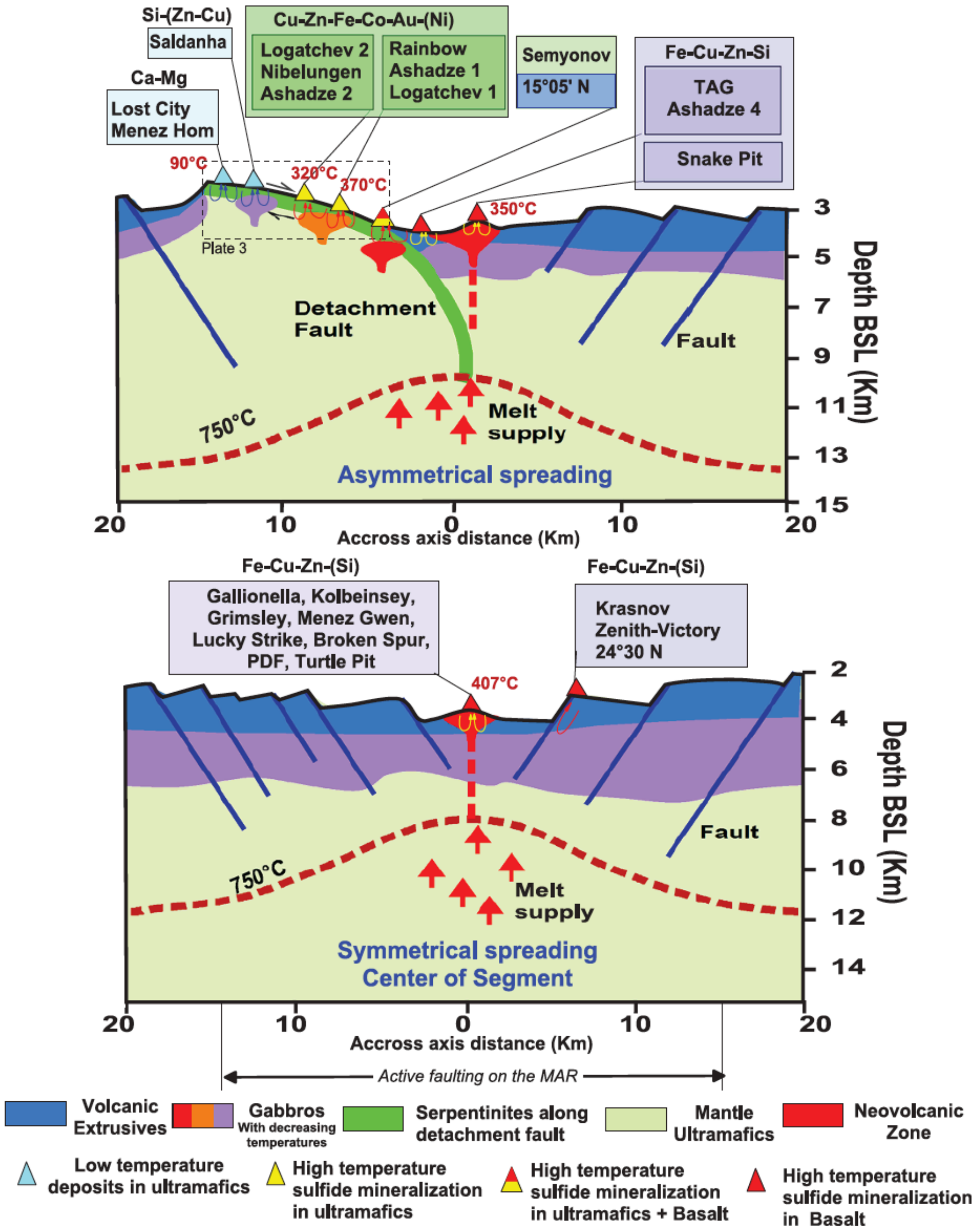

Figure 4.12 Schematic model for the location and composition of major hydrothermal deposits along the Mid-Atlantic Ridge. ***Upper panel*** *– cross section of the MAR showing vent locations related to detachment faults (heavy green line). Positions of vents are at the scale of their distance from the axis (Lost City, 15 km; Saldanha, 12 km; Logatchev 2, 12 km; Ashadze 2, 9 km; Nibelungen, 9 km; Logatchev 1, 8 km, Rainbow, 6 km; Ashadze 1, 4 km; Semenov, ~2 km; 15°05'N, ~2 km; Krasnov, 7 km; Zenith-Victory, 9 km. Note that black smokers with a temperature of 320°C are seen as far as 12 km off-axis at Logatchev 2. Many sites associated with detachment faults are also controlled by non-transform discontinuities.* ***Lower panel*** *– cross section of the MAR showing vent locations associated with Mid-Ocean Ridge Basalts. (Reproduced from Fouquet et al., 2010)*

The location of some of the active and inactive vents in the Russian claim area, with respect to the topography of the axial valley are shown in Figure 4.13

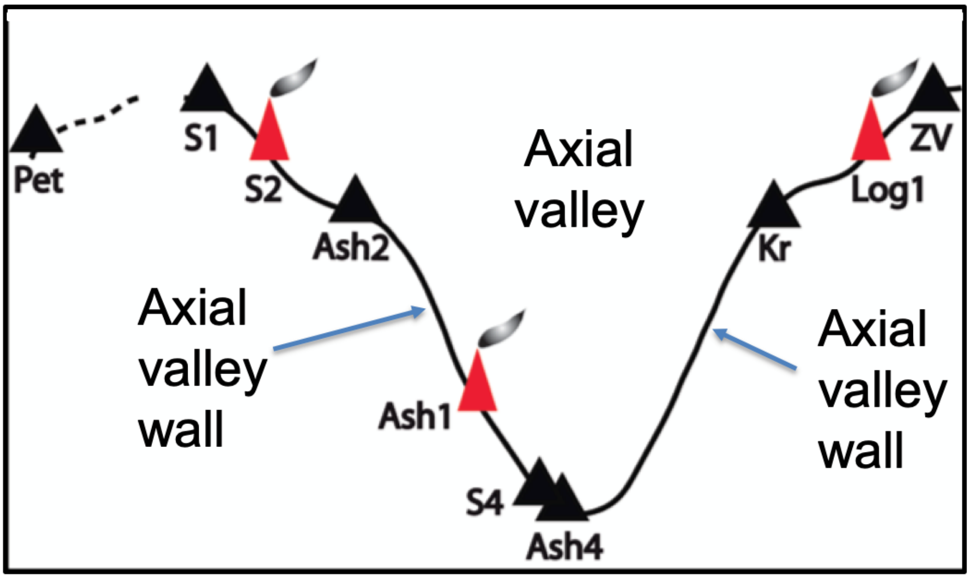

Figure 4.13 Location of some known active and inactive vent sites with respect to the axial valley (Active vent sites in red). Pet – Peterburgskoe; S1,2,4 Semenov; Ash Ashadze; Kr Krasnov; Log Logatchev; ZV Zenith-Victoria (Figure courtesy of A. Gebruk)

4.4 Relationship of active to inactive vent sites

Many vents on the MAR have been active over thousands of years and some up to 200,000 years (Cherkashov, et al., 2017) although all of them experience several discrete active periods of hydrothermalism interspersed with inactive periods (Figure 4.14). Periods of activity may be brought to an end by reductions in supply of hydrothermal fluids or obstructions to the flow e.g. clogging of chimney conduits or volcanic activity (Van Dover, 2019). Cherkashov et al. (2017) analysed data from several locations and concluded that there have been distinct periods when hydrothermal activity was at a peak such as during the last glacial maximum.

Eventually vent sites become permanently inactive due to: i) the movement of the plate away from the ridge axis and thus movement of the site away from the heat source, ii) the site becomes covered with lava flows, or iii) the vent fluids find a new route to the seabed (Van Dover, 2019). Thus, there can be three states of a hydrothermal vent:

- Active – emitting hydrothermal fluids and maintaining hydrothermal vent communities of animals
- Inactive – temporarily dormant and lacking hydrothermal vent communities, but able to resume venting at some time in the future
- Extinct – permanently inactive due to loss of driving force of hydrothermalism probably due to moving away from the ridge axis by plate tectonics or being covered with lava flow (Van Dover, 2019).

There is no method to distinguish between inactive and extinct vent sites, though those located further away from the ridge axis are more likely to be extinct.

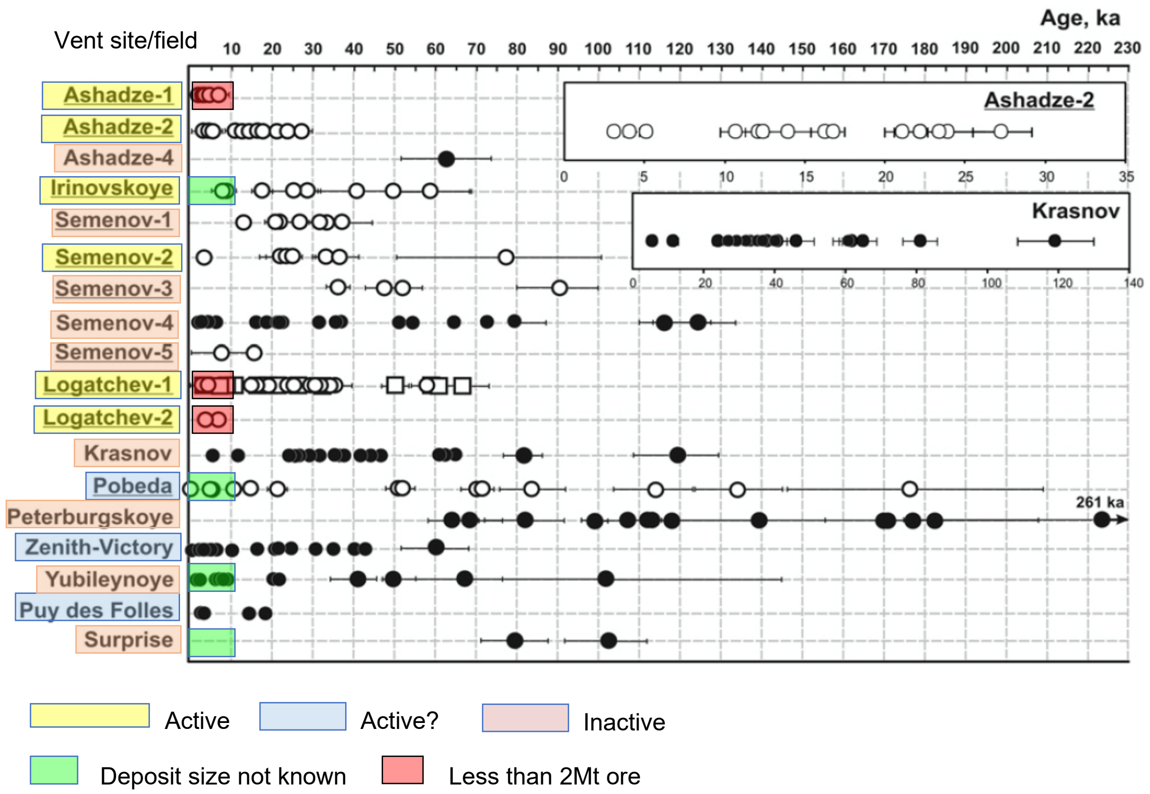

Figure 4.14. Dating results with the 1σ variability for SMS deposits at the Russian claim area on the mid-Atlantic Ridge of the North Atlantic. Symbols represent periods of activity. Figure based on data from Cherkashov et al., 2017. (For further explanation see Cherkashov, et al., 2017).

Extinct vents may become covered by thin layers of lava or may remain exposed at the seabed where sediments will gradually cover them, although they are likely to remain exposed or shallowly buried for kilometres to tens of kilometres away from the ridge axis.

4.5 Location of vent sites along the MAR

A considerable amount of scientific effort has been put into locating hydrothermal vents since they were first discovered in 1977. A database of active vent fields and sites is maintained by Interridge (https://vents-data.interridge.org/), which lists a number of details including: location, water depth, biology, and tectonic setting. New vent sites are discovered regularly, especially in more remote parts of the ocean. Figure 4.15 shows the location of vent fields on the North Atlantic MAR based on the Interridge database. There are no vent fields listed in the Interridge database in Areas Beyond National Jurisdiction (ABNJ or the ‘Area’) between the southern boundary of the Icelandic extended continental shelf claim and the northern boundary of the Portuguese extended continental shelf claim.

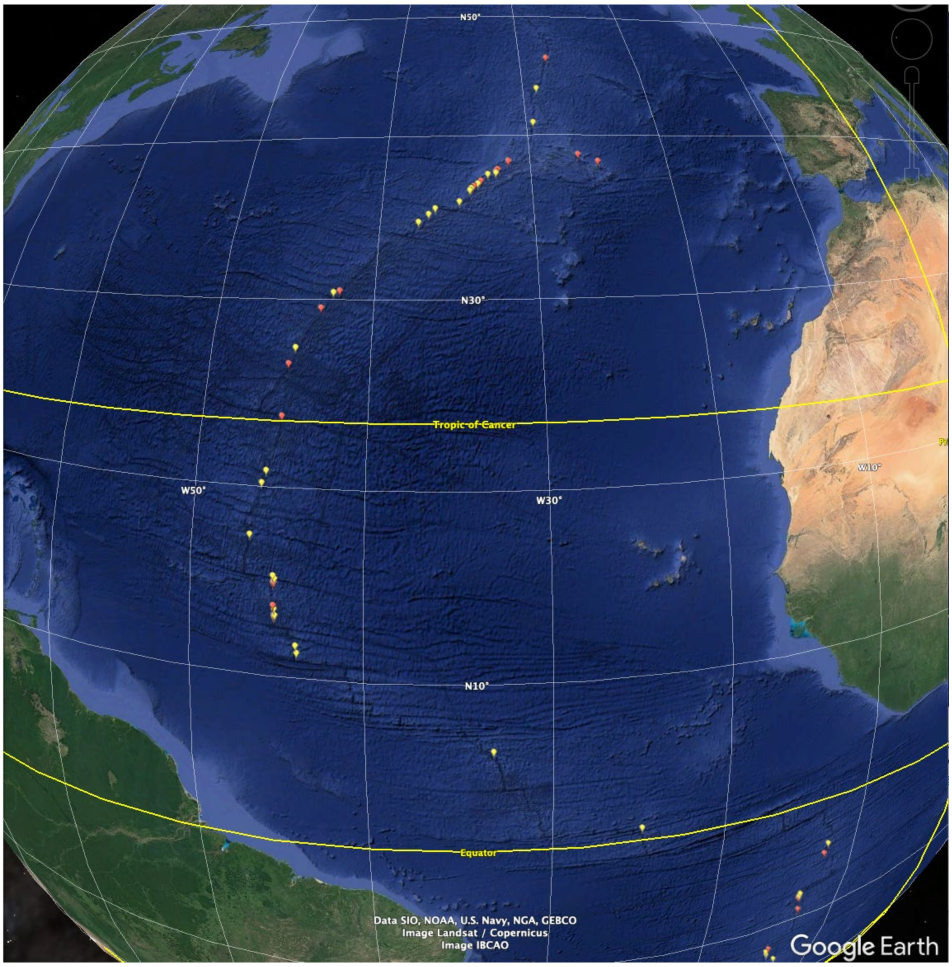

Figure 4.15. Location of vent sites listed in the Interridge database and plotted on Google Earth map. Vent sites that are known to be active are coloured red. Those coloured yellow are inferred to be active but not proven to be so. Vent data from http://vents-data.interridge.org/ *(Beaulieu and Szafranski, 2019).*

The Interridge database lists 18 active hydrothermal vent sites on the North Atlantic MAR (including the Reykjanes Ridge), plus 28 which are inferred as being active and 14 which are listed as inactive (Table 4.1). In the area of the ridge between the southern end of the Portuguese EEZ and the equator the Interridge database lists 9 active, 15 active-inferred and 14 inactive vent sites. The deepest site is Ashadze 4 at 4530 m and the shallowest is the Steinaholl Vent Field south of Iceland at 350 m.

Table 4.1 List of vent sites on the MAR from south of Iceland to the equator. Data extracted from the Interridge vents database v3.4 http://vents-data.interridge.org/ (Beaulieu and Szafranski, 2019).

Name ID	Activity	Latitude	Longitude	Maximum or Single Reported Depth	Full Spreading Rate (mm/a)
Steinaholl Vent Field	active, confirmed	63.1	-24.5333	350	19.1
Reykjanes Ridge, Area A	active, inferred	62.45	-25.433	500	19.3
Reykjanes Ridge, Area B	active, inferred	59.8167	-29.6833	1000	20
Moytirra	active, confirmed	45.4833	-27.85	2900	22.5

MAR, 43 N	active, inferred	43	-29	3400	22.8
South Kurchatov	active, inferred	40.467	-29.55	2900	23.1
Menez Gwen	active, confirmed	37.8417	-31.525	865	19.9
Bubbylon	active, confirmed	37.8	-31.5333	1000	19.9
Lucky Strike	active, confirmed	37.2933	-32.2733	1740	20.2
Evan	active, confirmed	37.2667	-32.2833	1775	20.2
Menez Hom	active, confirmed	37.15	-32.4333	1802	20.2
Lucky Strike segment, southern end	active, inferred	37.05	-32.42	2600	20.2
North FAMOUS	active, inferred	36.967	-32.967	2500	20.3
Saldanha	active, confirmed	36.5667	-33.4333	2300	20.5
AMAR	active, inferred	36.3833	-33.65	2600	20.5
Rainbow	active, confirmed	36.23	-33.902	2320	20.6
S AMAR 1	active, inferred	36.083	-34.083	2630	20.7
S AMAR 2	active, inferred	35.967	-34.183	2240	20.7
N Oceanographer	active, inferred	35.283	-34.867	2600	20.9
S Oceanographer	active, inferred	34.867	-36.433	3460	21.1
S-OH1	active, inferred	34.533	-36.85	3000	21.2
S-OH2	active, inferred	34.067	-37.483	3250	21.4
Lost City	active, confirmed	30.125	-42.1183	800	22.6
MAR, 30 N	active, inferred	30.0333	-42.5	3400	22.6
Broken Spur	active, confirmed	29.17	-43.1717	3100	22.9
MAR, 27 N	active, inferred	27	-44.5	2900	23.4
TAG	active, confirmed	26.1367	-44.8267	3670	23.6
MAR, 25 50'N	inactive	25.8083	-44.9833	3000	23.7
MAR, 24 30'N	inactive	24.5	-46.1533	3900	24
MAR, 24 20'N	inactive	24.35	-46.2	3200	24
MAR, 23 35'N	inactive	23.5833	-45	3500	24.1
Snake Pit	active, confirmed	23.3683	-44.95	3500	24.1
MAR, 22 30'N	inactive	22.5	-45.005	2800	24.3
Puy des Folles	active, inferred	20.5083	-45.6417	2000	24.7
Zenith-Victory	inactive	20.1292	-45.6225	2390	24.7
St. Petersburg	active, inferred	19.8666	-45.8666	3400	24.7
MAR, 17 09'N	active, inferred	17.15	-46.42	3100	25.2
MAR, 16 46'N	inactive	16.795	-46.38	3300	25.2
Krasnov	inactive	16.64	-46.475	3900	25.2

MAR, 15 50'N	inactive	15.8667	-46.6667	3000	25.2
MAR, south of 15 20'N fracture zone	active, inferred	15.0833	-45	3000	25.5
MAR, 14 54'N	active, inferred	14.92	-44.9	3500	25.5
Logatchev	active, confirmed	14.752	-44.9785	3050	25.5
Logatchev 5	inactive	14.75	-44.97	3100	25.5
Logatchev 2	active, confirmed	14.72	-44.938	2760	25.5
Logatchev 3	active, inferred	14.7083	-44.9667	3100	25.5
Logatchev 4	inactive	14.7063	-44.9083	2000	25.5
Semyenov	active, confirmed	13.5137	-44.963	2440	26
MAR, 13 19'N OCC	active, inferred	13.3333	-44.9	3000	26.2
Ashadze 2	active, confirmed	12.9917	-44.9067	3300	26.2
Ashadze 3	active, inferred	12.986	-44.861	4200	26.2
Ashadze	active, confirmed	12.9733	-44.8633	4200	26.2
Ashadze 4	inactive	12.97	-44.85	4530	26.2
Neptune's Beard	active, inferred	12.91	-44.9	4100	26.2
MAR, 12 48'N	inactive	12.8	-44.7883	2400	26.2
MAR, 11 26'N	active, inferred	11.4482	-43.7035	3835	26.9
MAR, 11 N	active, inferred	11.038	-43.6483	4010	26.9
Vema Fracture Zone	inactive	10.85	-41.8	3600	27
Markov Deep	active, inferred	5.91	-33.18	3500	28.8
MAR, segment south of St. Paul system	active, inferred	0.5	-25	3500	30.7

Between 11°N and the equator there are only two known vent sites, whilst north of 11°N to the southern end of the Portuguese extended continental shelf claim vent sites are more frequent (Figure 4.15, Table 4.1). Within the latter interval if we take only the known active and active-inferred vent sites their separation distance is an average of 105 km with a maximum separation distance of 322 km between Snake Pit and Puy de Folles. These calculations however are likely to change depending on 1) the discovery of new active vent sites based on further exploration and 2) whether active-inferred sites are eventually confirmed as active or inactive.

4.6 References

These are included with the references at the end of Chapter 5 “Contract areas and the mining process”

5. Contract areas and the mining process

5.1 Existing ISA contract areas on the northern Mid-Atlantic Ridge

The total area awarded for exploration by the ISA is defined in ISBA/16/A/12/Rev.1 Regulation 12 as follows:

1. *For the purposes of these Regulations, a "polymetallic sulphide block" means a cell of a grid as provided by the Authority, which shall be approximately 10 kilometres by 10 kilometres and no greater than 100 square kilometres.*
2. *The area covered by each application for approval of a plan of work for exploration for polymetallic sulphides shall be comprised of not more than 100 polymetallic sulphide blocks which shall be arranged by the applicant in at least five clusters, as set out in paragraph 3 below.*
3. *Each cluster of polymetallic sulphide blocks shall contain at least five contiguous blocks. Two such blocks that touch at any point shall be considered to be contiguous. Clusters of polymetallic sulphide blocks need not be contiguous but shall be proximate and confined within a rectangular area not exceeding 300,000 square kilometres in size and where the longest side does not exceed 1,000 kilometres in length.*
4. *Notwithstanding the provisions in paragraph 2 above, where an applicant has elected to contribute a reserved area to carry out activities pursuant to article 9 of annex III to the Convention, in accordance with regulation 17, the total area covered by an application shall not exceed 200 polymetallic sulphide blocks. Such blocks shall be arranged in two groups of equal estimated commercial value and each such group of polymetallic sulphide blocks shall be arranged by the applicant in clusters, as set out in paragraph 3 above.*

As of November 2019, three contracts have been signed by the ISA for exploration on the northern MAR (Figure 5.1). The individual contract blocks in each contract area are closely tied to the ridge axis but up to 6 contiguous blocks lie across the ridge axis. This creates a corridor at least 30 km wide each side of the ridge axis where contract blocks have been identified for exploration. Several of the blocks cover known active hydrothermal vent sites whilst others cover known inactive vents. Many of the blocks cover areas of ridge where active vents have not yet been detected.

If the contractor has not contributed a reserved area (paragraph 4 above) but has an exploration contract for up to 100 blocks then the relinquishment process operates as outlined in ISBA/25/LTC/8. Exploration contracts last for up to 15 years during which time the contractor shall relinquish parts of the area allocated to it in accordance with the following schedule:

a) By the end of the eighth year from the date of the contract, the contractor shall have relinquished at least 50 % of the original area allocated to it;

b) By the end of the tenth year from the date of the contract, the contractor shall have relinquished at least 75 % of the original area allocated to it;

Relinquished areas revert to the Area and thus become available for new contracts. At the end of the fifteenth year from the date of the contract, or when the contractor applies for exploitation rights, whichever is the earlier, the contractor shall nominate an area from the remaining area allocated to it to be retained for exploitation. Thus, exploitation areas will be very much smaller than exploration areas.

ISBA/25/LTC/8 provided clarity on how relinquishment could occur. Each 10km x 10km block can be subdivided into 1km x1 km cells and the requisite number of cells returned to the Authority to achieve the correct percentage. Relinquishment may be undertaken by full blocks or individual cells within multiple blocks with no restriction on which cells or blocks are to be returned.

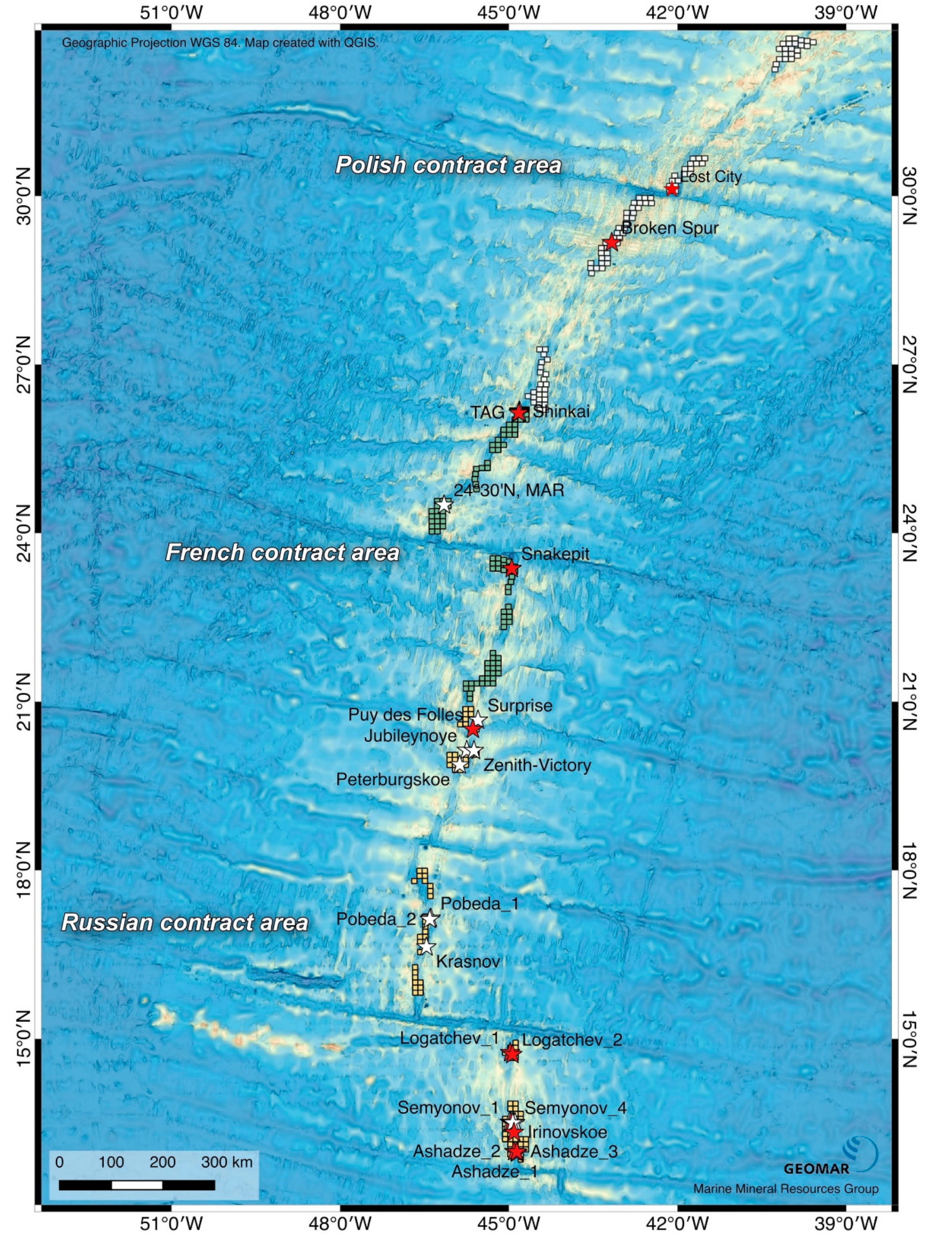

Figure 5.1. Polymetallic sulphide blocks (each block is ≤ 10 km × 10 km) approved for exploration by the ISA in the North Atlantic (yellow blocks: Russian Federation, green blocks: France, white blocks: Poland) and the locations of known active vent ecosystems (red stars) and inactive sulphide mounds (white stars). Reproduced from Van Dover et al. (2018).

5.2 Resource potential

The full resource potential for PMS deposits on the MAR remains unknown. Most hydrothermal vent systems lose much of their metal content to the surrounding water in hydrothermal plumes. Active vent sites are still in the process of precipitating metals so their metal content may be relatively low (see for example the young vents sites Ashadze 1 and Logatchev 2 in Figure 5.1 that have low metal contents). Petersen et al. (2016) suggest that tens or hundreds of thousands of years may be needed to create the largest deposits and even then metal grades may be poor. Vents related to detachment faults may be much longer lasting and therefore have the potential to create larger deposits (Petersen et al., 2016).

Overall only a small proportion of known vent sites have commercially attractive accumulations of PMS deposits, however, many more active vent sites remain to be discovered. The identification of inactive vent sites will add substantially to the number of potential locations with commercial prospects (Petersen et al., 2017).

After PMS deposits have been mapped in two-dimensions by a combination of geological / geophysical methods and seabed sampling, the three-dimensional scales of the deposits and their total ore tonnage must be calculated from subsurface drilling information. To date very few deep-sea deposits have been drilled and less than half of these have mineable resources (Petersen et al., 2016). In the Atlantic comprehensive drilling has only been achieved for the TAG deposit (Hannington et al., 1998), although some drilling has taken place on the Logatchev field (Petersen et al., 2007, 2009), which revealed a ‘small deposit’.

Using the drilling data Hannington et al. (1998) estimated the TAG mound to contain 3.9 Mt of sulphide ore with an estimated average copper grade of 2.8 wt% and around 0.5 gram/ton of gold. The bulk of the metals (70%) including virtually all of the Zn, Ag, Pb and Au plus 80-85% of the Cu are concentrated in the upper 5 m of the mound, with 15-20% of the total Cu being located in the deeper stockwork (Hannington et al., 1998). These metal concentrations compare to the range of Cu concentrations in the extensively mined Cyprus ophiolites of 0.2 to 7.7 wt%, with an average close to 2 wt%, whilst gold ranges from 0.1 to 2 gram/ton (Hannington et al. (1998). Lehrmann et al. (2019) report that although zinc may be deposited in mounds during hydrothermal activity, once this activity ceases zone refining processes may result in the zinc being remobilized or removed from the mounds. Copper, however, appears to be preferentially retained within the upper parts of the structure which may suggest only the upper few metres of the mounds have economic potential.

Estimates have been made of the potential ore tonnages in the Russian contract area (Cherkashov et al., 2010, 2013), but these have not been confirmed by drilling (Table 5.1).

Deposit A = active, I = inactive	**Latitude N**	**Water depth m**	**Area km²**	**Maximal age ka**	**Resource Mt**
Ashadze-1 (I), 2 (A),4 (I)	12°58.5'	4200	0.058	1 – 7.2 ± 1.8 2 – 27.3 ± 1.8	5.2
Semyenov 1 (I), 2 (A), 3(I), 4(I), 5(I)	12°59.5'	2400–2600	0.361	123.8 ± 9.7	40
Logatchev-1(A), 2 (A)	13°31'	2900–3100	0.039	1 – 58.2 ± 4.4 2 – 7.0 ± 0.3	1.9
Krasnov (I)	14°45'	3700–3750	0.161	119.2 ± 12.2	12.8
Peterburgskoe (I)	14°43'	2800-2900	1.12	176.2 ± 59.1	2.9
Zenith-Victoria (I)	16°38'	2370–2390	0.495	176.2 ± 59.1	15.2
Puy des Folles (?)	20°08'	1940–2000	0.858	59.5 ± 8.4	11.9
TAG (active mound) (A)	20°30.5'	3670	0.031	18.2 ± 4.4	4

Table 5.1. Estimates of resources for a range of hydrothermal fields in the Russian claim area and the estimate for the TAG field. Note most of these fields are located at active vent sites (column 1). Compiled from Cherkashov, et al., (2010) and Cherkashov et al. (2013). Information on TAG (Active mound) is from Hannington et al. (1998).

It is likely that commercial mining practice will extract at least one Mt of ore per year (Petersen et al., 2016 suggest up to 2 Mt per year). Thus, some of the deposits listed in Table 5.1 could take several years to mine. What is unclear is what the lower cut-off will be to the volume of exploitable resource which will depend on a number of factors such as metal ore grade, operating costs and market prices.

5.3 Detection of ore bodies

As explained above ores are formed at active hydrothermal vents along the ridge axis and in areas adjacent to the ridge axis. Such areas of active venting are relatively easy to detect by measuring geochemical anomalies in water column profiles or during near bottom surveys, in both cases using sensor packages (Baker, 2017). This is because plumes show up as anomalies in the water column in the potential temperature/salinity ratio and nearer the seabed as light scattering and transmission anomalies due to particulates. Increasingly, Autonomous Underwater Vehicles (AUVs) are being used to detect plumes since they can cover larger areas than tethered Remotely Operated Vehicles (ROVs) (Schmid et al., 2019).

However, better targets for exploitation may be the inactive and extinct vent sites. The extinct vent sites are likely to contain the largest resources since they have completed the whole cycle of metal formation as opposed to active hydrothermal sites and inactive sites, which may continue to precipitate (or resume precipitation of) metals for many years. In many cases inactive and extinct vents are co-located with active vent sites. For example, the Semenov field contains five vent sites only one of which is hydrothermally active (Cherkashov, et al., 2017; Firstova, et al., 2019) (Figure 5.2). In these cases, the search for active venting can lead to the discovery of inactive and extinct vent sites. However, beyond a few kilometres from the ridge axis all vents will be extinct because the tectonic plates spread away from the ridge axis and transport the vent sites away from the hydrothermal fluid sources. Detection of these ore bodies is much more difficult, especially those further away from the ridge axis where they are increasingly likely to be covered by sediment layers or basalt flows. In these cases, exploration using ROV or AUV-based mapping of bathymetry will need to be aided by geophysical measurements such as magnetic and self-potential sensors (Cherkashov et al., 2010; Kawada and Kasaya, 2018).

Technology is currently being developed to prospect for ore bodies that are not associated with active hydrothermal venting including ore bodies buried by thin sediment layers (Holz et al., 2015; Petersen et al., 2017; Kawada and Kasaya, 2017). There are no statements as to how thick the sediment cover could be before prospecting becomes unfeasible and this will probably only be determined once equipment is operational. Petersen et al. (2017) estimate that ore bodies should remain detectable for at least 20 km on each side of the ridge axis.

Sediment in the deep sea is derived from plankton fallout, dust and, near mid-ocean ridges, hydrothermal deposits (Dutkiewicz et al., 2015). In mid ocean oligotrophic regions sediment accumulation rates are often in the order of 2 cm/kyr. Combining this rate with the rate of plate motion (typically 2.4 cm/yr^{-} for the North Atlantic) indicates that 20 m of sediment cover could be expected some 12-15 km away from the ridge axis in each direction. Closer to the Azores sediment accumulation rates are higher (Figure 4.6) and 20 m of sediment cover may be attained much closer to the ridge axis.

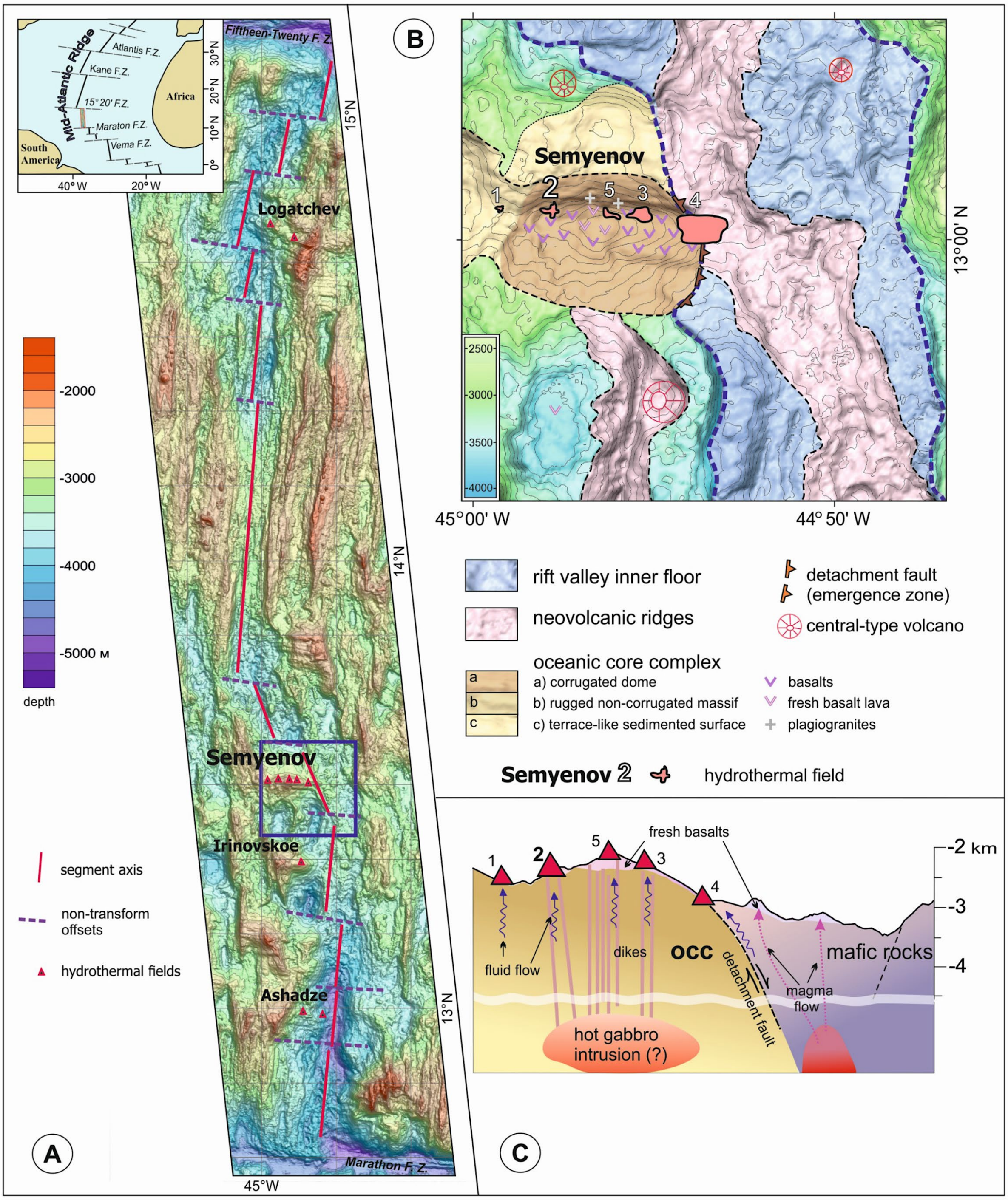

*Figure 5.2 The Semenov vent field in the Russian claim area. (**A**) Shaded-relief bathymetric map of the Mid-Atlantic Ridge between the Fifteen–Twenty Fracture Zone and the Marathon Fracture Zone, showing the location of the hydrothermal fields. The contour interval is 200 m. The box corresponds to the area of Figure B. (**B**) Morphostructural setting of the Semyenov hydrothermal fields. (**C**) Interpretative cross-section of the MAR rift valley in the Semyenov cluster (this figure was modified from Pertsev et al., 2012); vertical exaggeration 3:1. Vent site 2 is active whilst all others are inactive. Reproduced from Firstova et al., 2019.*

The generation of new crust along the ridge axis may prevent sediment layers developing at all within a few kilometres either side of the axis and beyond this the presence of rocky terrain with steep slopes may mean that sediment layers do not begin to build up until even further away. Hard rocks, including ore bodies, may therefore be found at or near the seabed at distances considerably further than 15 km from the ridge axis. Eventually the sediment layers will fill the irregular topography and all rocks will be buried with sediments becoming increasingly thick reaching hundreds of metres thick in the abyssal plains.

Current exploration contracts extend up to 30 km each side of the ridge axis (Figure 5.1) and even with the development of new sensing techniques exploration is unlikely to extend much more than this.

5.4 Mining scenario

The exploitation phase of deep-sea mining for PMS has not begun yet so there are no accounts of actual mining practice. However, the Japanese Ministry of Economy, Trade and Industry (METI) and the Japan Oil, Gas and Metals National Corporation (JOGMEC) conducted successful test mining for PMS in a water depth of 1,600 m off Okinawa Prefecture in August/September 2017 (METI, 2018). The test mining methodology is shown in Figure 5.3 and indicates mining on flattened surfaces by tracked vehicles with ore being piped to a support vessel with subsequent transfer to barges for transport to shore (METI, 2018; Okamoto et al, 2019).

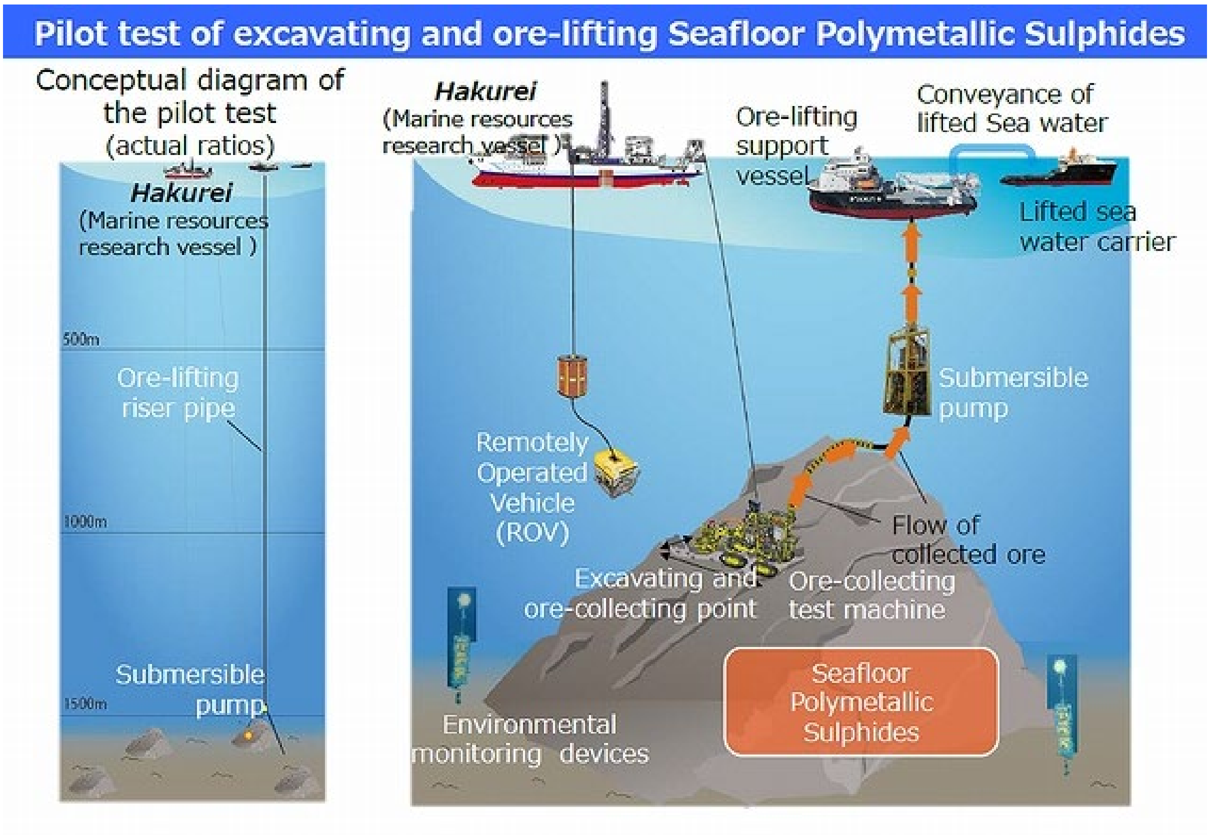

Figure 5.3 Mining scenario applied to test mining off Japan in 2017. Reproduced from a press release by the Japanese Ministry of Economy, Trade and Industry (METI[1]).

The processes carried out by Japan are similar to those that were proposed by Nautilus Minerals for mining the Solwara 1 site in the Bismarck Sea off Papua New Guinea. Nautilus Minerals developed three seafloor instruments for mining polymetallic sulphides: bulk cutter, auxiliary cutter and collecting machine. These instruments are modifications of mining tools used elsewhere in the mining industry, for example in land-based coal mines and offshore dredging and diamond mining (Gwyther, 2008). The

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[1] World's first success in continuous ore lifting test for seafloor massive sulphides: http://www.meti.go.jp/english/press/2017/0926_004.html

mining process would involve the auxiliary cutter levelling the seabed in preparation for the bulk cutter that would mine in a similar way to coal cutting machines. The two cutting machines would disaggregate the rock, leaving it for the collecting machine that would draw it in as slurry and pass it to the riser system. Ultimately a hole will be created in the seabed, similar to land-based mines, which in the case of Solwara 1 could be 18-30 m deep and cover 0.11 km^2. In addition, the overburden would need to be removed, which for Solwara 1 consists of an estimated 130,000 tons of unconsolidated sediment plus 115,000 tons of waste rock (Gwyther, 2008). This would need to be pumped to an area of seabed outside the mined area. The plume generated by these operations was predicted to deposit 0.18 to 500 mm of sediment over an area of 2.3 km^2.

The mining, retrieval and shipping processes can be divided into the following actions.

1. Removal of overburden at the seabed, which could include sediment and non-ore bearing rocks. These materials are likely to be pumped across the seabed to an area away from the mine site
2. Levelling of the rugged seabed to form flat benches. This will be achieved by the auxiliary or multi-axis cutter. This vehicle could either be connected directly to the riser pipe (Ishiguro et al., 2013) or it could leave crushed ore in swathes on the seabed waiting for the collector vehicle as in the Nautilus example[2]. Note: the original Nautilus Minerals plan was for the riser pipe to be connected directly to the mining vehicles (Gwyther, 2008).
3. Open-cut mining using a bulk or drum cutter. This vehicle operates on the flat benches where it cuts at a higher capacity than the auxiliary cutter. The same options exist for direct connection to the riser pipe (Ishiguro et al., 2013) or the cutting of swathes of ore to be collected by a collector vehicle.
4. Transfer of the ore to the surface support vessel via a riser pipe (otherwise known as a Vertical Transport System (VTS) or Riser and Lift System (RALS)). A discussion of various riser systems is given in Frimanslund (2016) together with a detailed description of the VTS system that would have been used by Nautilus Minerals. The VTS is likely to consist of a fully enclosed riser and lifting system, similar to those seen in the oil and gas industry as well as separate pipes for returning tailings to the seafloor or water column. A flexible hose will likely be required to connect the seafloor mining tools to the VTS. A pump system will be required to lift the slurry within the VTS; depending on the depth of the resource and the lift system used, it is possible that several pumps and booster stations will be required. The ore will be transferred as a slurry, which according to Gwyther, (2008) will comprise a ratio of seawater to ore of 9:1.
5. Dewatering of slurry on support vessel. The water will need to be removed from the slurry as soon as it arrives at the ship so that the sulphides can be stored dry. The removed water will be returned to the ocean. Nautilus Minerals suggested particles larger than 8 microns would be retained with smaller particles being a component of the returned water (Gwyther, 2008). Nautilus Minerals also proposed that the returned water could be used to drive the subsea slurry pump located at the bottom of the riser pipe.
6. Transfer to barges for transport to shore. Barges will attend the mine site at periodic intervals to be filled with ore. The transfer process may be in a wet or dry state. If the ores need to be rewetted, then they will require a second dewatering on the barge, with discharge of this water back to the ocean.

An alternative method of mining PMS resources has been proposed by BAUER Maschinen GmbH (Schrobenhausen, Germany) and Technip (Paris, France) based on trench-cutter technology (Spagnoli

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[2] Nautilus Minerals mining technology – How it will all work: http://www.nautilusminerals.com/irm/content/how-it-will-all-work.aspx?RID=433

et al., 2015). This mining tool would be capable of vertical mining and would be easily relocatable on the seafloor. In the model shown in Figure 5.4 the ores would be collected in containers for direct transfer to the ship, thus limiting the production of plumes from seafloor mining operations and shipborne dewatering.

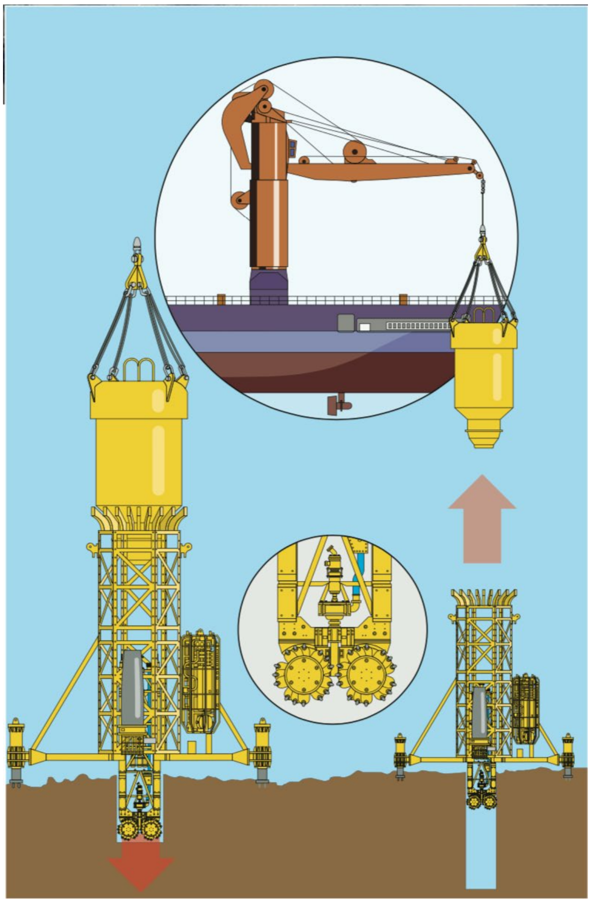

Figure 5.4 The proposed Bauer deep-sea mining tool showing vertical cutting head and container lift system (https://www.deepsea-mining-alliance.com/en-gb/news)

5.5 Potential areas of impact

Deep-sea mining is likely to have at least 4 areas of impact:

1. **The mine site.** PMS deposits are three-dimensional and will involve mining a pit in the seabed. The size of the mine will be dependent on the size of the ore body but may be less than 1 km2 in many cases. For example, the Solwara 1 mine site, which is estimated to have 2.3 Mt of mineral resource (Lipton, 2012), was planned to cover an area of 0.112 km2. In addition to this there may be some overburden removal and relocation elsewhere on the seabed. If the mine site includes active hydrothermal vents with vent-obligate fauna, these will be destroyed by the mining. The presence of active vents with vent-obligate fauna that are located close to inactive vents with high mineral content may make it difficult to avoid impact on vent communities, which will be affected by sediment plumes even if they are not targeted directly by mining. For example, the Semenov field has an estimated 40 Mt of ore and comprises five sites, with site 2 being active and hosting

vent-obligate fauna (Cherkeshov et al., 2017). This site is located about two and three kilometres away from inactive sites 5 and 1 respectively (Figure 5.2).

2. **The mining plume.** The mining vehicles will generate plumes of water laden with small particles that can flow away from the mine sites and may bury or smother seafloor organisms and habitats and potentially prevent recolonisation (Levin et al., 2016; Clark and Smith, 2013). Impacted organisms may include corals, sponges and a wide variety of other fauna that are attached to hard rock surfaces as well as any benthopelagic fauna living near the seabed that cannot escape the plume. The plumes may be relatively small in volume because the PMS substrate is hard and most of the material generated may be too large or too dense to be suspended in the water. However, the act of mining sulphide deposits will expose metal surfaces to oxidation and this may release metals and metalloids into the seawater (Fuchida et al., 2017; Simpson and Spadaro, 2016: Brown et al., 2017) and fine-grained sulphide particles (Fuchida, et al., 2017; Hauton et al., 2017). Fuchida et al. (2019) observed different metal dissolution behaviours between the non-oxidized and oxidized hydrothermal sulphides suggesting that instantaneous metal release from sulphides into seawater will not occur before or during the crushing and lifting processes of seafloor mining as opposed to oxidized phases that rapidly release metals and metalloids into seawater. Thus, the mining plumes may contain contaminants (Fallon et al, 2018, Knight et al., 2018) and these will be transported away from the mine site in currents. This may lead to significant releases of contaminant elements, such as cadmium, arsenic, antimony and copper, especially if weathered crushed ore is stockpiled on the seabed for any length of time (Fuchida, et al., 2019; Weaver and Billett, 2019).
3. **Returned water plume.** When the ores are received by the mining vessel they will be dewatered and the waste water returned to the ocean. At present the ISA recommendation (ISBA/16/LTC/7) states "*The discharge may occur below the thermocline layer and the oxygen-minimum zone, and preferably at the seabed*". The dewatering process cannot remove all the smallest particles and those smaller than a few tens of μm will be discharged in the returned water. In many cases toxic metals attach preferentially to fine particles. Even though the discharge plume may be diluted very quickly within the environment (Gwyther, 2008), it may still have biological effects, especially through bioaccumulation. Therefore, discharge plumes have the potential for wide ranging effects at scales larger than those evident directly at the mine site, and in both the pelagic and benthic environment (Weaver and Billett, 2019). A scientific workshop to discuss the potential effects of plumes on midwater ecosystems was held in Hawaii in 2018 and the results are reported in Drazen et al., (2019). Their recommendations included minimising effects in the mesopelagic zone by releasing water below 1000 metres depth; the production of a midwater haze due to enhanced suspended particle concentrations should be avoided; research is needed on the bathypelagic and abyssopelagic zones (from ~1000 m depths to just above the seafloor) and more modelling of plume behaviour and its biological effects should be conducted.
4. **Removal of overburden and waste rock.** In some cases, the ore body may be covered by layers of sediment that will need to be removed and dumped locally on the seabed. Such was the case for Solwara I, that was planned to be mined by Nautilus Minerals as described above. This transported material could smother sensitive fauna either directly or via a plume. During mining operations waste rock with low or absent metal content may be similarly dumped nearby on the seabed.

Additional areas of potential impact include light from surface vessels and deep-sea vehicles plus noise from surface vessels, deep-sea vehicles and the riser pipe.

5.6 References

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6. Physical Oceanography of the North Atlantic

6.1 Introduction and scope

This review covers the broad topic of the Physical Oceanography of the North Atlantic, from the equator to Iceland, considering both flow patterns and the resulting distributions of temperature, salinity, oxygen and turbidity. Particular attention is paid to the Mid-Atlantic Ridge (MAR), from the perspective of its impact on large-scale flows as well as the smaller scale flow processes that define its local environment. These smaller scale processes have been very sparsely investigated, so examples drawn from other ocean basins (largely the South Atlantic) have been included where they are clearly of direct relevance to the North Atlantic.

6.2 Large-scale circulation

6.2.1 Overview

The large-scale circulation of the North Atlantic consists of largely wind-driven, surface-intensified gyre circulations (Fig. 6.1) interacting with a significant (compared to the Pacific, (Weaver et al. 1999)) density-driven meridional overturning component (Kuhlbrodt et al. 2007; Bower et al. 2019) in which warm surface waters are drawn to high latitudes where they are transformed and returned as dense, deep waters. It is the open connection to the Nordic Seas and the Arctic that permits this strong overturning circulation, mediated by the relatively shallow ridge between Greenland and Scotland which must be traversed by newly formed deep waters.

Flows can, for convenience, be broadly split into surface, intermediate and deep/bottom layers (here loosely defined by water characteristics). Although these layers do interact, through vertical motion and mixing, this interaction is sufficiently small that temperature, salinity and other water properties are largely retained and identifiable over vast horizontal distances. This is especially the case for deeper waters which are not modified by contact with the atmosphere. The preservation of identifying properties allows oceanic water to be subdivided into a complex series of water masses, the broadest groupings of which are described here. The properties of mining plumes may similarly be conserved and traceable if concentrations remain at detectable levels.

In deep ocean basins, currents tend to be stronger in the upper water column than the lower water column, since most forcing occurs at the surface (winds and the effects of heating/cooling). Significant flows do exist at depth, however, with a global average of measured near-bottom current speed in depths over 1500 m being 8-9 cm s^{-1} (Turnewitsch et al. 2013; Scott et al. 2010), although this value appears high for the central North Atlantic and may reflect bias of measurements toward areas with strong flows. Note also that this average includes instantaneous current speeds due to varying components such as tides and eddies and is considerably greater than the speed of the time-averaged flow that leads to net displacements. Tidal currents comprise a depth-invariant component of typically a few centimetres per second in the deep ocean plus a more complex ‘internal tide’ resulting from interaction of the tide with topography. So, tidal current speed may actually increase with depth, and the importance of tidal currents relative to the underlying flow components is greatest near the bed.

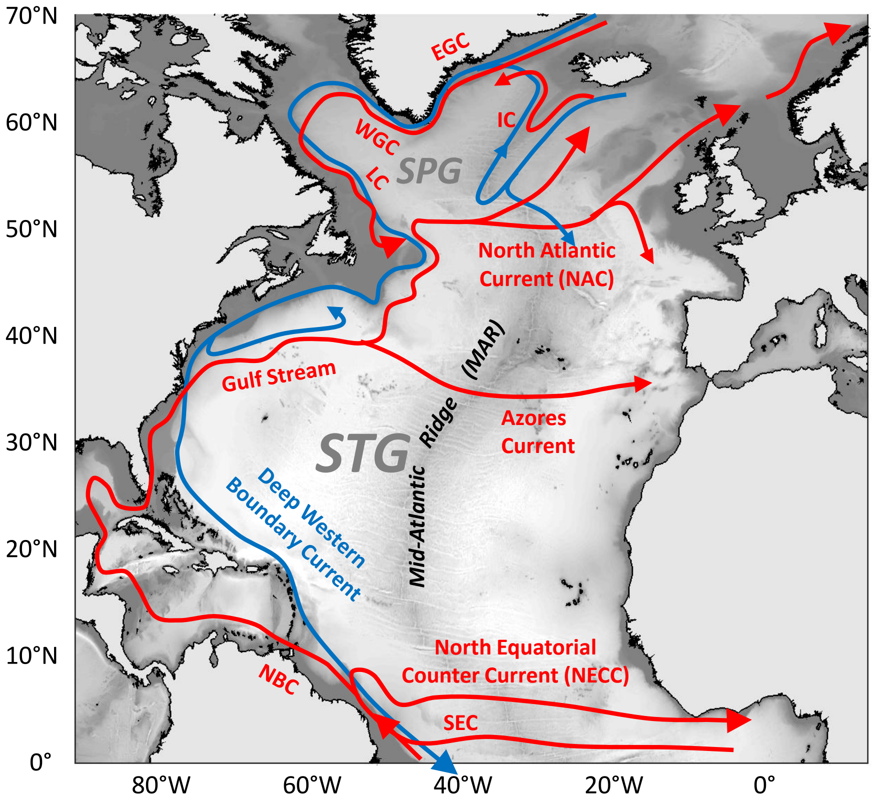


***Figure 6.1**: The principal features of the North Atlantic surface circulation (red) and deep circulation (blue). WGC: West Greenland Current, EGC: East Greenland Current, LC: Labrador Current, IC: Irminger Current, NBC: North Brazil Current, SEC: South Equatorial Current. The Sub-Polar Gyre, SPG and Sub-Tropical Gyre, STG meet in the North Atlantic Current.*

The long-term mean and slowly varying components of flow (with a timescale of days or longer) tend to locally follow the seabed topography (i.e. follow depth contours). While this topographic influence is present throughout the water column, it reduces with height above the bed. So, deep flows are strongly steered by, or locked to, topography, while surface flows are less constrained, can more readily cross depth contours, and are more prone to eddying. For this reason, although flow complexity exists at all levels in the water column, deep flow complexity (Xu et al. 2010) (Fig. 6.2) is steadier in time because it is locked to invariant topography.

6.2.2 Surface layer currents

The broad pattern of surface flows in the Atlantic consists of a pair of large, rotary gyre circulations, the clockwise sub-tropical gyre and the anti-clockwise sub-polar gyre to the north of 45-50ºN (Fig. 6.1) (Fratantoni 2001; Reverdin et al. 2003).

The sub-tropical gyre is strongly intensified against its western boundary as the Gulf Stream (Fofonoff 1981), which originates in the Caribbean and follows the North American shelf until 20ºN where it heads broadly to the east/northeast into open water, becoming the multi-branched and highly variable North Atlantic Current (NAC). While peak current speeds within the Gulf Stream exceed 2 ms^{-1}, mean flows within the NAC in the central North Atlantic are considerably slower and strongly modified locally by eddies and meanders. A southern branch of the NAC is drawn into the Azores Current, a coherent eastward flow to the south of the Azores at 35ºN directed towards the entrance to the Mediterranean, compensating the entrainment of water into the underlying Mediterranean outflow plume (Özgökmen et al. 2001; Jia 2000). The southward and westward return portions of the subtropical gyre, the Canary Current and North Equatorial Current, are broad, weak and largely obscured by other variability.

The NAC also forms the southern limb of the subpolar gyre, consisting of the general flow of the northern flank of the NAC to the northeast towards the Nordic Seas and its recirculation around the Irminger and Labrador Seas back to the North American shelf. The NAC initially branches as the Irminger Current, which is strongly constrained by the relatively shallow topography of the northern MAR (Reykjanes Ridge), before merging with a series of coastal currents, the East Greenland Current, West Greenland Current and Labrador Current to complete the recirculation.

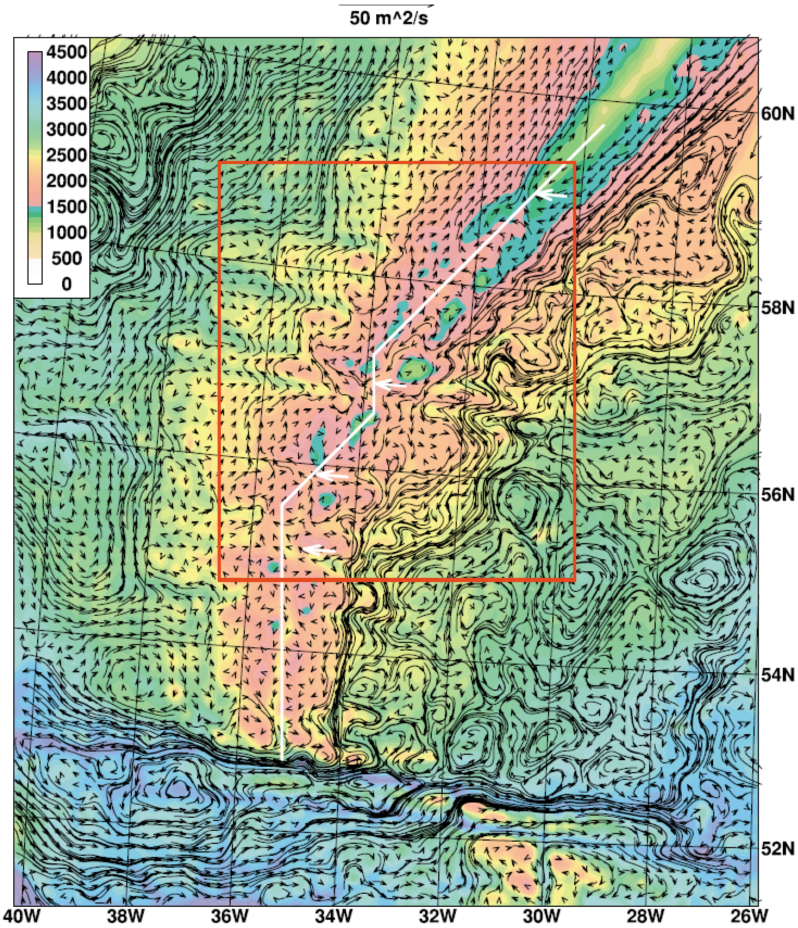


***Figure 6.2**: Modelled transport of dense water (potential density greater than 27.8 kg m^{-3}) in the area of the Charlie-Gibbs Fracture Zone and Reykjanes Ridge. Arrow length shows the volume transport per unit width (m^{2} s^{-1}). Underlying colouring shows bottom depth, and flow complexity results from the tendency to follow depth contours (Reproduced from Xu et al. 2010).*

The tropical Atlantic has a persistent, though somewhat seasonal, set of largely east-west currents (Lumpkin and Garzoli 2005; Stramma and Schott 1999; Philander 2001). The west-flowing South Equatorial Current (SEC) is broad and shallow (100 m) forming the northern limb of the South Atlantic subtropical gyre. Its northern branch (nSEC) extends north of the equator to around 4ºN, feeding the North Brazil Current (NBC) flowing to the northwest along the Brazilian coast. Much of the NBC 'retroflects', turning back on itself to return eastward as the North Equatorial Counter Current (NECC) between 4ºN and 10ºN which effectively forms a tropical gyre with the South Equatorial Current. The broad west-flowing North Equatorial Current (NEC) between 10ºN and 20ºN forms the southern limb of the northern hemisphere subtropical gyre but is considerably weaker than the nSEC and NECC.

Where surface circulations are persistent and sufficiently intense, they are clear in satellite altimetry (Fig. 6.3). These more persistent flows cross the MAR in three key regions corresponding to the NAC north of 45ºN, the Azores Current around 35ºN, and the equatorial current system south of 10ºN. Although surface flows are not directly in contact with the seabed, their dynamics are influenced by seabed topography to the extent that they tend to cross the MAR at locations where the ridge crest is broken by deep connections between basins. Reflecting its high level of eddy variability, the locations where the NAC crosses the MAR are not fixed. They include the Charlie-Gibbs Fracture Zone (CGFZ, 52-53ºN), the Faraday Fracture Zone (50-51ºN), and the area around 49ºN, with the crossing varying between single and multiple branches (Bower and von Appen 2008). This variation is on inter-annual timescales and is also apparent in surface thermal fronts (Miller et al. 2013).

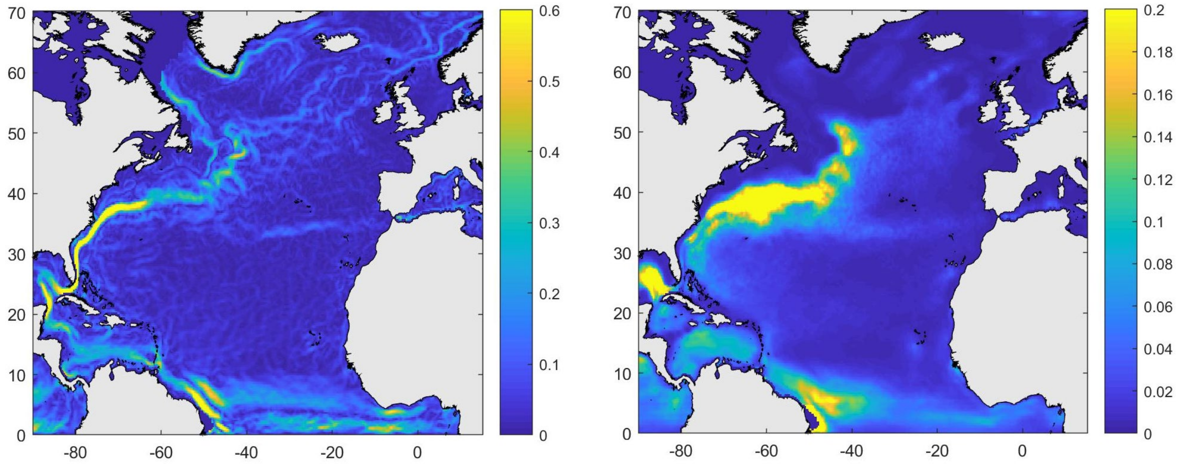


***Figure 6.3**: (a) Mean surface geostrophic flow speed (ms^{-1}), and (b) eddy kinetic energy (m^{2}s^{-2}) from ten years of satellite altimetry (2009-2018). Values locally exceed the colour scales in high energy areas. (Generated using EU Copernicus Marine Service information, product identifier SEALEVEL_GLO_PHY_L4_REP_OBSERVATIONS_008_047).*

6.2.3 Intermediate layer currents

The major surface current structures typically extend through much of the upper water column, and potentially deeper, usually weakening with depth. Observations of deeper flows, and pathways, are more difficult to obtain, however, being beyond the reach of satellite techniques, so understanding is pieced together from distributions of water properties as well as studies using subsurface floats and current meter moorings.

Two particularly extensive sets of observations of subsurface floats (Lavender et al. 2005; Bower et al. 2002) clarify many of the intermediate flow features of the northern North Atlantic, in particular of the NAC, its interaction with the MAR, the subpolar gyre, and connections to the subtropical gyre to the south. At the level of the thermocline (200-800 m), around half of the floats crossing the MAR within the NAC did so at the CGFZ, while the remaining crossings occurred at other fracture zones south of CGFZ to 45ºN (Bower et al. 2002). Most of these floats entered the subpolar gyre to the north without passing into the Nordic Seas. West-bound crossings of the MAR (Reykjanes Ridge) occurred to the north of the CGFZ at various latitudes. Mean speeds prior to and after crossing the MAR were 2 cm s^{-1} and dominated by mesoscale eddying, but convergence of the flow at the CGFZ elevated the mean there to 5 cm s^{-1}. A similarly extensive dataset of floats tracking pressure surfaces at 400, 700 or 1500 decibars (approximately metres) provided excellent coverage north of 44ºN and partial coverage to 25ºN, in particular of the subpolar gyre, confirming many of the features described above (Lavender et al. 2005). The most intense flows at 700 m were the boundary flows on the continental slopes of Greenland and Labrador, which exceeded 10 cm s^{-1}. Strong flows not exceeding 5 cm s^{-1} also occurred to the east in the CGFZ and traced the bathymetry of the Reykjanes ridge to cross back from the eastern to the western basin. Flows to the south of the NAC were generally weak. In addition, the variability (meandering) of the NAC was found to increase closer to the surface as topographic control weakened.

Tracer analysis has been used to estimate transport timescales for intermediate water. Anthropogenic chlorofluorocarbons, temperature and salinity was used to identify and track Labrador Sea Water at 1000-2000 m, which was traced from the Labrador Sea across the North Atlantic to its eastern boundary, presumably via the CGFZ. For a period in the 1990s this transport took 4-5.5 years (Sy et al. 1997), a mean speed of 1.5-2 cm s^{-1}.

Further south, floats released at 700 m on the flanks of the MAR to the SE of the Azores (clusters at 33ºN on the eastern flank and 36ºN on the western flank) dispersed widely in both eastern and western basins (Ollitrault and Colin de Verdière 2002), but the MAR provided a significant barrier in this region. Despite the floats being above the depth of the ridge crest, only one float crossed between basins. Their transport and dispersion were again dominated by mesoscale eddying, showing greater dispersion in the more energetic western basin. After 2-3 years, the floats on the Western flank of the MAR had become distributed across much of the western basin of the North Atlantic between 30ºN and 55ºN, whereas the floats in the eastern basin had been transported to the east by the deep expression of the Azores Current and dispersed more slowly.

6.2.4 Deep layer currents

The densest water in the North Atlantic is of Antarctic Origin (Antarctic Bottom Water, AABW) occupying depths in excess of 4000 m. AABW crosses the equator from the western basin of the South Atlantic, initially forming a boundary current on the western flank of the MAR from 8-16ºN before becoming more diffuse in the western basin (Warren 1981). Clearly, waters beneath the MAR crest are only able to cross between the western and eastern basins where a sufficiently deep connection exists. AABW crosses the MAR at the Romanche Fracture Zone (0-2ºN) but this component remains topographically restricted from spreading more widely in the North Atlantic. More significant in this respect is the Vema Fracture Zone (11ºN) (Eittreim et al. 1983) which provides a deep link through which an estimated one third of the AABW supply from the South Atlantic is able to cross to the eastern basin and spread as boundary currents to the east and to the north along the flank of the MAR (McCartney et al. 1991).

Lying above AABW is a complex of water masses grouped as North Atlantic Deep Water (NADW) comprising dense waters formed in the Nordic Seas and the Labrador Sea mixed with ambient Atlantic water and entrained AABW. Deep water inflows from the Nordic Seas enter the North Atlantic by spilling over shallow topography between Greenland and Iceland (Denmark Strait Overflow Water) and between Iceland and Scotland (Iceland-Scotland Overflow Water, ISOW). The equatorward flow of NADW forms the deep component of the Atlantic's Meridional Overturning Circulation (Dickson and Brown 1994; Bower et al. 2019). These deep flows travel with shallow topography to their right, so they are most pronounced in the western basin and ultimately concentrate against the North American shelf as a deep western boundary current (Fig. 6.1).

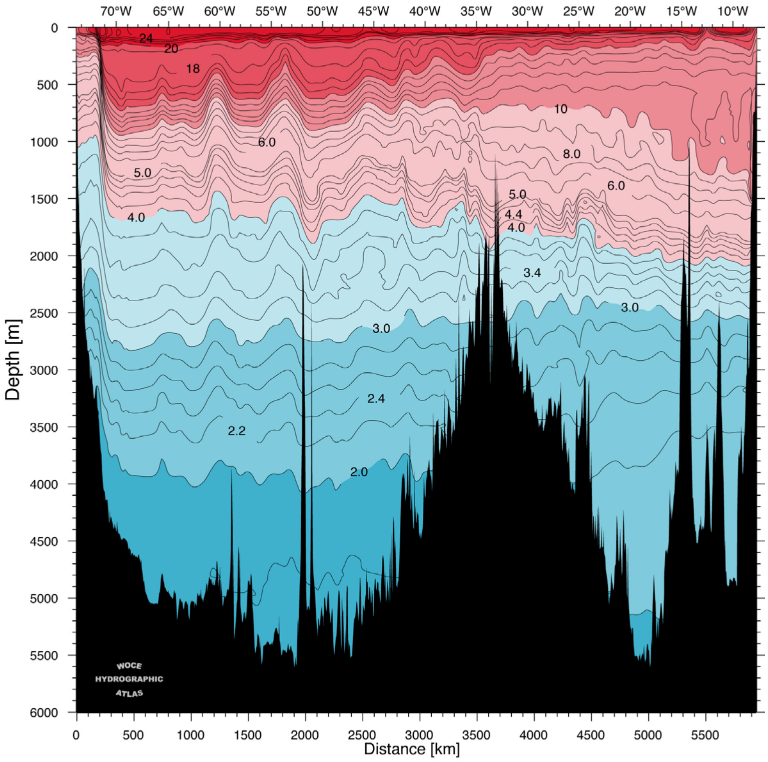
The component of the deep flow that most influences the MAR is that of ISOW which, after crossing the Iceland-Scotland ridge, traverses the slope to the south of Iceland (Saunders 1996) and flows southwest along the eastern flank of the Reykjanes Ridge (Kanzow and Zenk 2014). The majority of ISOW is thought to cross the MAR at the Charlie-Gibbs Fracture Zone (Dobrolyubov et al. 2003; Saunders 1994), although model simulations suggest that leakage across the ridge may also occur at points to the north (Xu et al. 2010), and some also ISOW influence is also seen south of the CGFZ (Read et al. 2010; Xu et al. 2010). While the mean situation in the CGFZ is of eastward flow of the NAC at the surface and westward flow of ISOW at depth, the deep flow is dynamically coupled to the upper flows and so is strongly correlated with it. When a strong branch of the NAC is present at the CGFZ, the flow of ISOW may reverse, so the ability of ISOW to reach the western basin is intermittent (Saunders 1994; Xu et al. 2018; Schott et al. 1999). Once in the western basin, ISOW turns to flow north along the western flank of the MAR and circulates around the Irminger Basin.

Model simulations of the flow of ISOW in the vicinity of the Northern MAR suggest that superimposed on the largescale transport is a highly complex, topographically-steered pattern (Xu et al. 2010) (Fig. 6.2) emphasising that locally measured flows near seabed topography are more strongly influenced by that topography than by large scale flow pathways. So, while these pathways are revealed by the distribution of water properties (section 3), they are difficult to observe directly by measurements of currents because of local factors. Moreover, even the rather complex-looking simulations of (Xu et al. 2010) significantly under-resolve the full complexity of the topography.

6.3 Distribution of water properties

The basic hydrography of the North Atlantic is well described by Tomczak & Godfrey (2003, Chapter 15). The presence of water masses with distinct properties reflecting their regions of origin provides clear evidence of flow pathways and their response to bathymetry. Figs. 6.4 and 6.5 show an east to west transect of water properties at 36ºN and a south to north transect in the eastern basins of the South and North Atlantic.

(a)



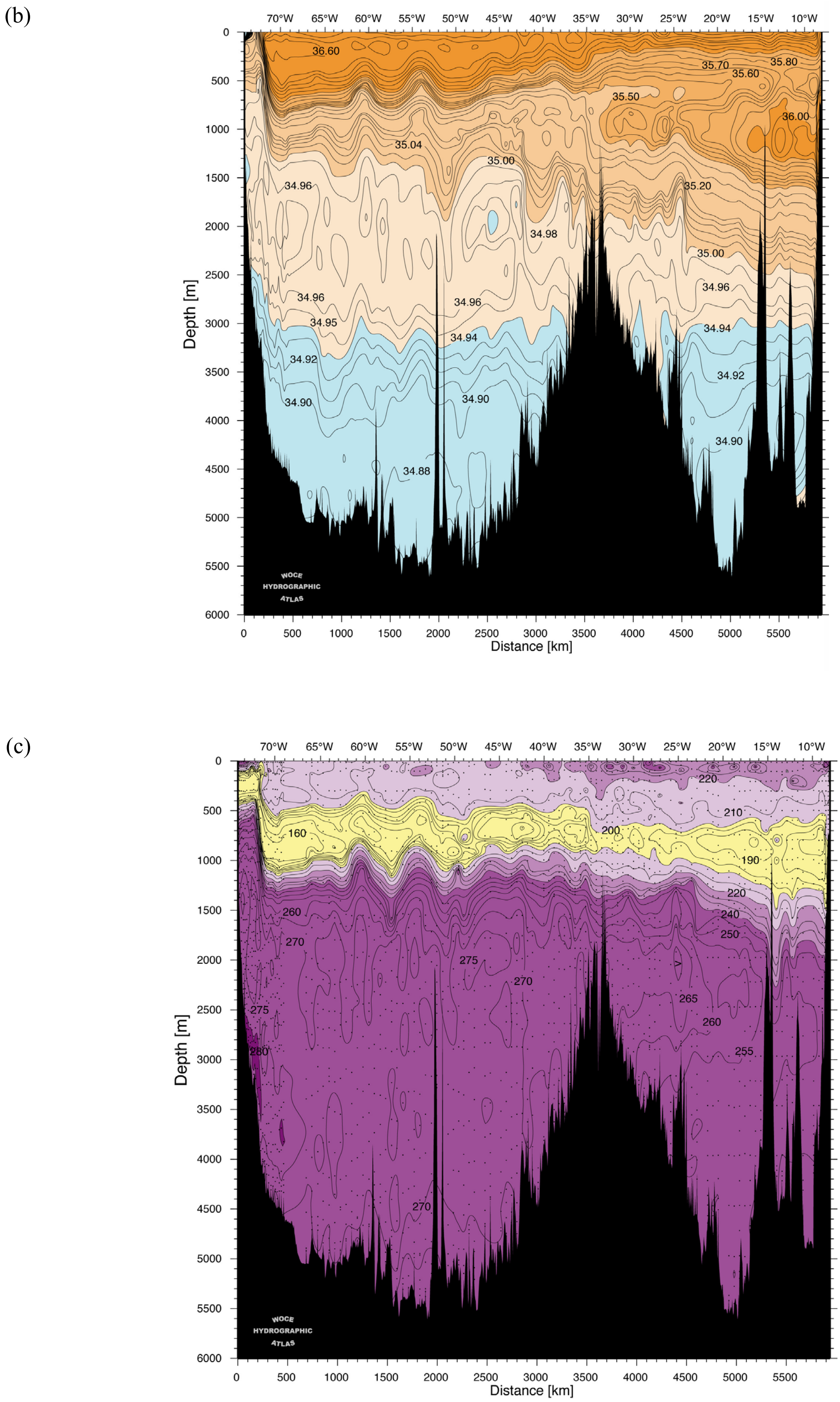


Figure 6.4: *West-east sections of (a) potential temperature (°C), (b) practical salinity and (c) oxygen concentration (µmol kg*$^{-1}$*) across the North Atlantic at 36°N (WOCE line A03), from the WOCE Atlantic Ocean Atlas (Koltermann et al. 2011) based on 1990s data.*

6.3.1 Temperature and salinity

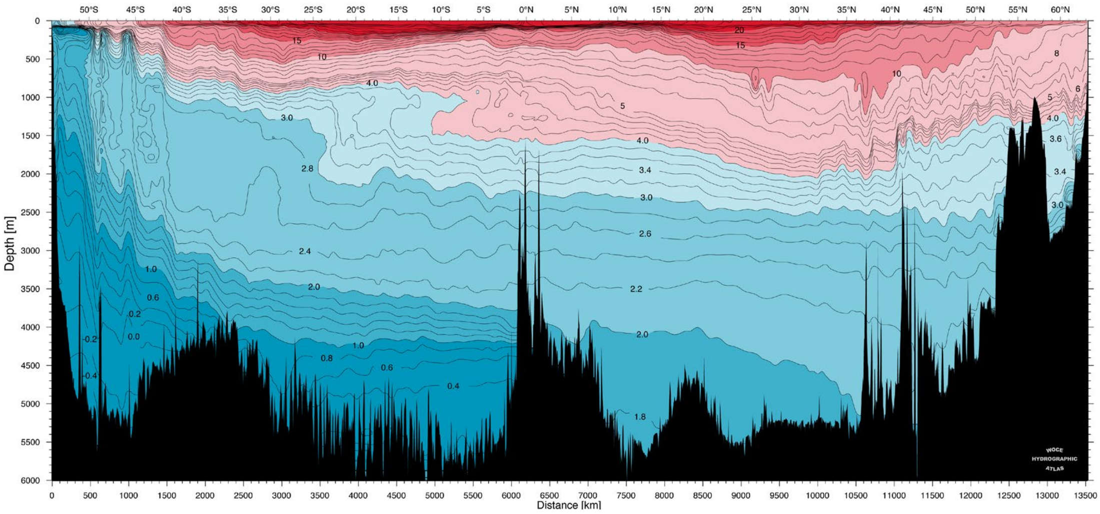
Surface temperature and salinity are highly variable due to atmospheric influences, but they clearly reflect the pattern of surface gyre circulation, with the northern flank of the NAC corresponding to the subpolar front dividing the cool water of the subpolar gyre from the warmer subtropical gyre.

In global terms, the surface layer of the North Atlantic has a particularly large winter mixed layer depth (de Boyer Montégut et al. 2004), with the deepest mixing occurring in the NE Atlantic, Irminger Sea, southern Labrador Sea and along the path of the NAC. Depths in excess of 100 m develop in October-November and reach a peak of 500 m or more in places, before being much reduced during April, May and largely erased by June. These mixing depths set the depth of the permanent pycnocline.

A feature of the North Atlantic at intermediate depths is the inflow of Mediterranean Water, a dense water mass that spills over the sill at the entrance to the Mediterranean, descends and spreads across the North Atlantic as a saline anomaly relative to the upper NADW of the same density (Fig. 6.5). This spreading is initially at around 1000 m, with the spreading layer breaking into rotating lenses termed ‘meddies’. The salinity anomaly can be traced extensively, into the western basin and across the equator, deepening as it spreads.

As described previously, North Atlantic Deep Water (NADW) represents a complex of water types from differing sources in the Labrador and Nordic Seas. Waters from these sources mix with ambient Atlantic water but still retain slightly differing properties and remain distinguishable. The upper layer of NADW, at intermediate depths, derives from the Labrador Sea, whereas lower layers have their origin in the Nordic seas via overflows in the Denmark Strait or between Iceland and Scotland.

(a)



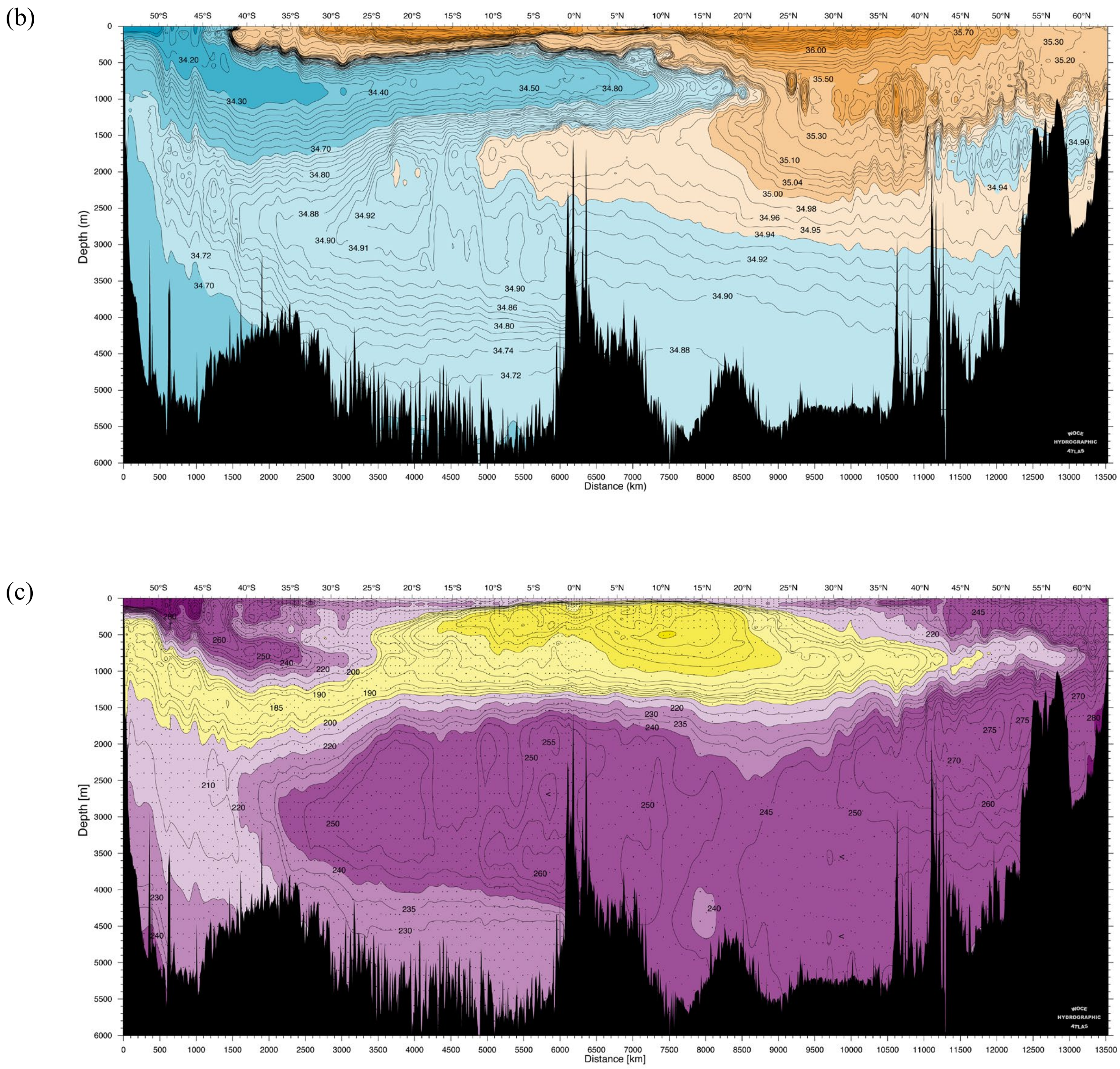


***Figure 6.5**: South-North sections of (a) potential temperature (°C), (b) practical salinity and (c) oxygen concentration (µmol kg^{-1}) in the eastern basins of the Atlantic (WOCE line A16), from the WOCE Atlantic Ocean Atlas (Koltermann et al. 2011).*

Antarctic Bottom Water (AABW) differs from North Atlantic Deep Water (NADW) in being relatively cool, fresh and dense. It also has reduced oxygen and high silicate. As AABW spreads in the North Atlantic it gradually warms through mixing with overlying NADW. So, the coolest AABW (potential temperature < 0ºC) is in the western basin near the equator, and temperatures increase from there to the north, and spreading in the eastern basin from the Vema and Romanche Fracture zones. The topographic barrier of the MAR is clearly apparent in water column profiles which diverge significantly between eastern and western basins at levels below the ridge crest. West of the MAR, water cools and freshens more rapidly with depth than east of the MAR reflecting the greater influence of AABW.

6.3.2 Oxygen

The North Atlantic is, in broad terms, characterised by high oxygen levels resulting from its deep winter mixing and plentiful supply of deep water. Oxygen concentrations are high in surface waters, at depths that interact with the surface through winter mixing, and in deep waters which retain their oxygen signature from their formation regions (Fig. 6.5). While deep and bottom waters all have high oxygen concentrations, variation is useful in separating distinct deep-water sources within the water masses grouped as NADW, which fill much of the lower water column. Lower oxygen concentrations also clearly differentiate the influence of AABW below 4000 m (Fig. 6.5).

Between the oxygenated surface and deep waters, beneath the permanent pycnocline, an oxygen minimum exists. This minimum is most pronounced at low latitudes, becoming deeper and less pronounced at high latitudes, reflecting the deepening of the well-oxygenated winter mixed layer with latitude. The oxygen minimum layer always lies above the level of the crest of the MAR. Models and observations suggest decreasing oxygen concentrations in upper and intermediate waters of the North Atlantic, including at the oxygen minimum (Stendardo and Gruber 2012; Stramma et al. 2009), although values remain high compared to those in comparable areas of the Pacific (Karstensen et al. 2008). The lowest concentrations in the eastern tropical Atlantic were around 40 µmol kg^{-1} in 2008.

6.3.3 Turbidity

The distribution of suspended particulate matter in the North Atlantic has been comprehensively described by a number of authors (Biscaye and Eittreim 1977; Eittreim et al. 1976; Gardner et al. 2017). A typical water column profile shows high levels of particles in surface waters as well as, in places, in the lower water column as a benthic nepheloid layer. Between these two lies a mid-water minimum. The particulate concentration at this minimum appears to reflect the biological productivity of the overlying waters, being low in the centre of the subtropical gyre and elevated beneath upwelling zones off North Africa and Iberia, as well as more generally in the northeast Atlantic. Upper ocean productivity apparently sets a background particulate concentration for the water column as a whole (Eittreim et al. 1976).

The presence of a strong bottom nepheloid layer is thought to represent resuspension of material from the seabed. The particulate load of the lower water column largely mirrors the distribution of strong currents as well as areas with high eddy energy at depth (Biscaye and Eittreim 1977). There is a skew towards the western basin and the highest water column loads (>1000 µg cm^{-2}) are found beneath the Gulf Stream and NAC. In areas without such high eddy energy, nepheloid layers are weak or non-existent (Gardner et al. 2017).

Resuspension of material to maintain a nepheloid layer need not be a constant process but can result from intermittent periods of elevated current speed and resuspension. These periods have been termed ‘benthic storms’ and may result from the penetration of surface eddies to the seabed or the meandering of currents. While such events have typically been observed beneath energetic currents such as the Gulf Stream and its eddies (Hollister and McCave 1984; Isley et al. 1990), currents to 27 cm s^{-1} have also been recorded in the much less energetic abyssal eastern basin (Klein and Mittelstaedt 1992). Over the MAR, the deep penetration of surface eddies is expected to be curtailed to beneath the level of the highest topography, so it is unclear whether eddies produce currents in valleys and canyons that are sufficiently strong to resuspend material from the seabed.

6.4 The local flow environment of the MAR

6.4.1 The axial valley – stratification, mixing and compensating flows

The axial valley of the MAR is far from continuous, being reasonably approximated as a series of basins separated by sills (Thurnherr 2000). Such chains of basins can be further grouped into disjoint segments with variable connection to waters of similar depth to either side of the ridge or to fracture zones crossing the ridge. Waters within the rift valley may differ markedly from those at similar depths off the ridge (Fehn et al. 1977), and tend to be weakly stratified, reflecting topographic blocking of denser off-ridge waters and efficient mixing within the valley itself (Saunders and Francis 1985). Local factors mean that water properties may also differ markedly between segments. Within closed axial valley segments, mean flows arise locally to redress horizontal density gradients created by mixing and hydrothermal heat input (with mixing estimated to be the dominant factor) (Saunders and Francis 1985; Fehn et al. 1977). These mean flows are relatively weak, with their speed relative to local tidal flows determining whether tidal reversals occur, or whether flow is more persistently unidirectional. The tidally-reversing case appears more frequent (Thurnherr et al. 2002). Mean flow is directed towards lower densities as denser water seeks to displace more buoyant water drawn down from above by mixing. It should be noted that the direction of flow in any given MAR segment will depend on local factors, principally the direction in which the segment is open to external waters and cannot be inferred from large-scale patterns of flow or water properties.

Detailed observations within the axial valley are relatively few. Within the well-studied segment from 35.5ºN to 36.7ºN, a mean flow of 0.01-0.03 m s^{-1} to the NE in the bottom few hundred metres was found to compensate an along-valley density gradient of -0.9×10^{-5} kg m^{-3} km^{-1} (Thurnherr et al. 2002). Decreasing density largely resulted from increasing temperature but was partially mitigated by increasing salinity. Along valley flows were locally intensified over sills, with a maximum daily-averaged flow recorded of 0.14 m s^{-1} near the Rainbow hydrothermal vent site (see 5.3).

6.4.2 The ridge flanks – mixing-driven upslope flow

Mixing against a sloping boundary can also create a horizontal density gradient which drives a compensating upslope flow (Phillips et al. 1986). In many areas, the flanks of the MAR are incised by canyons perpendicular to the ridge axis, with the base of these canyons rising towards the ridge crest. Measurements in the South Atlantic have shown mixing-driven residual flow along the seabed in such a canyon towards the ridge crest (Thurnherr et al. 2005), and similar flow is expected at topographically similar sites elsewhere. Indeed, a general tendency is expected for flow near the bed on the flanks of the MAR to be towards the ridge crest, with such flow concentrated in canyons (St. Laurent et al. 2001), although such broad patterns will be confounded locally by additional complexity and variability.

6.4.3 Sills – intensified hydraulic flows and mixing

Where a flow passes over a topographic obstruction (for example, if a sill obstructs flow along the axial valley of the MAR) hydraulic processes can lead this flow to plunge down the downstream flank of the obstruction, as an intensified, and turbulent, bed flow (Fig. 6.6). In the Lucky Strike segment of the axial valley at 37.3ºN, 2-week averaged velocities at the sill crest and instantaneous velocities in the bottom 200 m downstream exceeded 0.1 m s^{-1}, with this bottom-intensified flow extending for around 5 km before returning to a thicker, slower structure (St Laurent and Thurnherr 2007). Associated levels of turbulence and mixing were elevated to the extent that such sites may contribute significantly to the mixing budget of the abyssal ocean. Similarly, at the Rainbow hydrothermal site (36.2ºN), intensified and unidirectional near-bed flows reaching 0.14 m s^{-1} have been recorded over a sill (Thurnherr 2006), and high levels of mixing inferred. More recent observations from a nearby site on the same sill have, however, revealed a more tidal structure to the currents. Associated intense turbulent bursts were also apparently tidal, extending to 400 m above the seabed and often detached from the bed (van Haren et al. 2017; van Haren 2019).

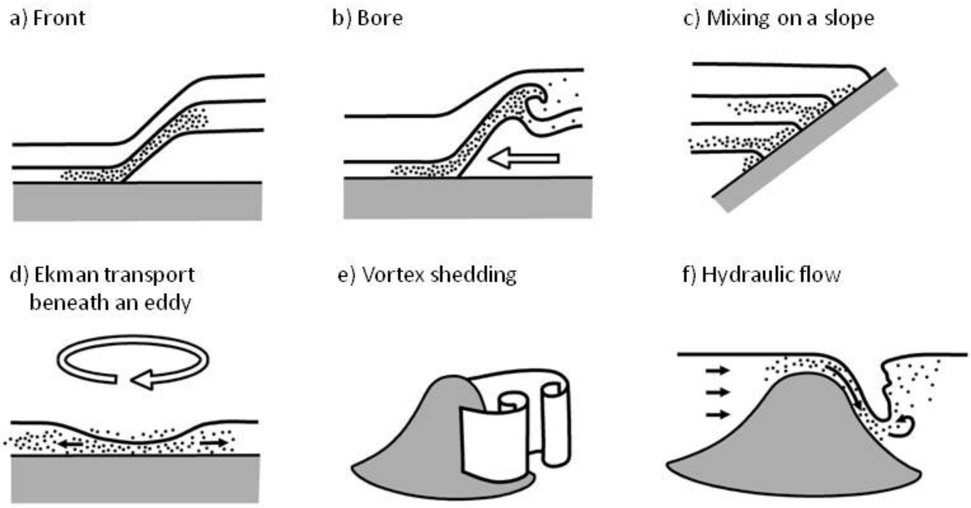


Figure 6.6: *Near-bed flow processes that may influence the behaviour of plumes in the deep sea. Based, in part, on (Richards 1990).*

6.4.4 Local tidal processes – internal tides, lee waves and bores

Depth-averaged tidal current speeds away from coastal/shelf areas are small (typically a few cm s^{-1}). Topographic effects, however, can greatly enhance tidal effects locally, extracting energy from the back and forth motion of the water column as a whole (Egbert and Ray 2000) and feeding a range of more complex, frequently bottom-intensified, and potentially turbulent, behaviours. As a result, observed mixing levels show a bottom-intensified structure and tend to be higher above areas of more complex topography such as the MAR (Polzin et al. 1997), although the nature of this turbulence is that it is patchy, occurring sporadically in time and location. A turbulent event may be attached to the bottom or detached from it in the overlying water column.

The details of tidal interaction with the MAR, and the partitioning of the energy involved between local processes and radiated internal tides, remain poorly understood. Much is inferred from model studies and analogy with shallow water processes. Exceptions include a set of highly detailed observations from moored thermistor chains (van Haren et al. 2017; Van Haren et al. 2014; van Haren 2019), and observations from a MAR site near 49ºN where tidally-pulsed flow over a low point in a ridge formed internal lee waves, upslope-propagating bore-like fronts, and turbulent bursts (Dale and Inall 2015) (Figs. 6.6, 6.7). Away from the MAR, highly turbulent, similar upslope-propagating fronts have also been observed at ~500m depth on the flanks of the Great Meteor Seamount (van Haren 2005), at 470m on the continental slope in the Faeroe-Shetland Channel (Hosegood and van Haren 2004) as well as at 1400m on the Biscay continental slope at (van Haren 2006), suggesting that they are frequent features of sloping topography across a broad range of depths. Such sites might expect sudden turbulent bursts, current or temperature changes, resuspension, and vertical velocity driving near-bottom water higher into the water column. While these fronts often appear to be tidal in origin, they are rather variable in both their occurrence and timing (Dale and Inall 2015) and their dynamics are incompletely understood. A similar but downslope-propagating feature associated with resuspension of bed material was observed at the foot of the continental slope at 3000m on the flanks of the Rockall Trough (Bonnin et al. 2006).

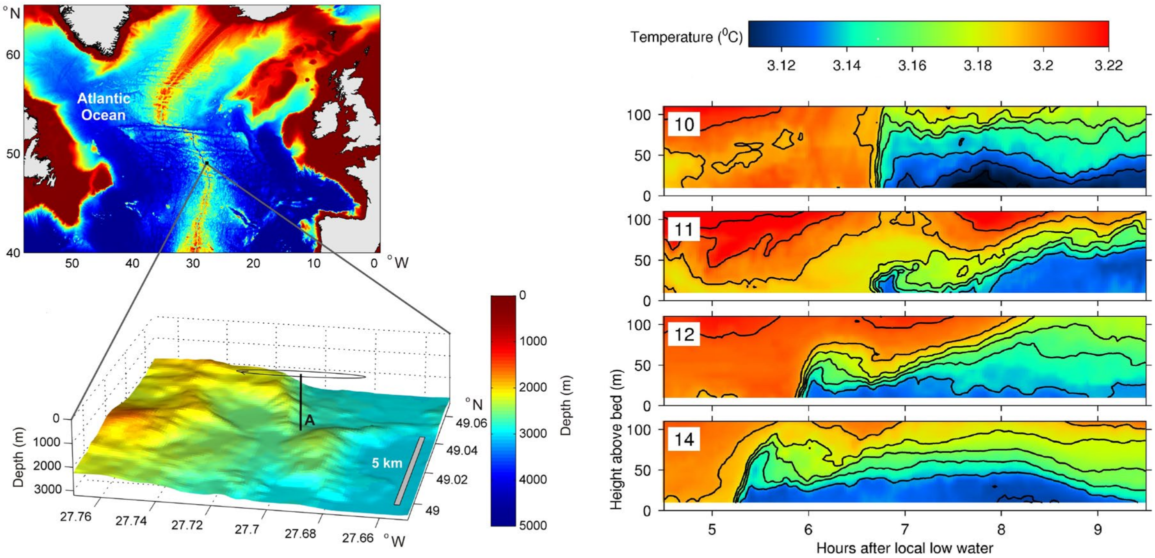


***Figure 6.7**: Bottom trapped pulses of cool/dense water travelling over a topographic saddle amid complex MAR topography (Dale and Inall 2015). Left panel: Location and bathymetry. Right panel: Time series of temperature over the bottom 100 m of the water column. The inset number is the sequential tidal cycle in the record.*

6.4.5 Influence of natural hydrothermal vents and plumes

Hydrothermal vents locally modify water density and therefore influence the flows surrounding a vent site across a broad range of length scales, potentially extending to the ocean basin scale (Speer and Helfrich 1995). A vent plume is initially warmer and more buoyant than its surroundings, so rises through the water column entraining ambient water and becoming denser as it does so. When the increasingly dense plume matches the density of the ambient water column, the plume water and the water it has entrained spread more horizontally. Perhaps counter-intuitively, a rising hydrothermal plume in the Atlantic reaches density equilibrium with its surroundings as a relatively cool temperature anomaly (Speer and Rona 1989; Thurnherr and Richards 2001) due to entrainment of fresher, cooler water at depth. Conversely, the temperature anomaly is warm in the abyssal Pacific where the ambient salinity gradient is reversed. Vent plumes rise hundreds of metres above their source (330 m for a modelled Atlantic example (Speer and Rona 1989), comparable with observations of 360 m at the TAG vent field (Rona et al. 1986). Near their source, plume waters form multiple thin layers (10-20 m), visible through their particle load and resulting turbidity, whereas further from the source these layers coalesce into a smoother nepheloid layer of hundreds of metres in vertical extent (German et al. 1996). As plume waters spread after reaching equilibrium with ambient waters, they veer under the Coriolis force, tending to form anticyclonic (clockwise in the North Atlantic) vortices (Speer and Marshall 1995; Helfrich 1994; Speer 1989), although these can be unstable and break into sub-vortices (Helfrich and Battisti 1991). Predicted flows within vortices are comparable to ambient mean flows and tides (Speer 1989; Speer and Helfrich 1995), so vortices are likely to be subject to additional distortion by flows that they encounter, as well as nearby topography.

More substantial volcanic events can produce ‘megaplumes’ that rise 1 km above their source, retaining a distinct temperature signature and developing a rotating eddy structure with a diameter of 10-20 km and current speeds exceeding 0.1 ms^{-1} (D'Asaro et al. 1994; Woods and Bush 1999). These eddies potentially have a lifespan of years (D'Asaro et al. 1994) and would be capable of retaining and transporting plume fluid during this period. Such features have not been directly observed in the Atlantic, although volcanic events of an appropriate magnitude have been detected on the MAR (Dziak et al. 2004).

6.4.6 General comments on the nature of the small-scale physical environment

The preceding sections paint a picture of complex and frequently turbulent flows, with considerable spatial variability on small scales and unpredictability in time. Indeed, (Polzin et al. 1997) confirm the increase in turbulent mixing with depth. This, at first glance, appears at odds with the decrease of current speeds with depth, which implies that energy levels decrease. This decrease in energy is countered, however, by decreasing stratification, meaning that less energy is required to overcome vertical density differences, so deep flows can more easily move vertically. With the increasing importance of vertical motion comes a decrease in the typical horizontal scales of flow (the internal Rossby radii decrease), meaning that deep flows are more fully three-dimensional. This poses a challenge for both measurement of the deep flow environment and for flow modelling, where the horizontal resolution of hydrodynamic models must be fine while the hydrostatic dynamical approximation used to simplify large-scale ocean modelling becomes questionable. Models do not adequately represent the true nature of flow-topography interaction in three dimensions, and the sensitivity of predictions to model resolution is problematic, even at larger scales (Zilberman et al. 2009). The reality is that flow structures may differ dramatically between sites separated by a few hundred metres or considerably less (Dale and Inall 2015).

6.5 Variability

The physical environment of the MAR reflects large-scale flow patterns, including surface flows such as the NAC and equatorial current system, and elements of the deep component of the overturning circulation, particularly to the north of the CGFZ. Therefore, the MAR is to some extent likely to be impacted by variability in these components of circulation. Tidal interaction with topography and resulting mixing-driven flows, in contrast, receive predictable tidal forcing and are only likely to change substantially if there are significant changes in stratification at abyssal depth. It is presumed that such a change could only take place relatively slowly.

6.5.1 Basin scale

The large-scale overturning and gyre circulations show variation in their strength and structure, including both oscillatory variability and long-term underlying trends. Key modes of Atlantic variability are the Atlantic Multi-decadal Oscillation (AMO) (Buckley and Marshall 2016) and the North Atlantic Oscillation (NAO) (Eden and Jung 2001) which are both evident in sea surface temperature anomalies. Models suggest the AMO is related to variability in the overturning circulation (Yeager and Robson 2017; Trenary and DelSole 2016), however the timescales of such variability are too long to be well represented in existing observational records and mechanisms remain controversial. New programmes, measuring the overturning circulation in unprecedented detail, are revealing that is has very considerable variability on the relatively short timescales measured to date (Lozier et al. 2019; Frajka-Williams et al. 2019).

6.5.2 Mesoscale

Perhaps of more direct impact for the MAR is mesoscale variability (scales of order 100 km and timescales of months) including eddies and meanders of the mean flow. The bulk of the energy contained in oceanic flows is contained in eddies and other varying components rather than in the underlying mean flow, however the distribution of the energy of this varying component (Eddy Kinetic Energy, EKE) frequently mirrors the underlying mean flows from which it is derived. In the North Atlantic, EKE is highest along the path of the Gulf Stream, the North Atlantic Current, the Azores Current and in the tropics south of 10N (Fig. 6.3). The exceptions are coastal and boundary currents, such as the East and West Greenland Currents, which are more strongly constrained and have lower EKE. Outside these areas of strong mean flow, EKE is low, but may still be orders of magnitude larger than the mean energy.

While mesoscale flows may take the form of eddies, which enclose a body of water and materially transport it (such as Gulf Stream rings, or 'meddies' of intermediate depth Mediterranean water), the central Atlantic is better described as a complex of meandering and interacting mesoscale features which do not so much enclose and transport water as divert and add complexity to the path of flow through a region. The interpretation of local flow patterns requires careful reference to mesoscale structure (Read et al. 2010). The dominance of the mesoscale is very clearly seen in the paths of drifters and floats in the North Atlantic, both at the surface (Fratantoni 2001; Reverdin et al. 2003) and intermediate (Ollitrault and Colin de Verdière 2002; Lavender et al. 2005) depths, and leads to complex patterns of dispersion of dissolved tracers (and plumes) which are drawn out into elongated filaments (Ledwell et al. 1993).

The equatorial current system has its own distinct mode of variability, since its horizontal and vertical shear are unstable and lead to the development of tropical instability waves (TIWs). In the northern hemisphere these produce a peak in EKE at 4-5ºN with a pronounced maximum during the late northern hemisphere summer when the North Equatorial Counter Current is also strongest (Von Schuckmann et al. 2008).

6.6 Influence of the physical environment on mining activities on the MAR

6.6.1 Plume behaviour

Detailed understanding of small-scale local flow, its variability, and the potential for turbulence, is of high importance for understanding the fate of suspended material, since a large proportion of such material settles within seconds to minutes of being suspended. Mid-ocean ridge environments are complex with a range of flow processes, variability on small length scales and a potential for patchy turbulence (Fig. 6.7). For this reason, it is difficult to generalise about sites and their expected plume behaviour. Hydrodynamic modelling is also difficult in these environments, as simulations may not converge acceptably as model resolution is refined. Direct observations of the flow environment of individual sites would therefore be of great benefit, to determine the background flow direction, variability, and any significant local responses to topography, such as intensified hydraulic flow over sills, propagating bores.

Natural hydrothermal plumes differ markedly from mining-induced plumes in their buoyancy characteristics. Whereas natural plumes are buoyant at their seabed source and equilibrate through entraining surrounding fluid as they rise through the water column, mining plumes will be less buoyant than surrounding fluid due to their sediment load, so they are expected to initially sink. While this may initially restrict plumes with a near-bed source to the bottom few metres or tens of metres, there are a number of processes that can mix a bottom layer higher into the water column or directly lift it from the bed, including passing fronts/bore, and mixing driven intrusions from slopes (Fig. 6.7). Predictions of plume behaviour are highly dependent on the exact nature (size distribution) of the suspended particle load and the nature of its release.

6.6.2 Large scale dispersion from the MAR

Large-scale surface currents interact with the MAR in three key regions: In the north, where the North Atlantic Current crosses the MAR in a broad and variable zone between 49ºN and 53ºN; in the Azores current at around 35ºN; and in the equatorial current system south of 10ºN (Fig. 6.3). These surface current systems penetrate at least to intermediate depths including the MAR crest and it is expected that surface and intermediate waters in these regions could disperse relatively rapidly away from the MAR. Drifter and float studies suggest that basin-wide dispersion occurs on timescales of the order of a few years.

Deep flows in contact with the MAR topography may be influenced by shallower current systems (for instance, in the regulation of deep flow through the CGFZ by NAC variability), but the topographic constraint means that deep flows are more likely to flow along the MAR than across it, so they have less capacity for transporting material away from the MAR. They are also relatively slow. Large scale deep flows that interact with the MAR occur largely to the north of the CGFZ where overflow water from the Iceland-Scotland Ridge (ISOW) travels to the southwest along the eastern flank of the Reykjanes Ridge, crosses the MAR at the CGFZ, then travels to the northeast along the western flank. At depths greater than 4000 m there is also flow of Antarctic Bottom Water (AABW) across the MAR in the Romanche and Vema fracture zones.

At other latitudes, mean deep flows are expected to be more locally driven by mixing processes that relate to the bathymetric circumstances of individual ridge segments. While some ridge segments are well studied and the direction of the mean deep flow is known (Thurnherr et al. 2002), it is difficult to infer flow directions for less well studied segments and direct measurements are required. These flows are not, however, expected to transport deep water away from the MAR.

6.7 References

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7. Cumulative impacts

7.1 Introduction

The “Recommendations for the guidance of contractors for the assessment of the possible environmental impacts arising from exploration for marine minerals in the Area” (ISBA/25/LTC/6) recognises the importance of collating all baseline data generated by contractors to the ISA to be used for addressing cumulative impacts through the REMP process. Contractors to the ISA are obliged under Regulation 33 of the “Regulations on prospecting and exploration for polymetallic sulphides in the Area” (ISBA/16/A/12/Rev.1) to ensure effective protection for the marine environment from harmful effects which may arise from activities in the Area, in accordance with Recommendations issued by the Legal and Technical Commission. There is therefore a direct obligation requiring contractors to provide their baseline data from which potential cumulative impacts can be assessed. Cumulative impacts are defined as "Impacts resulting from incremental changes caused by other past, present or foreseeable actions" (ISBA/25/LTC/6)

Assessment of cumulative impacts in Europe is commonly attempted and provides some relevant information for assessment and management. Assessment of cumulative impacts was first required by the European Environmental Impact Assessment (EIA) Directive (85/337/EEC, since amended by further Directives) and by the EC Habitats Directive (92/43/EEC), where they are called “in-combination” impacts. More recently, the European Strategic Environmental Assessment (SEA) directive (2001/42/EC) also requires assessment of “secondary, cumulative, synergistic, short, medium and long-term permanent and temporary, positive and negative effects” (Annex 1, f, 2001). Furthermore, both appropriate assessment and screening under the European Habitats Directive requires consideration of “in combination” impacts (Article 6.3, 1992), which are taken to be synonymous with cumulative impacts.

Cumulative impacts can occur at a greater extent than the sum of all the individual impacts in space and time. Evaluating these impacts is challenging and requires 1) scoping and impact identification techniques to identify how and where an indirect or cumulative impact or an impact interaction would occur, and 2) evaluation techniques to quantify and predict the magnitude and significance of impacts based on their context and intensity (Walker and Johnston, 1999). This is an important part of regional environmental assessment and management planning (Therivel, 2010).

Box 1: Cumulative impacts can be additive, neutralising or synergistic.

Additive impacts are caused by the sum of all the individual impacts

Antagonistic (or neutralising) impacts are impacts that cancel each other out, i.e. the net effect is close to zero

Synergistic impacts are caused when the cumulative impacts are greater than the sum of the individual impacts

From an environmental perspective, impact interactions are typically classified into those that are greater than (synergistic) or less than (antagonistic) their additive effects (Boyd and Brown, 2015). These can affect ecosystems in different ways and predictions of the interactions, particularly in unstudied systems, presents a challenge. For example, both synergistic and antagonistic interactions may be common in marine food webs (Griffith *et al.*, 2012). In addition, synergistic and antagonistic interactions may operate at different levels of ecosystem functioning; for instance, antagonistic interactions may act on populations of individual species (Brown *et al.*, 2013) but the combined population impacts may lead to synergistic effects to communities (Kirby *et al.*, 2009). The interplay of different environments, impacts and scales give rise to many different permutations of change (Boyd and Brown, 2015). The cumulative effects of interactions also depend on whether the impacts are positive or negative. Antagonistic interactions can have a negative effect even if the individual effects are positive, for example ocean fertilisation can occur with iron enrichment and increasing carbon dioxide concentrations (Salter *et al.*, 2014), but the combined effect of both leads to pH-mediated changes to trace metal speciation (important for iron availability to marine biota) and reduced overall productivity (The Royal Society, 2005).

The management of cumulative impacts is increasingly important (Duarte, 2014) but presents challenges (Dunstan *et al.*, 2019). As illustrated, pressures from one or more sources may interact and result in non-linear consequences, and can be the product of different exposures, time lags, or threshold responses (Johnson, 2016). Cumulative impacts can result from a single activity repeatedly producing a single pressure, a single activity producing multiple pressures, multiple activities producing a single pressure, or multiple activities producing multiple pressures (Foley *et al.*, 2017). In the coastal ocean, statistical tools and models are often applied to better predict the effects of multiple pressures (Uthicke *et al.*, 2016), but these are difficult to develop and to parameterise in less well known areas. In addition to the challenge of prediction, there is a challenge of managing cumulative impacts (Johnson, 2013). In most cases activities are managed separately and regulated by different governing bodies (Ardron and Warner, 2015) complicating an integrated approach.

In the context of deep-sea mining, cumulative impacts are important (Gjerde *et al.*, 2016; Gollner *et al.*, 2017; Levin *et al.*, 2016; Van Dover, 2014). There is particular concern that cumulative impacts could lead to regional-scale effects, including losses of brood stock, genetic diversity, species, trophic interactions and complexity, and resilience, together with changes in community structure, genetic isolation, and the possibility of species extinctions, and species invasions (Van Dover, 2014). Several potential cumulative impacts of relevance to deep-sea mining have been identified including: 1) multiple mining events, 2) interactions with other activities, such as fishing, other commercial harvesting, scientific research, tourism, marine debris/litter, bioprospecting, and cables/communication infrastructure and 3) climate change (including ocean acidification, deoxygenation, warming and changes in POC flux) (Levin *et al.*, 2016; Washburn *et al.*, 2019). Experts have expressed greatest concern about the vulnerability of ridge habitats to cumulative impacts resulting from multiple mining events and fishing activities (Levin *et al.*, 2016; Washburn *et al.*, 2019).

Here, we describe and evaluate the potential cumulative impacts that could occur for deep-sea mining. For the purpose of this description, we focus on the northern Mid-Atlantic Ridge between the southern boundary of the Icelandic extended continental shelf (ECS) claim south of Iceland to the equator, exclusive of the Brazilian Exclusive Economic Zone (EEZ) around the islands of St Peter and St Paul (Fig 7.1).

7.2 Considerations for potential cumulative impacts

The extent of cumulative impacts at a local to regional scale will be controlled by the same environmental factors that influence the impacts from single operations. These include the environmental conditions at the sites, such as currents, temperature, density and their spatial and temporal variability (Amorim *et al.*, 2017). They also include the habitat types and ecosystems found in the area and their sensitivities (Van Dover *et al.*, 2018). The characteristics of individual species and their populations are also important, with factors like species life histories, reproductive mode, trophic dynamics, function within the ecosystem, population size and connectivity being critical in determining their vulnerability (Hauton *et al.*, 2017).

The potential for cumulative impacts (Table 7.1) is dependent on the spatial location of mining operations as well as the magnitude, duration and spatial extent of impacts resulting from them. The location of mining activities will be driven by the resource availability, legal framework and potentially technological, economic or environmental considerations (Jones *et al.*, 2018a; Lusty and Murton, 2018). The impacts of mining could vary greatly dependent on technology and mitigation measures put in place (Cuvelier *et al.*, 2018).

Direct impacts

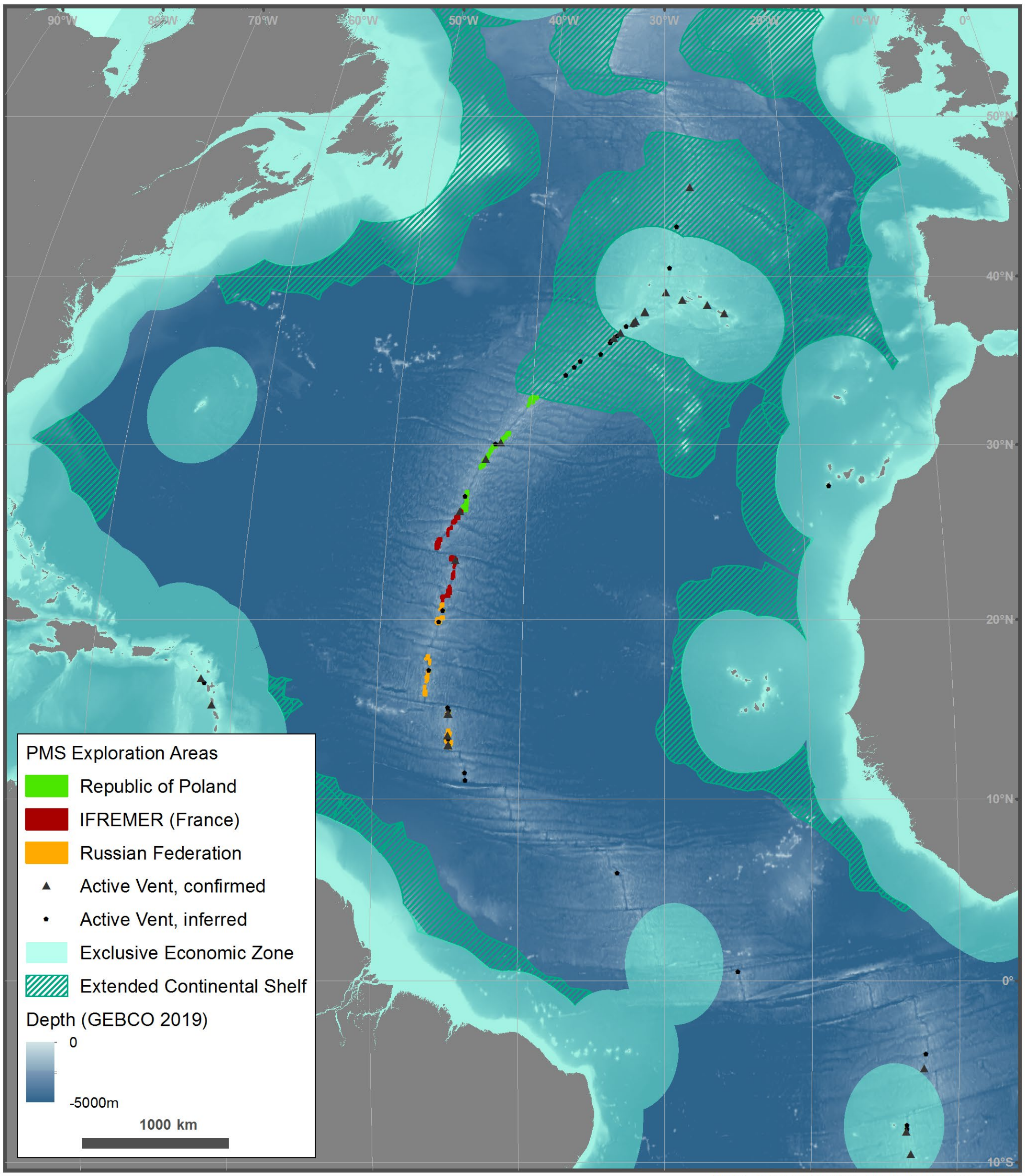
Many of the most severe impacts from mining (Table 7.2), such as direct disturbance to the seafloor from seabed collection, only occur at the mine site and the same area of seafloor is unlikely to be mined more than once. With sufficient separation, cumulative impacts will be limited to interactions with non-mining impacts. However, there is the potential for multiple direct impacts, such as those targeting resources associated with the same rare communities, such as hydrothermal vent communities potentially, to lead to cumulative effects, such as impacts on connectivity between populations.

Indirect impacts

The most likely contribution from mining to cumulative impacts are the impacts that extend over wider areas than the mine site itself. These impacts are mostly associated with plumes that are enriched in suspended particles or chemicals (Boschen *et al.*, 2013). Modelling work for the Mid-Atlantic Ridge suggests that plumes may extend over several times the area of the mining operation (Aleynik *et al.*, 2015). Plume impacts may extend throughout the water column, impacting surface (0-200m), pelagic (200 – 50m off bottom) as well as benthic (seabed to 50m off bottom) environments.

Table 7.1: Summary of types of cumulative effects and their characteristics based on (Spaling, 1994)

Type of cumulative effects	**Characteristics**
Incremental (additive) (repeated actions of a similar nature in space and time)	effects of additional impacts over time
Time lags or delayed effects	effects over time
Cross-boundary movement	impacts occur elsewhere
Fragmentation	fragmentation of habitats
Compounding/ synergistic effects	effects from multiple causes & processes, interaction of impacts & policies
Indirect effects; secondary or higher order effects	indirect and secondary impacts
Nibbling effects	continued small-scale impacts over area or time



Marine Geospatial Ecology Lab, Duke University (2020)

Figure 7.1: The case study area for this section is centred on the ridge axis from the southern boundary of the Iceland EEZ to the northern boundary of the equator. Existing French, Polish, and Russian Federation exploration contracts with the International Seabed Authority (ISA) for SMS are from the ISA database (www.isa.org.jm). Vent areas are from (Beaulieu et al., 2013). Map produced by Marine geospatial Ecology Lab, Duke University.

7.3 Types of cumulative impacts

7.3.1 Multiple mining operations

The cumulative impact of multiple mining operations has the potential to lead to additive and potentially synergistic effects. In many cases the spatial extent of the Mid-Atlantic Ridge, the large spacing between potential exploitation sites (Figure 7.1) and the likely time difference between operations will limit the potential for cumulative impacts. However, in some cases the scale of mining operations, deposits, the potential impacts of plumes and the slow recovery times of deep-sea ecosystems could provide potential for cumulative impacts (Figure 7.2). The most likely causes of cumulative impacts between mining operations are from **adjacent ongoing mining operations.** Ecosystem resilience will influence impact of adjacent ongoing mining operations. The layout of the existing exploration blocks suggests that there is potential for cumulative impacts of simultaneous (or near simultaneous) mining to occur in four ways (Figure 7.3):

1. Within a single block
2. Between adjacent blocks operated by one contractor
3. Between adjacent blocks operated by different contractors (France/Russia and France/Poland)
4. Between blocks in the Area and those within national jurisdiction (transboundary issues). For example, Polish exploration blocks are adjacent to the Portuguese extended continental shelf around the Azores, which may be subject to future mining activities under national jurisdiction.

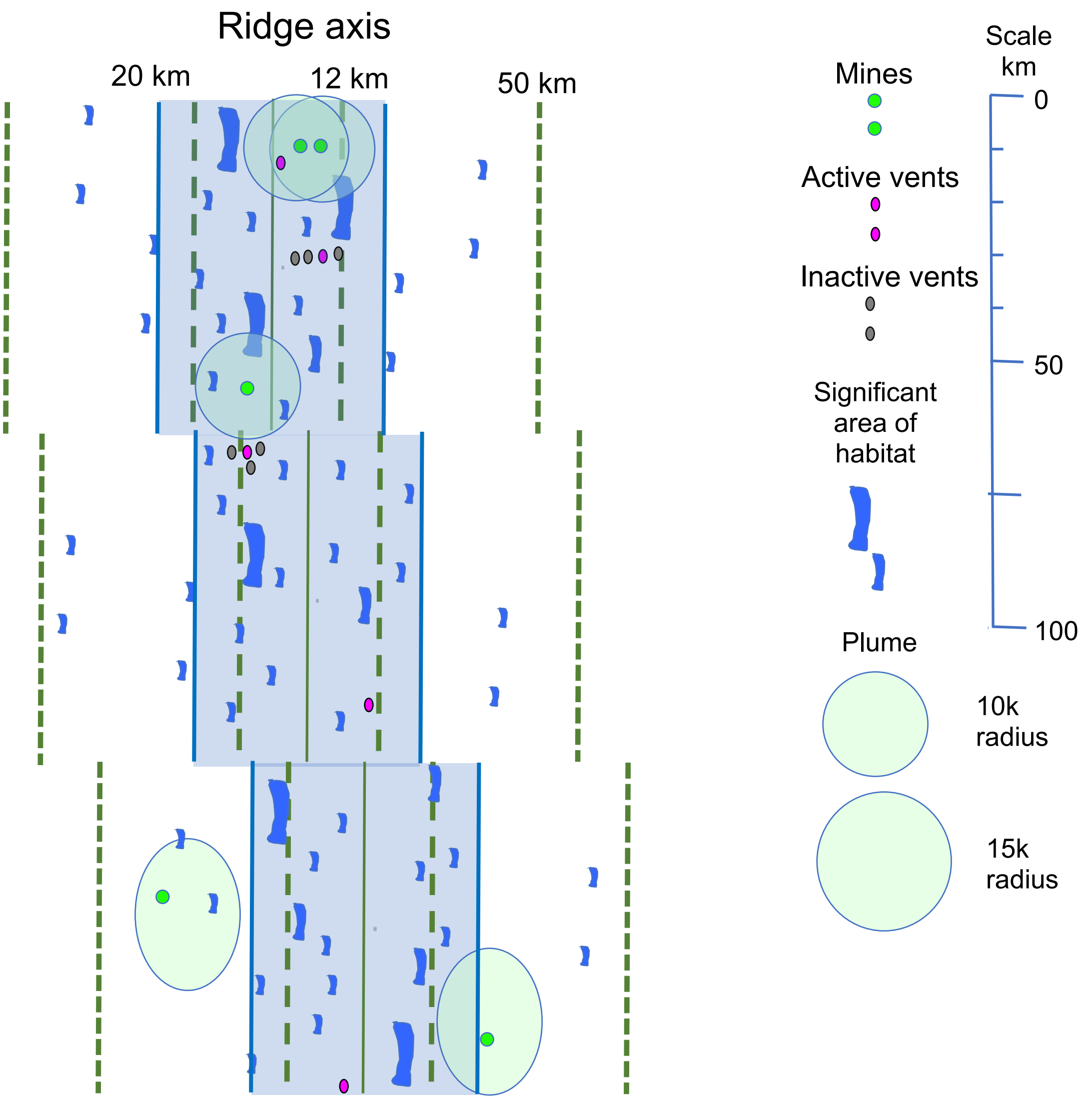


Figure 7.2: Conceptual figure showing the scale of possible impacts and habitats on the Mid-Atlantic Ridge (Weaver). Scales based on literature (Cherkashov et al., 2010; Niedzielski et al., 2013)

The relevance to the environmental impacts of the identity of the contractor and the legal regime in which they operate depends on whether different technological or legal situations will lead to different approaches for deep-sea mining. Different approaches will likely lead to different impacts (Table 7.1) and may affect the potential for cumulative impacts, particularly for nearby operations.

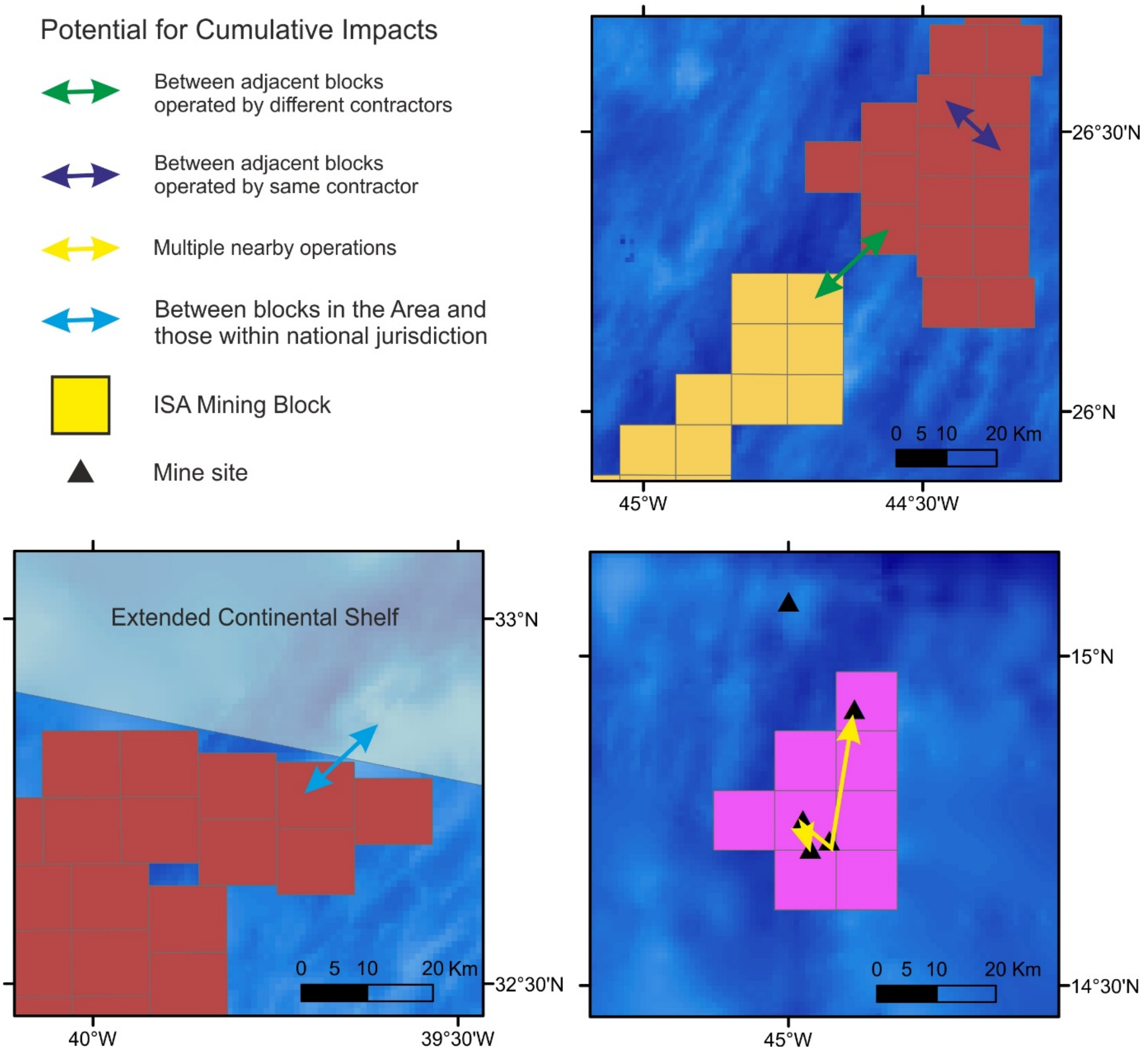


Figure 7.3: Maps showing potential for cumulative impacts. Maps are based on the spatial location of actual ISA exploration blocks (10 x 10km) and vent sites (as potential mining areas) for scaling. However, the figures do not imply any real mine location information or planned impact scenarios. Blue background represents seabed depth.

Profitable mining on the Mid-Atlantic Ridge may target numerous and relatively small SMS deposits (Lusty and Murton, 2018). Given efficient mining activities might target only the highest grade resources, each area may be mined in their entirety within months (Petersen *et al.*, 2016). This presents the potential for cumulative impacts from **single operations that move rapidly**. The impacts of rapidly mining many small targeted sites may be disproportionately high for those ecosystems, habitats or communities supported by that resource. Inactive sulphides are likely to be targeted but the ecosystems associated with these resources are poorly understood (Van Dover, 2019).

The potential for broad-scale alterations to the seafloor environment from deep-sea mining is unknown. Cumulative disturbance in the vicinity of hydrothermal vent sites has the potential to alter the hydrothermal stockwork (Humphris *et al.*, 1998), for example by redistributing seabed fluid flow to non-vent areas (Nakajima *et al.*, 2015). It should be emphasised that mining activities are not expected to arrest the hydrothermal system, but activities near vent systems will probably alter the distribution of venting activity on a local scale (metres to hundreds of metres) (Van Dover, 2011). The extent of inactive sulphides and whether particular communities are associated with them is unknown at the moment.

The ecological impact of cumulative mining events in a given region is difficult to assess. It requires understanding of the connectivity of populations, the number, size, and distribution of sources and sinks of larvae and dispersive juveniles and adults that are required to re-supply areas stripped of their biota (Van Dover, 2011). If multiple source populations are wiped out then current connectivity pathways will be removed or stressed, reducing recovery. Habitat loss or degradation attributable to cumulative mining events seems likely to be associated with chronic reduction in population size and increased isolation (Stockwell *et al.*, 2003), which in turn can impede recovery (Van Dover, 2011). Even if major changes do not occur, mining impacts are likely to reduce resistance and resilience of communities making cumulative impacts of sequential mining, or other disturbances, more likely to cause ecosystem-scale consequences.

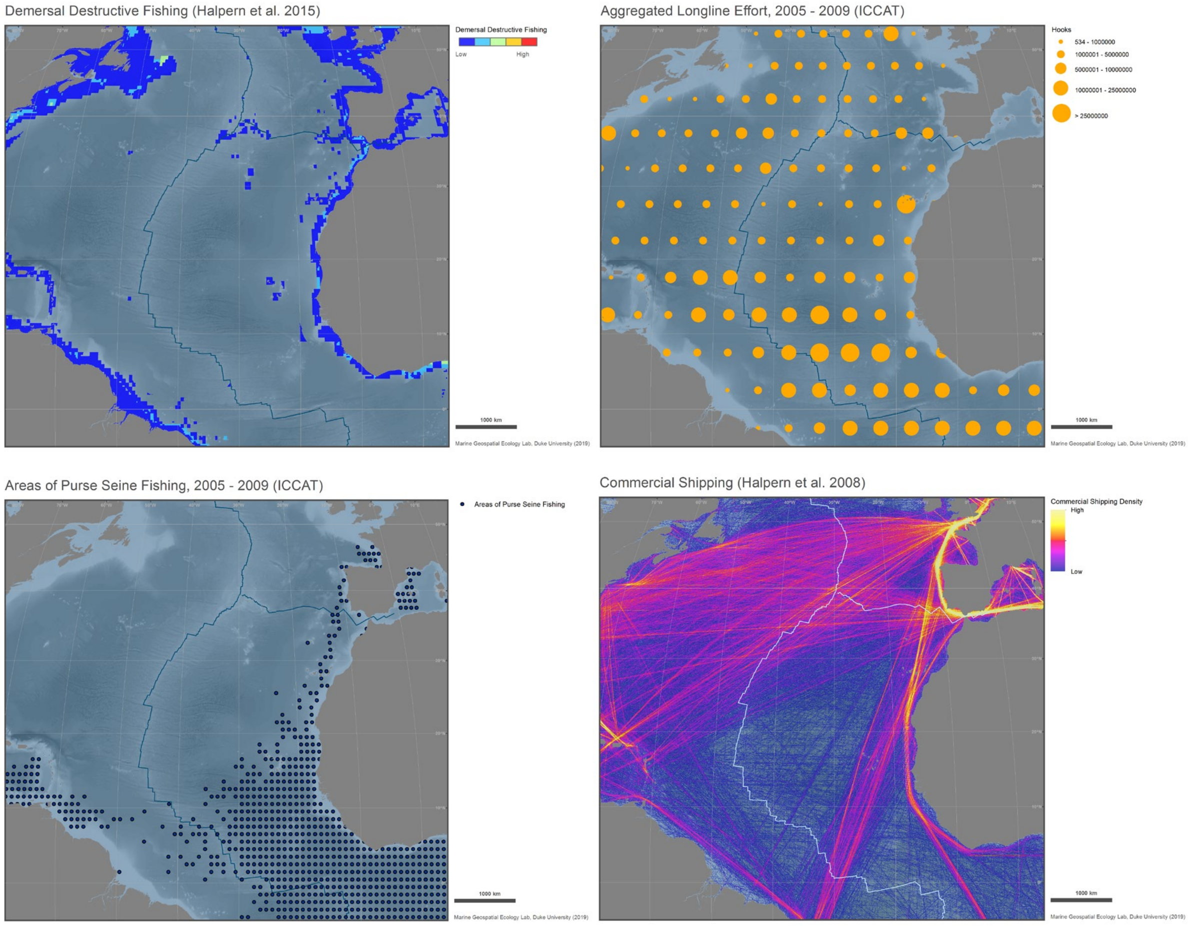
Table 7.2: Expected impacts and effects of mining on the Mid-Atlantic Ridge (modified from (Van Dover, 2014))

Physico-chemical impacts (cause)
Loss of habitat
Degradation of habitat quality (altered topography, substrata)
Modification of fluid flux regimes (flow rates, distribution, chemistry)
Sediment plume and sedimentation
Potential release of harmful metal complexes owing to oxygenation and crushing of ore
Light, noise
Potential biological effects (response)
Elimination or reduction of local populations and decreased reproductive output
Loss of larvae/zooplankton
Local, regional, or global extinction of rare species
Decreased seafloor primary production
Modification of trophic interactions
Decreased local diversity (genetic, species, habitat)
Mortality or impairment owing to toxic sediments
Altered behaviours
Regional effects
Losses of: brood stock, genetic diversity, species, trophic interactions and complexity, resilience; changes in community structure, genetic isolation, species extinctions, species invasions

7.3.2 Fishing and other harvesting

Historical data from the open ocean clearly suggest that overfishing has led to major impacts on target species and fundamentally altered marine ecosystems (Jackson *et al.*, 2001; Morato *et al.*, 2006; Pitcher, 2001). With the decline of shallow coastal waters resources, increasing demand, and new technology, fisheries are expanding offshore (Christensen *et al.*, 2003; Myers and Worm, 2003; Pauly *et al.*, 2003) and into deeper waters (Garibaldi and Limongelli, 2003; Gianni, 2004; Koslow *et al.*, 2000). Catches of open ocean target species, such as shark, billfish and tuna, are larger above seamounts (Morato *et al.*, 2010) and on mid-ocean ridges (Vecchione *et al.*, 2010). As a result, these areas are subject to extensive fishing activity (Queiroz *et al.*, 2016). The Mid-Atlantic Ridge also harbours a relatively high biomass (Fock *et al.*, 2002) and wide variety of demersal fish (Bergstad *et al.*, 2008), some of which are the target for fishing activities (Bensch *et al.*, 2009). Deep-water fish are generally considered to be long-lived (tens to greater than a hundred years) and have slow growth, late maturity and low fecundity (Morato *et al.*, 2006), which makes them particularly susceptible to impacts and slow to recover from fishing, but also to other activities.

On a broad scale established fisheries do cover some of the area of the MAR (Figure 7.4). Whether there will be exact spatial overlaps between areas of mining exploitation and either demersal or pelagic fisheries is still to be determined. Even without direct overlap there can be potential for cumulative impacts between mining and fishing activities. Potential effects may be one sided, only affecting the fishery and not the mining operation, and could include increased mortality resulting from particulates or increased chemical contamination of fish, rendering stocks unsalable. Potential additive impacts could occur where both mining activities and fishing independently lead to increased mortality. Synergistic impacts have been observed between climate change and fishing, where synchronous changes in fish numbers and sea temperature have established an extensive trophic cascade favouring lower trophic level groups over economic fisheries (Kirby *et al.*, 2009). Although the mechanisms are not clear, it is possible that two-way potential synergistic effects of mining and fishing could be observed, for example if mining impacts nursery areas for fish, while fishing directly reduces adult populations and spawning stocks. It is also possible that the impacts of fishing activities on the seafloor, such as habitat alteration and plume formation (Jennings and Kaiser, 1998), act in combination with the effects of mining to exceed a particular ecological threshold that was not exceeded by each impact individually. It is also possible that a three-way potential cumulative impact could occur between fishing, climate change and mining activities.


Demersal Destructive Fishing (Halpern et al. 2015)

Aggregated Longline Effort, 2005 - 2009 (ICCAT)

Areas of Purse Seine Fishing, 2005 - 2009 (ICCAT)

Commercial Shipping (Halpern et al. 2008)

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Figure 7.4: Spatial distribution of some potential cumulative impacts in the Atlantic. A) Demersal fishing, adapted from Halpern et al. (2008). B) Aggregated longline fishing effort for all flags, data from ICCAT. C) Occurrence of purse seine fishing for all flags, data from ICCAT (2005-2009). D) Commercial shipping, adapted from Halpern et al. (2008). Maps from Cleary et al, 2019 (available at https://ran-s3.s3.amazonaws.com/isa.org.jm/s3fs-public/files/documents/datareport-19nov-lowres.pdf)

7.3.3 Climate Change

The effects of climate change on the deep ocean include warming (Levitus *et al.*, 2000), oxygen loss (Breitburg *et al.*, 2018), acidification (Gehlen *et al.*, 2014), changes in ocean circulation (Toggweiler and Russell, 2008) and changes to surface productivity (Steinacher et al., 2010) that reduce food supplies to the seafloor (Jones et al., 2014). These changes are projected to exceed their typical ranges within the next century (Sweetman *et al.*, 2017). Current projections suggest that climate-related impacts will occur in all areas targeted for deep-sea mining, including the Mid-Atlantic Ridge (Sweetman *et al.*, 2017). The impacts of climate change will lead to effects on deep-sea life including direct impacts to key biological processes including metabolic rates, growth, and reproduction leading to increases in mortality and range shifts. Circulation variations will alter connectivity among populations and limit their ability to recover. This will lead to direct effects on ecosystems and the functions and services they provide. It is likely that cumulative effects from climate drivers and mining disturbance will interact.

Present projections suggest that the bathyal Atlantic (200-3000m depth), of which a significant proportion is on the MAR, is expected to experience dissolved Oxygen changes of –0.68 to 2.05% and changes in the flux of particulate organic carbon (food supply) to the seafloor of –36.27 to 4.79% between present conditions and 2100 (Sweetman *et al.*, 2017). Temperature is expected to decline in the bathyal Atlantic by –0.32 to 4.41 °C by 2100. The bathyal Atlantic Ocean is expected to become more acidic in the same period with pH changing by –0.37 to –0.01 units by 2100 compared to present conditions (Sweetman *et al.*, 2017). These changes are expected to lead to ecosystem-scale changes in the deep sea, such as major reductions in seafloor biomass (Jones *et al.*, 2014).

In the coming decades, climate-induced changes will affect all areas of mining interest. As such, it is important to consider these changes in conjunction with mining impacts to improve the effectiveness of environmental management. For example, it may be important to try to manage and differentiate impacts, such as species loss, directly caused by local mining from those generated at distance or by climate change (Levin *et al.*, 2019). Local and regional baseline data can be used to validate climate projections in order to avoid, mitigate and reduce mining impacts. Incorporating climate change into the management process for mining is an important consideration for cumulative impact assessment.

7.3.4 Other potential impacts

A range of other potential anthropogenic impacts have been identified that may lead to cumulative impacts with mining activities (Benn *et al.*, 2010). These include scientific research and bioprospecting, marine debris/litter, and cables/communication infrastructure. Civilian and military disposal activities occur in the deep sea, but typically not in the area of the Mid-Atlantic Ridge (Benn *et al.*, 2010).

Marine scientific research uses a range of equipment to sample the marine environment including dredges and trawls, grabs, corers, submersibles, moorings. Much of this equipment has only a single impact of a few square meters, although trawling, particularly for fisheries research, can disturb larger areas (Benn *et al.*, 2010). Marine scientific research may cause cumulative impacts with mining if the research is focussed in a small spatial area or linked to the monitoring of impact (Jones *et al.*, 2018b). The impacts of bioprospecting are currently negligible (Synnes, 2007), but may increase.

Marine litter is pervasive, with visible macroplastics observed in deep areas of the Mid-Atlantic Ridge (Pham *et al.*, 2014). Microplastics are even more common (Kane and Clare, 2019). The impacts of litter on deep-sea environments are poorly known (Law, 2017) but are not expected to lead to significant cumulative impacts with deep-sea mining.

Cables and communication infrastructure extend between all major land masses and hence are present in the deep ocean (Benn *et al.*, 2010). Although they may reach thousands of kilometres in length, the width of most cables is a few centimetres. The presence of subsea cables is certainly important for determining the spatial location of mining activities, although the cumulative impacts are economic rather than environmental.

The potential for cumulative impacts has been summarised (Halpern *et al.*, 2008) by combining information on expected individual impacts. Such analysis suggests that much of the Mid-Atlantic Ridge may receive cumulative pressures of fishing, climate change and pollution. Such additive analyses may underestimate true cumulative impacts, particularly with the addition of mining pressure. The effects of mining could exacerbate other changes. Mining could affect deep-sea biota with resulting feedbacks on other ecosystem processes, functions and services. Disturbance of microbes, removal of animals, combined with changing temperature, and oxygen depletion by sediment plumes, are likely to alter the carbon sinks. Such carbon sinks provide an important deep-sea ecosystem service, removing carbon from the biosphere, though the magnitude of these effects needs to be validated.

7.4 Potential for unexpected consequences of cumulative impacts

Marine ecosystems can undergo large, abrupt, and surprising changes in response to cumulative impacts, including those caused by both additive and synergistic stressors (Selkoe *et al.*, 2015). Theory and empirical evidence suggest that many complex systems have system boundaries (also called thresholds or tipping points) beyond which the system will rapidly reorganize into an alternative regime (Holling, 1973; Petraitis *et al.*, 2009; Scheffer and Carpenter, 2003). Tipping points result from nonlinear relationship between ecosystem condition and intensity of an impact (Selkoe *et al.*, 2015). Well known examples of tipping points include collapsing fish stocks, cascading effects of eutrophication or overfishing, or climate-driven shifts in food webs (Rabalais *et al.*, 2010). Despite many examples, rapid ecological shifts are often not predicted (or modelled) usually because we assume linear, additive, and gradual ecological responses to impacts of human uses or natural drivers (Selkoe *et al.*, 2015). Major ecosystem-level changes can be socially, culturally, and economically costly (Doak *et al.*, 2008; Scheffer *et al.*, 2009; Travis *et al.*, 2014) and careful management based on best available data is important to reduce the chances of their occurrence.

7.5 Summary

- Cumulative impacts can lead to greater effects than the sum of individual constituent impacts. These impacts can occur at a regional or ecosystem level.
- The effects or mode of action of cumulative impacts are poorly known, especially in the deep ocean, leading to high uncertainty. Modelling techniques for individual pressures and cumulative impacts exist and will facilitate assessment of potential impacts and their likelihood.
- The science of estimating cumulative impacts is still in development, but existing methodologies, when combined, can provide adequate robustness for management.
- Cumulative impacts can occur from multiple mining activities as well as the combined impacts of mining and other anthropogenic pressures on the marine environment, including climate change
- There is a potential for a wide range of cumulative impacts to occur during mining operations on the Mid-Atlantic Ridge

- Marine ecosystem responses to individual, additive or synergistic stressors can be large, abrupt, and surprising.

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8. Introduction to the Biological chapters

The biology section is by far the longest in this document. To facilitate easier use of this information we have divided it into two separate chapters: 1) surface and midwater biology; and 2) benthic biology. This short introductory chapter relates to both the pelagic and benthic habitats. References for the whole biology section (Chapters 8 – 10) are included at the end of the benthic biology section (Chapter 10).

This document is structured, as far as possible, to reflect the content which is expected to be required in Environmental Impact Statements (EIS) to be submitted to the International Seabed Authority (ISA) as detailed in the ISA Draft Regulations for Exploitation document (ISBA/25/C/WP.1, Annex IV). The template for EIS within ISBA/25/C/WP.1 spans the surface (0 to 200 m water depth), mid-water (200 m to 50 m above seafloor) and benthic (seafloor to 50 m above seafloor) environments (Figure 8.1). The Regional Environmental Management Plan (REMP) for the northern Mid-Atlantic Ridge (MAR) is only anticipated to address the seafloor beyond national jurisdiction (the Area) along the northern MAR. However, the inclusion of the surface and mid-water environments within the EIS template supports the inclusion of these environments within the Biological section, to support the establishment of regional environmental baselines from the surface to the seafloor and to provide the context within which future contractor EIS documents may be viewed.

The Biological section is broadly structured to reflect the division of the marine environment as envisioned in ISBA/25/C/WP.1, however, within this section it was necessary to combine the surface and mid-water environments. Along the MAR, there does not appear to be a physical boundary at 200 m which prevents movement of pelagic species between the mid-water and surface environments, although photosynthetic activity of phytoplankton would be restricted to the photic zone, which is often above 200 m. Many of the MAR pelagic fauna move between the surface and mid-water as defined by ISBA.25.C.WP.1, and there does not appear to be sufficient information available to classify any of the species considered as ‘surface’ restricted, apart from seabirds, which do not tend to dive deeper than 200 m. To reduce repetition within this document, the surface and mid-water environments are subsequently addressed together, acknowledging that ISBA/25/C/WP.1 treats these environments separately.

Within the benthic, and combined surface and midwater environments, an attempt has been made to cover the range of biological components included within the EIS template of ISBA/25/C/WP.1, and the required aspects of their biology, such as regional distribution, temporal variation, trophic relationships, ecosystem function, connectivity, and resilience and recovery. However, it was not possible to provide information on all of the biological components featured in the EIS template within this document. Priority was given to providing a detailed account of all the biological components in the benthic environment, as the seafloor is expected to be the focus for developing a REMP for the northern MAR. Within the surface and mid-water environments, detailed accounts are given for the nekton (fishes, sharks, squid) and air-breathing fauna (sea birds, turtles, marine mammals). Air-breathing fauna, such as marine mammals and turtles, can feed at the seabed in some areas, but in this document are only addressed within the combined surface and mid-water environment. It was not possible within this version of the document to provide accounts of the microorganisms and plankton (both phytoplankton and zooplankton) in the combined surface and mid-water environment, although these do feature within the EIS template of ISBA/25/C/WP.1, and are important components of the northern MAR surface and mid-water ecosystems. Future versions of this document may be able to address these biological components.

In general, the most information is available for the regional distribution of biological components. Typically, there is less information available for temporal variation and trophic relationships. Far less information is available regarding ecosystem function, connectivity, and resilience and recovery. Within this version of the document, it was not always possible to address all these aspects of the biological components considered, where this is the case, this is clearly identified within the text. Generally, there is more biological information available for the section of the MAR south of Iceland but North of the Azores than there is South of the Azores to the equator. This generally reflects the efforts of two large international science projects, MAR-ECO (Patterns and processes of the ecosystems of the northern mid-Atlantic) and ECOMAR (Ecosystems of the Mid-Atlantic Ridge at the Sub-Polar Front and Charlie-Gibbs Fracture Zone), which both focussed on this northern section of the MAR.

The information provided within this section focuses on studies conducted along the northern MAR between the southern extent of the Icelandic Extended Continental Shelf Submission and the equator. However, where pertinent, information outside of this area is included to provide a more holistic regional context for the biological components under consideration. Where information is limited or absent on biological components, or aspects of their biology, this is identified within the text. The Biological section is not an exhaustive account of the biological components of the northern MAR but provides an informative first assessment, which can be updated as more information becomes available.

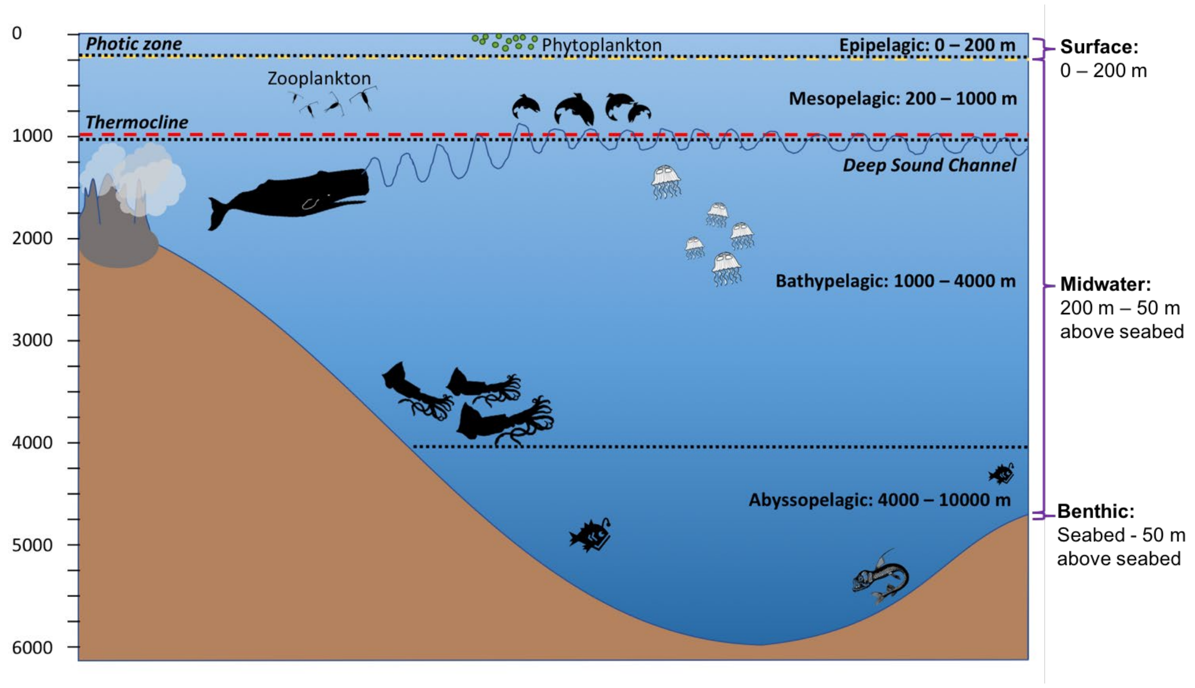

Figure 8.1. Schematic representing the division of the marine environment as used within the Biology Chapter: surface (0 – 200m depth); mid-water (200m – 50m above seafloor); and benthic (seafloor and 50m above seafloor). Courtesy of Rachel Boschen-Rose.

9. Biology of the Surface and Mid-Water Environment

The Mid-Atlantic Ridge (MAR) has a profound role in the circulation of the water masses in the North Atlantic Ocean (Bower *et al*., 2002a; Heger *et al*., 2008; Keller *et al.*, 1975; Rossby, 1999; Søiland *et al*., 2008; Sy *et al*., 1992), as discussed in the Physical Oceanography Chapter. The complex hydrographic setting around the MAR in general and the presence of the ridge itself leads to enhanced vertical mixing and turbulence that results in areas of increased productivity over the MAR (Falkowski *et al*., 1991; Heger *et al*., 2008; Read *et al*., 2010). The presence of the northern MAR disrupts the ocean circulation creating regions of high biomass that may arise from topographic influences on water circulation (St Laurent & Thurnherr 2007), bathymetrically induced fronts (Morato *et al*., 2018; Scales *et al*., 2014), and upwelling nutrient-rich deep water. As a result of these factors, the MAR concentrates biomass over its flanks and summits creating mid ocean regions of high productivity (Priede *et al*., 2013a).

The dominant water masses over the northern MAR between Iceland and the Azores show three different hydrographic regimes, dividing the water column environment into: 1) cold, sub-polar conditions north of the Sub-Polar Front; 2) warm, sub-tropical conditions south of the Sub-Polar Front; and 3) the frontal region itself which blends the characteristics of both areas (Bower *et al*., 1998; Pierrot-Bults, 2008; Søiland *et al*., 2008; Sy, 1988; Sy *et al*., 1992). Warm, saline water from the Mediterranean Sea also reaches the high latitudes, crossing the MAR over deep gaps in the ridge, demonstrating that sea-floor topography can constrain even upper-ocean circulation patterns (Bower *et al*., 2002b; Sy, 1988). Shallower portions of the MAR, such as the Reykjanes Ridge, act like a barrier to water movements, while deep west-to-east fracture zones, such as the Charlie-Gibbs and Vema Fracture Zones, seem to guide the spatial and temporal distribution of thermal fronts and water masses (Belkin *et al*., 2009).

The combined surface and mid-water environment of the northern MAR (surface to 50 m above seafloor) is a vast environment spanning thousands of meters' water depth. This pelagic environment is one of the least understood habitats globally, and there is often little information about the pelagic fauna, especially those residing in the mid-water. As well as influences from different water masses, the MAR pelagic environment also exhibits large gradients in light, heat, and availability of surface-derived food, all of which are generally negatively correlated with depth. In general, life in the deep sea decreases logarithmically with depth, with biomass declining roughly ten-fold for every 2000 m increase in depth (Priede, 2017) in both the benthic and pelagic realms. Over the MAR there are is an important difference, there is a fish biomass maximum at 1500-2300 m, and within 200 m of the sea floor 'near bottom' the biomass of mid-water fish may exceed that in the surface layers (Sutton *et al.,* 2008, Figure 9.1). Thus, compared with open ocean the presence of the MAR has the effect of greatly concentrating biomass compared with adjacent open water areas.

The pelagic environment of the MAR has a diverse fauna including nekton: fishes, sharks, cephalopods (squid and octopus) and crustaceans (shrimp); and air-breathing fauna: seabirds, sea turtles and marine mammals. In the following section, the regional distribution, temporal variation, trophic interactions, connectivity, ecosystem function, and resilience and recovery of the northern MAR pelagic fauna are considered in detail. The majority of the information on the mid-water nekton of the northern MAR originates from the MAR-ECO and ECOMAR field programs, which were focused on the MAR section north of the Azores towards Iceland. Far less information is available on the pelagic fauna occurring between South of the Azores and the equator.

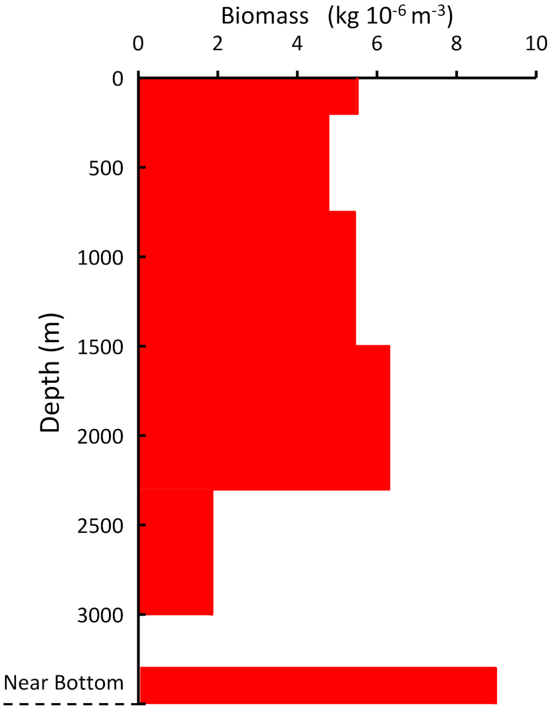

Figure 9.1. The vertical distribution of deep-pelagic biomass (wet weight) over the North Mid-Atlantic Ridge (Replotted from data in Sutton et al.*, 2008). 'Near bottom' includes all samples within 200 m of the sea floor irrespective of depth from the surface (range 750 – 2300 m). Courtesy of Monty Priede.*

9.1 Regional distribution

9.1.1 Biogeography

The pelagic environment of the northern Mid-Atlantic Ridge (MAR) under consideration (South of the Iceland Extended Continental Shelf Submission to the equator) spans four of the world's mesopelagic ecoregions (Figure 9.2) as recognised by Sutton *et al.*, (2017). The northern limit of this extent is defined by the Sub-Polar front located in the region of the Charlie-Gibbs Fracture Zone. Acoustic surveys of the MAR show a maximum of back scattering associated with the Sub-Polar front, the Charlie-Gibbs Fracture Zone and the area south of 52°N indicating a peak of mid-water pelagic biomass in this region (Opdal *et al.,* 2008).

North of the Sub-Polar front is the Northwest Atlantic Subarctic ecoregion which is the only major ocean region with deep-water connection to the Arctic and has a distinctive cold-water boreal faunal assemblage some of which are carried to the south in eddies that propagate from the frontal region (Miller *et al*., 2013; Heger *et al.,* 2008). The North Atlantic Drift ecoregion impinges on the MAR between approximately 51°N and 43°N and is a continuation of the Gulf Stream in the form of an eastward flowing eddy-field region which biologically acts as a transition ecotone between the boreal fauna to the north and subtropical fauna to the south. The dominant ecoregion is the Central North Atlantic from 43°N to 5°N which is a broad area of warm water with stable conditions and a distinctive faunal composition. Based on differences in the mid-water pelagic fish assemblages Judkins & Haedrich (2018) proposed a subdivision at latitude 23°N between a northern fauna with boreal affinities and a southern fauna with tropical influences. South of 5°N is the Tropical and West Equatorial Atlantic ecoregion with easterly winds and oligotrophic conditions. The four different ecoregions intersected by the northern MAR each have different fauna, although some fish, cephalopod and shrimp species are found across multiple ecoregions.

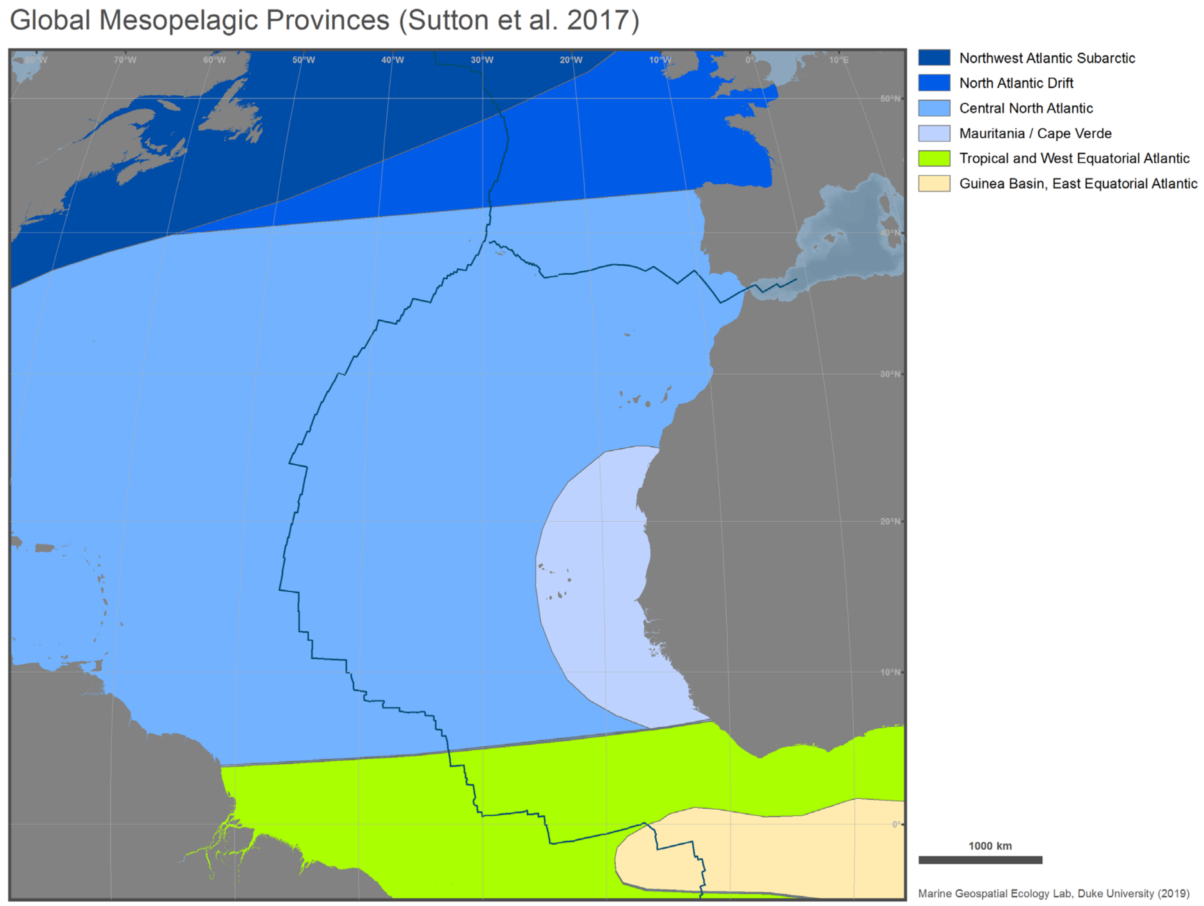

Figure 9.2. Mesopelagic Ecoregions of the North Atlantic Ocean. Map reproduced with permission from Cleary et al.*, 2019. Data taken from Sutton* et al.*, 2017. Map available: https://ran-s3.s3.amazonaws.com/isa.org.jm/s3fs-public/files/documents/datareport-19nov-lowres.pdf.*

9.1.2 Mid-water nekton

9.1.2.1 Fishes

The pelagic fish fauna of the northern MAR, often associated with deep-scattering layers detected by sonar, is dominated by vast numbers of small (typically < 10 cm long) forage fish (prey species to larger game fish), bristlemouths (Gonostomidae), lanternfishes (Myctophidae), hatchetfishes and pearlsides (Sternoptychidae) and deep-sea smelts (Bathylagidae). Associated with these are less abundant but larger predatory species, including Gulper eels (Eurypharyngidae) snipe eels (Nemichthyidae), sawtooth eels (Serrivomeridae) and dragonfishes (Stomiidae) that have various adaptations for stealthily intercepting and consuming their prey (Sutton *et al.*, 2008). Many of these fishes, both prey and predators, have bioluminescent organs used either for communication or for camouflage in the twilight and darkness of the deep (Priede, 2017; Table 9.1).

Within the Northwest Atlantic Subarctic ecoregion, to the North of the CGFZ, by far the most dominant mesopelagic fish species is the lantern fish *Benthosema glaciale*, accounting for over 90% of the catch in large trawls (Sutton & Sigurðsson, 2008). The bristlemouth *Cyclothone microdon* is also important but has been less well sampled (Sutton *et al.,* 2008).

Other myctophid lantern fish present in rank order of importance are *Protomyctophum arcticum, Myctophum punctatum*, Notoscopelus kroeyeri*, Lampanyctus macdonaldi, Lampanyctus crocodilus, Lampanyctus intricarius,* and *Lampadena speculigera.*

Species marked with an "*" are found almost exclusively over the MAR. Other species in rank order of importance are *Nansenia groenlandica*, Chauliodus sloani*, Bathylagus euryops, Nemichthys scolopaceus*, Schedophilus medusophagus*, Borostomias antarcticus, Normichthys operosus*, Arctozenus rissoi, Serrivomer beani, Paralepis coregonoides, Stomias boa ferox, Xenodermichthys copei, Argyropelecus hemigymnus, Maurolicus muelleri, Holtbyrnia anomala, Linophryne lucifer, Holtbyrnia macrops* and *Scopelogadus beanii* (Priede, 2017). Judkins & Haedrich (2018) identify a total of 140 fish species in the ecoregion with the species grouping *Benthosema glaciale, Bathylagus euryops*, *Lampanyctus macdonaldi, Cyclothone microdon, Maurolicus weitzmani¸ Borostomias antarcticus*, and *Melamphaes suborbitalis* considered to characterise the fauna having the highest geometric mean of the proportion of joint occurrences (GMPJO).

On the Reykjanes Ridge to the North of the CGFZ, Sutton & Sigurðsson (2008) found a dense deep-scattering layer (DSL) at 200-500 m depth on the West of the ridge with a high abundance of *Benthosema glaciale* and a more diffuse deeper DSL in the East. This was attributed to predominantly colder waters in the West. There is some evidence of increased fish biomass over the ridge with eight species occurring almost exclusively over the Reykjanes Ridge.

Within the North Atlantic Drift ecoregion, the fish fauna has affinities to the adjacent ecoregions to the North and South. As in the Subarctic, *Benthosema glaciale* is numerically the dominant fish species followed by *Cyclothone microdon* (Sutton *et al.,* 2008). Other important myctophids are, *Protomyctophum arcticum*, *Myctophum punctatum* and other species include the lightfish *Maurolicus muelleri*, the barbeled dragonfishes *Chauliodus sloani* and *Borostomias antarcticus*, the sawtooth eel *Serrivomer beanii*, deep-sea smelt *Bathylagus euryops* and Melaphaid *Scopelogadus beanii.* Judkins & Haedrich (2018) found a total of 120 species and identified the following grouping as most characteristic of the region: the myctophids *Protomyctophum arcticum* and *Notoscopelus kroyeri*, the lightfish *Maurolicus* muelleri, hatchetfish *Argyropelecus olfersii*, barbeled dragonfishes *Stomias boa ferox* and *Astronesthes niger* and deep-sea smelt *Bathylagichthys greyae.* These are not necessarily the most abundant but have a strong tendency to occur together in the North Atlantic Drift.

Sutton *et al.,* (2008) found a discrete assemblage of deep-living fish species at 750-2300 m depth dominated by three species; the bristlemouth *Cyclothone microdon*, deep-sea smelt *Bathylagus euryops*, and sawtooth eel *Serrivomer beanii*, that make up more than 50% of the fish biomass. At depths 200-750 m the myctophid *Benthosema glaciale* makes up more than 25% of the fish biomass. The fish fauna can be characterised as a relatively low diversity, high-abundance assemblage of vertical migrating fishes dominated by three species of lanternfishes (*Benthosema glaciale*, *Protomyctophum arcticum* and *Myctophum punctatum*) a dragonfish (*Chauliodus sloani*), a pearlside (*Maurolicus muelleri*) and a bristlemouth (*Cyclothone microdon*).

The Central North Atlantic ecoregion is a vast area extending from North of the Azores to almost the Equator in which Judkins & Haedrich (2018) found 255 fish species in the mesopelagic DSL, including species with a temperate distribution pattern such as the Myctophids *Hygophum hygomii*, *Lampanyctus pusillus, Lobianchia dofleini, Ceratoscopelus maderensis*, *Nannobrachium cuprarium*, *Bolinichthys indicus* and *Hygophum reinhardtii*; the hatchetfish *Argyropelecus aculeatus;* and barbeled dragonfish *Chauliodus danae.* Species which are considered broadly tropical also occurred here, including the myctophids Lampanyctus *nobilis*, *Lampanyctus vadulus* and *Diaphus luetkeni*; hatchetfish *Argyropelecus sladeni*; and bristlemouth *Gonostoma atlanticum*. Many species listed by Judkins & Haedrich (2018) occur mainly on the periphery of the North Atlantic and would not be expected on the MAR, where Sutton *et al*., (2008) found 168 mid-water fish species.

Species diversity is higher in the Central North Atlantic section of the MAR than on the more northerly sections, but biomass is lower. In the Azores region, Sutton *et al*., (2008) found 29 species of lantern fish, 19 of which could be regarded as dominant, leading them to suggest the term "Lanternfish Group" for an assemblage in which lanternfish contributed half of the abundance and one quarter of the biomass. At 750-1500 m depth, the pelagic assemblage was dominated by the bristlemouth *Cyclothone microdon*, loosejaw dragonfish *Malacosteus niger* and three large melamphaid species *Serrivomer beanii*, *Scopeloberyx robustus* and *Poromitra megalops*. At depths >1500 m there is a continuation of the same assemblage as found beneath the North Atlantic Drift comprising the bristlemouth *Cyclothone* *microdon*, the deep-sea smelt *Bathylagus euryops*, the sawtooth eel *Serrivomer beanii*, two melamphaids *Scopeloberyx robustus* and *Poromitra crassiceps* and a tubeshoulder *Maulisia microlepis*. There seems to be a general pattern of latitudinal change in species composition at depths <1500 m but relatively little species turnover at greater depths.

Judkins & Haedrich (2018) propose a latitudinal division in the central area at 23°N. To the North of this line, in descending rank order the most frequently occurring species are *Lobianchia dofleini, Diaphus rafinesquii, Ceratoscopelus maderensis, Notoscopelus resplendens, Lampanyctus crocodilus* and *Hygophum benoiti* (58-29% of samples). To the South, the most important species are *Ceratoscopelus warmingii, Lepidophanes guentheri, Gonostoma atlanticum, Diaphus brachycephalus, Lampanyctus nobilis, Argyropelecus hemigymnus, Diaphus luetkeni, Diaphus fragilis, Hygophum reinhardtii, Argyropelecus affinis, Sternoptyx diaphana* and *Diplophos taenia* (occurring in 83-28% of samples).

There is a significant number of widespread species that are found from temperate latitudes of the MAR in the North of the Central ecoregion through the tropics and into the South Atlantic including the lanternfishes, *Ceratoscopelus warmingii*, *Lepidophanes guentheri*, *Lampanyctus photonotus*, *Lepidophanes gaussi*, *Valenciennellus tripunctulatus*, *Diogenichthys atlanticus*, *Diaphus mollis* and *Lobianchia gemellarii*; and the bristlemouth *Sigmops elongatus*.

Within the Tropical and West Equatorial Atlantic, Judkins & Haedrich (2018) list 173 fish species but point out that only eight can be considered to have an affinity with this region. These include the barbeled dragonfishes *Astronesthes decoratus, Odontostomias micropogon*, *Astronesthes gudrunae* that rarely occur elsewhere and species that also occur in the Central North Atlantic; the lantern fish *Hygophum macrochir*, the barbeled dragonfish *Heterophotus ophistoma* and *Odontostomops normalops* (Sabertooth fish).

The Tropical and West Equatorial Atlantic can therefore be considered as a transition zone populated by species both from the North and South Atlantic but with a small number of more or less endemic predatory species. According to Kobyliansky *et al.,* (2010) the most abundant myctophid species in rank order are: *Ceratoscopelus warmingii*, *Bolinichthys photothorax*, *Lepidophanes gaussi*, *Lepidophanes guentheri*, *Nannobrachium cuprarium* and *Lampanyctus photonotus*. The light fish *Vinciguerria nimbaria*, bristlemouths *Cyclothone* sp., and hatchetfishes *Sternoptyx diaphana*, *Argyropelecus hemigymnus* also occur in large numbers.

Of the 205 species of fish logged by Sutton *et al*., (2008) on the northern MAR, 55 are represented by single specimens and 123 species are represented by 10 or fewer specimens (Table 9.1). The sum total of individuals in these 123 species accounts for just 0.65% of the total catch. Therefore, more than half the species present account for less than 1% of the catch. Some of these species with very low numbers such as the single specimen of the boarfish *Capros aper* are known to occur elsewhere in great abundance and are commercially fished, however a large proportion are intrinsically rare species that occur globally in low numbers. For example, 10 of the singleton species are oceanic deep-sea anglerfishes of the order Lophiiformes. They are iconic creatures of the deep sea, highly adapted to their dark and sparse energy environment with astounding diversity amounting to about 170 species in 12 families (Pietsch, 2009). There are more than 280 species of Stomiidae (barbeled dragonfishes) with various arrangements of jaws, light organs and barbels. Some species, as shown here, are quite abundant but many species are rare, known only from a few specimens. The Tetragonuridae (squaretails) have an unusual lifestyle in that they live for at least part of their life cycle inside gelatinous planktonic salp colonies, and do not occur in large numbers. The Cetomimidae (whalefishes) are found predominantly at depths greater than 1000 m and also do not occur in large numbers. These rare fish species are either highly specialised or pass most of their life at great depths with very low population numbers. Nevertheless, they contribute to the total species richness of the MAR and should not be discounted as 'noise' in statistical analyses of food webs, productivity or ecosystem function. For example, *Himatolophus* sp. (footballfishes) are rare deep-sea anglerfishes but have been twice recorded in the stomachs of sperm whales in the Azores (Clarke *et al*., 1993) and it is possible the whales actively search for this prey.

Table 9.1. Pelagic fishes of the Mid-Atlantic Ridge. Abundance (N) and Biomass are totals obtained in the survey of the northern Mid-Atlantic Ridge. Within each family, the species are ranked on order of numerical abundance. After Sutton et al.*, (2008).*

Order	Family	Species	Abundance N	Biomass wet weight (g)	NW Atlantic Subarctic	N Atlantic Drift	Central North Atlantic
Anguilliformes	Derichthyidae (longneck eels)	*Derichthys serpentinus*	16	466	Y	Y	Y
		Nessorhamphus ingolfianus	5	345	Y	Y	Y
	Nemichthyidae (snipe eels)	*Nemichthys scolopaceus*	9	449	Y	Y	Y
		Avocettina infans	1	33		Y	
	Serrivomeridae (sawtooth eels)	*Serrivomer beanii*	1062	78218	Y	Y	Y
		Serrivomer lanceolatoides	8	526			Y
Saccopharyngiformes	Eurypharyngidae (gulper eels)	*Eurypharynx pelecanoides*	95	7396	Y	Y	Y
	Saccopharyngidae (swallowers)	*Saccopharynx ampullaceus*	4	757		Y	
Argentiniformes	Opisthoproctidae (spookfishes)	*Opisthoproctus soleatus*	3	20		Y	Y
		Bathylychnops exilis	2	89		Y	Y
		Opisthoproctus grimaldii	2	2			Y
		Dolichopteryx longipes	1	7	Y		
	Microstomatidae (pencil smelts)	*Bathylagus euryops*	4543	190027	Y	Y	Y
		Bathylagichthys greyae	100	700			Y
		Melanolagus bericoides	15	308		Y	Y
		Nansenia sp.	14	886	Y	Y	Y
		Dolicholagus longirostris	4	40			Y
		Nansenia tenera	3	49		Y	Y
		Nansenia atlantica	2	61			Y
		Microstoma microstoma	1	31			Y
	Platytroctidae (tubeshoulders)	*Maulisia microlepis*	931	96481	Y	Y	Y
		Holtbyrnia anomala	283	11545	Y	Y	Y
		Normichthys operosus	261	5089	Y	Y	Y
		Holtbyrnia macrops	32	970	Y	Y	Y
		Searsia koefoedi	10	410	Y	Y	Y
		Sagamichthys schnakenbecki	4	51	Y	Y	
		Maulisia argipalla	2	121		Y	Y
		Maulisia mauli	2	132	Y	Y	Y
	Bathylaconidae	*Herwigia kreffti*	5	1167			Y

Order	**Family**	**Species**	**Abundance N**	**Biomass wet weight (g)**	**NW Atlantic Subarctic**	**N Atlantic Drift**	**Central North Atlantic**
		Bathylaco nigricans	2	375			Y
	Alepocephalidae (slickheads)	*Xenodermichthys copei*	43	1001	Y	Y	Y
		Bajacalifornia megalops	35	2461	Y	Y	Y
		Bathytroctes microlepis	8	1060		Y	Y
		Mirognathus normani	3	55		Y	
		Bathyprion danae	2	119		Y	Y
		Einara macrolepis	2	162			Y
		Photostylus pycnopterus	2	18	Y		
		Bathytroctes macrolepis	1	33		Y	
		Rouleina attrita	1	73.3	Y		
Stomiiformes	Gonostomatidae (bristlemouths)	*Cyclothone microdon*	7430	6557	Y	Y	Y
		Sigmops bathyphilum	564	10939	Y	Y	Y
		Sigmops elongatus	112	1973	Y	Y	Y
		Cyclothone braueri	82	34	Y	Y	Y
		Bonapartia pedaliota	71	151		Y	Y
		Cyclothone pallida	53	39	Y	Y	Y
		Margrethia obtusirostra	33	84			Y
		Gonostoma denudatum	18	207			Y
		Cyclothone pseudopallida	10	3	Y	Y	Y
	Sternoptychidae (hatchetfish & pearlsides)	*Maurolicus muelleri*	3379	4470	Y	Y	Y
		Argyropelecus hemigymnus	329	246	Y	Y	Y
		Sternoptyx diaphana	261	473		Y	Y
		Argyropelecus aculeatus	116	394	Y	Y	Y
		Argyropelecus olfersii	25	144	Y	Y	
		Sternoptyx pseudobscura	14	36	Y	Y	Y
		Valenciennellus tripunctulatus	6	1			Y
		Argyropelecus gigas	1	2			Y
	Phosichthyidae (lightfishes)	*Vinciguerria poweriae*	281	190		Y	Y
		Ichthyococcus ovatus	13	15		Y	Y
		Vinciguerria attenuata	5	3			Y
		Pollichthys mauli	2	1		Y	Y
	Stomiidae (barbeled dragonfishes)	*Chauliodus sloani*	897	21701	Y	Y	Y
		Stomias boa ferox	256	5963	Y	Y	Y
		Malacosteus niger	235	9453	Y	Y	Y

Order	Family	Species	Abundance N	Biomass wet weight (g)	NW Atlantic Subarctic	N Atlantic Drift	Central North Atlantic
		Borostomias antarcticus	139	11496	Y	Y	Y
		Melanostomias bartonbeani	11	381		Y	Y
		Photostomias guernei	8	40			Y
		Pachystomias microdon	5	189		Y	Y
		Astronesthes niger	4	30			Y
		Flagellostomias boureei	4	134		Y	Y
		Neonesthes capensis	4	65	Y	Y	Y
		Leptostomias sp.	2	64		Y	Y
		Aristostomias tittmanni	1	9			Y
		Astronesthes gemmifer	1	12			Y
		Bathophilus longipinnis	1	3			Y
		Bathophilus vaillanti	1	3			Y
		Melanostomias macrophotus	1	12			Y
		Photonectes margarita	1	40			Y
		Trigonolampa miriceps	1	393	Y		
Aulopiformes	Notosudidae (waryfishes)	*Scopelosaurus lepidus*	6	356	Y	Y	
		Ahliesaurus berryi	2	30			Y
		Scopelosaurus schmidtii	1	3			Y
	Scopelarchidae (pearleyes)	*Benthalbella infans*	4	48		Y	Y
		Scopelarchus analis	2	9			Y
		Scopelarchus guentheri	1	4			Y
	Evermannellidae (sabretooth fishes)	*Evermannella balbo*	11	91	Y	Y	
	Alepisauridae (lancet fishes)	*Alepisaurus brevirostris*	8	137		Y	Y
		Omosudis lowei	1	15			Y
	Paralepididae (barracudinas)	*Lestidiops sphyrenoides*	81	202		Y	Y
		Arctozenus risso	65	1048	Y	Y	
		Anotopterus pharao	27	5886	Y	Y	Y
		Lestidiops jayakari	14	143		Y	Y
		Magnisudis atlantica	8	60		Y	Y
		Paralepis brevirostris	5	44			Y
		Paralepis coregonoides	2	19.7	Y	Y	Y
Myctophiformes	Myctophidae	*Benthosema glaciale*	16640	24503	Y	Y	Y

Order	Family	Species	Abundance N	Biomass wet weight (g)	NW Atlantic Subarctic	N Atlantic Drift	Central North Atlantic
	(lantern fishes)	*Lampanyctus macdonaldi*	4095	101685	Y	Y	Y
		Notoscopelus kroyeri	3630	28919	Y	Y	Y
		Myctophum punctatum	2418	11217	Y	Y	Y
		Protomyctophum arcticum	1289	1246	Y	Y	Y
		Lobianchia dofleini	406	355		Y	Y
		Diaphus rafinesquii	315	711		Y	Y
		Hygophum hygomii	309	629			Y
		Diaphus holti	281	472			Y
		Electrona risso	237	789	Y	Y	Y
		Lobianchia gemellarii	216	1708		Y	Y
		Hygophum benoiti	214	310			Y
		Symbolophorus veranyi	191	672		Y	Y
		Notoscopelus bolini	145	736		Y	Y
		Nannobrachium atrum	139	967	Y	Y	Y
		Lampanyctus crocodilus	124	926	Y	Y	Y
		Ceratoscopelus maderensis	102	270		Y	Y
		Lampadena speculigera	94	2387	Y	Y	Y
		Bolinichthys indicus	52	66			Y
		Bolinichthys supralateralis	34	171	Y	Y	Y
		Lampanyctus intricarius	34	360	Y	Y	Y
		Lampanyctus pusillus	32	50			Y
		Lampadena anomala	30	844			Y
		Diaphus metopoclampus	28	111			Y
		Diaphus effulgens	18	201		Y	Y
		Lampanyctus photonotus	15	67			Y
		Lampadena urophaos atlantica	14	226		Y	Y
		Gonichthys cocco	13	12			Y
		Lampanyctus festivus	10	42			Y
		Hygophum reinhardtii	9	7			Y
		Lampadena chavesi	7	28			Y
		Diaphus mollis	5	6			Y
		Lepidophanes guentheri	4	6			Y
		Nannobrachium lineatum	3	25			Y

Order	Family	Species	Abundance N	Biomass wet weight (g)	NW Atlantic Subarctic	N Atlantic Drift	Central North Atlantic
		Taaningichthys bathyphilus	3	7		Y	Y
		Notolychnus valdiviae	2	0		Y	Y
		Benthosema suborbitale	1	2			Y
		Ceratoscopelus warmingii	1	1			Y
		Diaphus bertelseni	1	14			Y
		Diogenichthys atlanticus	1	2			Y
		Lepidophanes gaussi	1	4			Y
		Loweina interrupta	1	7			Y
		Nannobrachium achirus	1	8	Y		
		Nannobrachium cuprarium	1	1			Y
Gadiformes	Macrouridae (grenadiers, rattails)	*Coryphaenoides rupestris*	12	92	Y	Y	
		Bathygadus melanobranchus	3	6			Y
		Odontomacrurus murrayi	1	4			Y
	Moridae (deep-sea cods)	*Halargyreus johnsonii*	1	35		Y	
	Melanonidae (pelagic cods)	*Melanonus zugmayeri*	12	56		Y	Y
	Merlucciidae (hakes)	*Lyconus brachycolus*	1	62			Y
Ophidiiformes	Ophidiidae (cusk eels)	*Brotulotaenia crassa*	2	914			Y
Lophiiformes (Anglerfishes)	Melanocetidae (black sea devils)	*Melanocetus johnsonii*	3	333		Y	Y
	Oneirodidae (dreamers)	*Lophodolos acanthognathus*	10	105	Y	Y	Y
		Leptacanthichthys gracilispinis	4	24		Y	
		Chaenophryne draco	1	225	Y		
		Danaphryne nigrifilis	1	54	Y		
		Dolopichthys longicornis	1	4			Y
		Microlophichthys microlophus	1	70		Y	
		Oneirodes eschrichtii	1	156		Y	
		Oneirodes macrosteus	1	24			Y
		Phyllorhinichthys micractis	1	33			Y
	Ceratiidae	*Ceratias holboelli*	2	98		Y	Y

Order	Family	Species	Abundance N	Biomass wet weight (g)	NW Atlantic Subarctic	N Atlantic Drift	Central North Atlantic
	(seadevils)	*Cryptopsaras couesii*	1	99		Y	
	Gigantactinidae (whipnose anglers)	*Gigantactis vanhoeffeni*	1	166		Y	
	Linophrynidae (leftvent seadevils)	*Linophryne macrodon*	1	1			Y
Stephanoberyciformes	Melamphaidae (bigscale fishes)	*Scopelogadus beanii*	2152	47264	Y	Y	Y
		Melamphaes microps	255	5668	Y	Y	Y
		Scopeloberyx robustus	239	1159	Y	Y	Y
		Poromitra crassiceps	215	9456	Y	Y	Y
		Scopelogadus m. mizolepis	96	336		Y	Y
		Poromitra megalops	82	325	Y	Y	Y
		Poromitra capito	58	670			Y
		Scopeloberyx opisthopterus	11	7		Y	Y
		Melamphaes suborbitalis	7	102	Y	Y	Y
		Melamphaes typhlops	1	1			Y
	Rondeletiidae (redmouth whalefishes)	*Rondeletia loricata*	5	84		Y	Y
	Cetomimidae (flabby whalefishes)	*Gyrinomimus meyersi*	3	260		Y	
		Cetomimus sp.	2	101	Y	Y	
		Cetostoma regani	1	15			Y
		Procetichthys kreffti	1	73		Y	
	Megalomycteridae (bignose fishes)	*Ataxolepis apus*	1	0			Y
Beryciformes	Anoplogastridae (fangtooth)	*Anoplogaster cornuta*	26	2767	Y	Y	Y
	Diretmidae (spinyfins)	*Diretmus argenteus*	9	191		Y	Y
Gasterosteiformes	Syngnathidae (pipefishes)	*Entelurus aequoreus*	160	775	Y	Y	
Scorpaeniformes	Scorpaenidae (scorpionfishes)	*Sebastes mentella*	4	8014	Y		
		Sebastes sp.	4	3264	Y		
	Liparidae (snailfishes)	*Psednos* sp.	1	1		Y	
Perciformes	Percichthyidae	*Howella brodiei*	18	139		Y	Y

Order	Family	Species	Abundance N	Biomass wet weight (g)	NW Atlantic Subarctic	N Atlantic Drift	Central North Atlantic
	(oceanic basslets)						
	Epigonidae	*Epigonus constanciae*	1	1			Y
	(deepwater cardinal fish)	*Microichthys coccoi*	1	0			Y
	Carangidae (jacks)	*Trachurus picturatus*	1	16			Y
	Caristiidae	*Caristius maderensis*	1	34		Y	
	(manefishes, veilfins)	*Platyberyx opalescens*	1	319		Y	
	Zoarcidae (eelpouts)	*Melanostigma atlanticum*	5	18	Y	Y	
	Anarhichadidae (wolffishes)	*Anarhichas minor*	1	1056		Y	
	Chiasmodontidae	*Chiasmodon niger*	91	1838	Y	Y	Y
	(swallowers)	*Pseudoscopelus altipinnis*	9	266			Y
		Kali macrodon	5	413		Y	Y
		Dysalotus alcocki	4	130	Y	Y	Y
		Kali indica	4	270		Y	
		Kali macrurus	2	214		Y	Y
		Pseudoscopelus obtusifrons	1	68			Y
		Pseudoscopelus scutatus	2	35			Y
		Pseudoscopelus sp.*1*	1	68			Y
	Gempylidae (snake mackerels)	*Diplospinus multistriatus*	1	4			Y
	Trichiuridae	*Benthodesmus elongatus*	1	13		Y	
	(hairtails)	*Lepidopus caudatus*	1	4			Y
	Centrolophidae (medusafishes)	*Schedophilus medusophagus*	1	639		Y	
	Nomeidae (driftfishes)	*Cubiceps gracilis*	99	1616		Y	Y
	Tetragonuridae (squaretails)	*Tetragonurus cuvieri*	9	155			Y
	Caproidae (boarfishes)	*Capros aper*	1	2			Y
	Totals	229	56955		71	123	168

9.1.2.2 Cephalopods (squid and octopus)

Forty-one species of pelagic cephalopod molluscs were recorded on the North Atlantic Mid-Ocean Ridge by Vecchione *et al.*, (2010a) including 7 octopus species and 34 squids (Table 9.2). These range from large (up over 1 m total length) active species such as *Todarodes sagittatus* (Flying squid) to less active deep-sea species such as the tiny pelagic octopus *Bolitaena pygmaea* and the world's largest octopus *Haliphron atlanticus* (Seven-armed octopus) that can grow to more than 3 m long. Like the mid-water fishes, many of the cephalopods are bioluminescent and are camouflaged either by being transparent or dark coloured depending on the depth at which they live (Zylinski & Johnsen, 2011).

In the study of cephalopods of the MAR by Vecchione *et al*. (2010a) only a few species were considered to be Northern species characteristic of the cold waters North of the Sub-Polar Front. The most abundant was *Gonatus steenstrupi* (Armhook squid), followed by *Teuthowenia megalops* (Glass quid) and small numbers of *Chiroteuthis veranyi* (Long-armed squid). Seven other wide-ranging species of squid and one octopus were also recorded from the area. Rosa *et al.,* (2008) noted the total cephalopod species richness of 14 in the Atlantic Subarctic to be much lower than any other regions of the Atlantic Ocean.

Amongst the pelagic cephalopods only the rare new species of squid *Promachoteuthis sloani* (Young *et al.,* 2006) and cirrate octopus *Grimpoteuthis discoveryi* are recorded exclusively around the CGFZ. Others with affinities to the North Atlantic Drift region are squids *Brachioteuthis beanii*, and *Histioteuthis reversa* (Jewel squid) (Vecchione *et al.,* 2010a). The rest of the cephalopod fauna is made up of wide ranging species known from both North and South of this area, *Mastigoteuthis agassizii* (Whip-lash squid), *Bathyteuthis* sp. (Deep-sea squid), *Galiteuthis armata* (Glass squid), *Histioteuthis bonnellii* (Umbrella squid), *Planctoteuthis levimana*, *Todarodes sagittatus* (Flying squid), *Vampyroteuthis infernalis* (Vampire squid) and *Stauroteuthis syrtensis* (Glowing sucker octopus).

There is an increase in cephalopod species richness South of 40-44°N and Vecchione *et al.,* (2010a) noted 17 species of pelagic cephalopods that are not found further North (Table 9.3). In addition, there are eight species that are found both in the Central North Atlantic and in the North Atlantic Drift Ecoregions. Within the central area Rosa *et al.,* (2008) found a decrease in cephalopod diversity towards the South from a maximum around the Azores. There was generally lower diversity in the West Atlantic than in the East suggesting some kind of faunal divide in the vicinity of the MAR. There is a maximum species richness at around 15°C with fewer species at both lower and higher temperatures.

For cephalopods in the Tropical and West Equatorial Atlantic, data on the MAR are deficient. Rosa *et al*., (2008) report that species diversity tends to be lower in the equatorial ecoregion than further North, and attribute this to a very sharp thermocline with very little variation in water temperature in mid-water not favouring niche separation and a high number of species.

Table 9.2. Pelagic cephalopods of the Mid-Atlantic Ridge. After Vecchione et al.*, (2010a).*

Order	**Family**	**Species**	**Northwest Atlantic Sub-Arctic**	**North Atlantic Drift**	**Central North Atlantic**
Sepioidea	Sepiolidae	*Heteroteuthis dispar* (Odd bobtail squid)		Y	Y
Oegopsida	Bathyteuthidae	*Bathyteuthis* sp. (Deepsea squid)	Y	Y	Y
	Brachioteuthidae	*Brachioteuthis beanii*		Y	Y
	Chiroteuthidae	*Chiroteuthis mega*			Y
		Chiroteuthis veranyi	Y		

Order	Family	Species	Northwest Atlantic Sub-Arctic	North Atlantic Drift	Central North Atlantic
		(Long-armed squid)			
		Grimalditeuthis bonplandi			Y
		Planctoteuthis levimana	Y	Y	Y
	Chtenopterygidae	*Chtenopteryx sicula* (Comb-finned squid)			Y
	Cranchiidae	*Bathothauma lyromma* (Lyre cranch squid)			Y
		Galiteuthis armata (Armed cranch squid)	Y	Y	Y
		Helicocranchia pfefferi (Banded piglet squid)		Y	Y
		Leachia atlantica (Glass squid)			Y
		Taonius pavo (Glass squid)	Y	Y	Y
		Teuthowenia megalops (Glass squid)	Y	Y	Y
	Cycloteuthidae	*Discoteuthis laciniosa*			Y
	Enoploteuthidae	*Abraliopsis morisii*			Y
	Gonatidae	*Gonatus steenstrupi* (Armhook squid)	Y	Y	
	Histioteuthidae	*Histioteuthis bonnellii* (Umbrella squid)	Y	Y	Y
		Histioteuthis corona (Cock-eyed squid)			Y
		Histioteuthis meleagroteuthis (Cock-eyed squid)			Y
		Histioteuthis reversa (Elongate jewel squid)		Y	Y
	Joubiniteuthidae	*Joubiniteuthis portieri* (Joubin's squid)			Y
	Lepidoteuthidae	*Pholidoteuthis massyae* (Coffeebean scaled squid)			
	Lycoteuthidae	*Lampadioteuthis megaleia* (Firefly squid)		Y	Y
	Magnapinnidae	*Magnapinna* sp.			Y
	Mastigoteuthidae	*Mastigoteuthis agassizii* (Whiplash squid)	Y	Y	Y
		Mastigoteuthis hjorti			Y

Order	**Family**	**Species**	**Northwest Atlantic Sub-Arctic**	**North Atlantic Drift**	**Central North Atlantic**
		(Whiplash squid)			
		Mastigoteuthis magna (Whiplash squid)			Y
	Octopoteuthidae	*Octopoteuthis sicula* (Octopus squid)		Y	Y
	Ommastrephidae	*Todarodes sagittatus* (Flying squid)	Y		Y
	Onychoteuthidae	*Ancistroteuthis lichtensteinii* (Angel squid)			Y
		Onychoteuthis sp. (Club hook squid)			Y
	Promachoteuthidae	*Promachoteuthis sloani*			
	Pyroteuthidae	*Pterygioteuthis gemmate* (Enope squid)			Y
		Pyroteuthis margaritifera (Jewel enope squid)			Y
Octopoda	Stauroteuthidae	*Stauroteuthis syrtensis* (Glowing sucker octopus)	Y	Y	Y
	Alloposidea	*Haliphron atlanticus* (Seven-arm octopus)		Y	Y
	Bolitaenidae	*Bolitaena pygmaea*			Y
		Japetella diaphana			Y
	Ocythoidae	*Ocythoe tuberculata* (Football octopus)		Y	Y
Vampyroteuthidae	Vampyroteuthidae	*Vampyroteuthis infernalis* (Vampire squid)	Y	Y	Y

Table 9.3. Pelagic cephalopods of the Central North Atlantic Ecoregion, Mid-Atlantic Ridge

Central North Atlantic Ecoregion, not found further North	**Central North Atlantic & North Atlantic Drift Ecoregions**
Abraliopsis morisii	*Bathyteuthis abyssicola*
Ancistroteuthis lichtensteinii	*Brachioteuthis beanii*
Bolitaena pygmaea	*Haliphron atlanticus*
Chiroteuthis mega	*Helicocranchia pfefferi*
Chtenopteryx sicula	*Heteroteuthis dispar*
Grimalditeuthis bonplandi	*Histioteuthis reversa*
Histioteuthis corona	*Lampadioteuthis megaleia*

Histioteuthis meleagroteuthis	*Octopoteuthis sicula*
Japetella diaphana	
Joubiniteuthis portieri	
Leachia atlantica	
Mastigoteuthis hjorti	
Mastigoteuthis magna	
Ocythoe tuberculata	
Pholidoteuthis massyae	
Pterygioteuthis gemmata	
Pyroteuthis margaritifera	

9.1.2.3 Shrimp

The mid-water layers and the deep-sea scattering layer are also home to large numbers of pelagic decapod shrimps of the suborders Dendrobranchiata (with branching gills) and the infraorder Caridea (true shrimps). In a survey of the MAR from North of 60°N to South of 30°S, Cardoso *et al.,* (2014) identified a total of 65 species, 38 Caridea and 27 Dendrobranchiata. Of the fifty species found in the North Atlantic (Table 9.4), 32 are widespread or global species that also occur in other oceans.

In the Northwest Atlantic Subarctic ecoregion, the decapod crustacea of the deep-scattering layers are represented by two characteristic species *Parapasiphae sulcatifrons* and *Hymenodora gracilis* (Judkins & Haedrich, 2018). The same authors found no decapod shrimp species that favoured the North Atlantic Drift province. Species present were a mixture of those from the North or South with no particular affinity to this region.

Of all the ecoregions in the North and South Atlantic Oceans, the Central North Atlantic ecoregion has the highest number of decapod shrimp species, with 37 that show a preference for the region (Judkins & Haedrich, 2018). Of these, Cardoso *et al.,* (2014) found 12 that occur on the MAR although a few were only on the South MAR (Table 9.4).

For the Tropical and West Equatorial Atlantic ecoregion, Judkins & Haedrich (2018) list three species of decapod shrimp that are characteristic of the ecoregion, *Acanthephyra prionota*, *Acanthephyra acanthitelsonis*, and *Notostomus gibbosus*. The latter two of these species were recorded by Cardoso *et al.,* (2014) as occurring on the South MAR (Table 9.4). The equatorial or Romanche Fracture Zone may act as a biogeographic barrier to pelagic shrimps with the Eastward flow of Atlantic Bottom Water creating intense vertical mixing that modifies the water properties.

Table 9.4. Pelagic decapod shrimps of the Mid-Atlantic Ridge. After Cardoso et al.*, (2014). [1]Shrimp species identified by Judkins & Haedrich (2018) as having a preferred ecoregion. N: Occurs in the North Atlantic, S: Occurs in the South Atlantic, A: Atlantic Ocean endemic, G: Global, also in other oceans.*

Family	**Species**	**Regional/Global distribution**			**North Atlantic Ecoregion preference[1]**		
		North/ South Atlantic		**Atlantic/ Global**	**North West Atlantic Sub-Arctic**	**Central North Atlantic**	**Tropical & West Equatorial**
Suborder Dendrobranchiata (branching gills)							
Benthesicymidae	*Altelatipes falkenhaugae*	N		A			
	Bentheogennema intermedia	N	S	G			

Family	**Species**	**Regional/Global distribution**			**North Atlantic Ecoregion preference[1]**		
		North/ South Atlantic		**Atlantic/ Global**	**North West Atlantic Sub-Arctic**	**Central North Atlantic**	**Tropical & West Equatorial**
	Bentheogennema sp.		S	-			
	Gennadas brevirostris		S	G			
	Gennadas capensis		S	G		Y	
	Gennadas elegans	N		A			
	Gennadas gilchristi		S	A			
	Gennadas parvus		S	G			
	Gennadas scutatus		S	G		Y	
	Gennadas talismani		S	A		Y	
	Gennadas tinayrei	N	S	G		Y	
	Gennadas valens	N	S	A		Y	
Penaeidae	*Funchalia villosa*	N	S	G		Y	
	Funchalia woodwardia	N	S	G		Y	
Sergestidae	*Deosergestes corniculum*	N	S	A			
	Deosergestes henseni	N	S	A			
	Parasergestes armatus	N	S	G			
	Petalidium sp.		S	-			
	Sergestes arcticus	N		G			
	Sergestes atlanticus	N	S	G		Y	
	Sergestes pectinatus	N		G			
	Sergestes sargassi	N		G			
	Sergestes vigilax	N		G			
	Sergia creber		S	G			
	Sergia grandis	N	S	A			
	Sergia japonica	N		G			
	Sergia laminata		S	A		Y	
	Sergia robusta	N	S	A			
	Sergia splendens	N	S	G			
	Sergia tenuiremis	N	S	A			
Suborder Pleocyemata, Infraorder Caridea (true shrimps)							
Nematocarcinidae	*Nematocarcinus ensifer*	N		G			
	Nematocarcinus exilis	N		A			
Acanthephyridae	*Acanthephyra acanthitelsonis*		S	A			Y
	Acanthephyra brevirostris	N		G			
	Acanthephyra curtirostris	N	S	G		Y	
	Acanthephyra gracilipes	N		A			
	Acanthephyra pelagica	N	S	G			

Family	Species	Regional/Global distribution			North Atlantic Ecoregion preference[1]		
		North/ South Atlantic		Atlantic/ Global	North West Atlantic Sub-Arctic	Central North Atlantic	Tropical & West Equatorial
	Acanthephyra purpurea	N		A		Y	
	Acanthephyra quadrispinosa		S	A			
	Acanthephyra stylorostratis		S	G			
	Ephyrina benedicti	N	S	G			
	Ephyrina bifida	N		A			
	Ephyrina figueirai	N		A			
	Ephyrina ombango	N		G			
	Hymenodora gracilis		S	G	Y		
	Meningodora compsa	N		A			
	Meningodora miccyla	N		G			
	Meningodora mollis	N		G			
	Meningodora vesca	N	S	G			
	Notostomus elegans	N	S	G		Y	
	Notostomus gibbosus	N	S	G			Y
	Notostomus robustus	N	S	A			
Oplophoridae	*Oplophorus novazeelandiae*		S	G			
	Oplophorus spinosus	N	S	G		Y	
	Systellaspis braueri	N		A			
	Systellaspis cristata	N	S	G			
	Systellaspis debilis	N	S	G		Y	
	Systellaspis pellucida	N	S	G			
Pandalidae	*Stylopandalus richardi*	N	S	G		Y	
Pasiphaeidae	*Eupasiphae gilesi*	N		G			
	Parapasiphae sulcatifrons	N	S	G	Y		
	Pasiphaea ecarina	N		A		y	
	Pasiphaea hoplocera	N		G			
	Pasiphaea multidentata	N		A			
	Pasiphaea tarda	N		G			
Total		50	41	65			

9.1.3 Sharks and commercially important fishes

Alongside the mid-water nekton considered earlier in this section, the pelagic environment of the northern MAR also provides habitat for a number of larger fish species, many of which are commercially important top-predators, such as sharks, tunas and swordfish. It is not possible to address the regional distribution of all the commercially important fish species within the northern MAR pelagic environment, instead accounts of some of the common and key species are provided below.

9.1.3.1 Sharks

Within the Atlantic Ocean, *Prionace glauca* (blue shark) are the most commonly caught sharks in reported fisheries, followed by *Isurus oxyrinchus* (shortfin mako) (Queiroz *et al.,* 2016). Both *P. glauca* and *I. oxyrinchus* have been extensively tracked in the North Atlantic, with tracking data suggesting that these species spend considerable time along the northern MAR and may even follow the ridges' topography (Queiroz *et al.,* 2016). Other sharks recorded from the pelagic habitat overlying the MAR, include the *Lamna nasus* (Porbeagle shark), *Carcharodon carcharias* (white shark), *Rhincodon typus* (whale shark), and *Cetorhinus maximus* (basking shark). The following sections discuss the regional distribution of these six shark species in more detail.

9.1.3.1.1 Prionace glauca (blue shark)

Prionace glauca is the most abundant and probably the widest-ranging chondrichthyian (cartilaginous fish) in the Atlantic, occupying tropical, subtropical, and warm-temperate waters, on both sides of the North Atlantic (Kohler *et al.,* 2002; Figure 9.3). *Prionace glauca* generally occur from the surface to 350 m depth but have been known to dive to 1000 m (Campana *et al.,* 2011). It is an oceanic species capable of long-range seasonal latitudinal migrations. According to Coelho *et al.,* (2018), large mature adults tend to aggregate in the tropical Northeast, whilst the smaller immature sharks were found to aggregate in the temperate Northeast and Central North Atlantic. Young-of-the-year and small juveniles occur in particularly high abundance off the Iberian Peninsula and in the Bay of Biscay in the Northeast and around the Azores Islands in the Central North Atlantic, suggesting that these areas may be the main nursery grounds in the North Atlantic. The distribution of important aggregating areas for reproductively valuable adult female *P. glauca* in the Atlantic likely interacts with the wider Mid-Atlantic Ridge region in the equatorial Atlantic over the Romanche transform fault and south-west of the Cabo Verde. Juvenile habitats also occur west and north of the Azores.

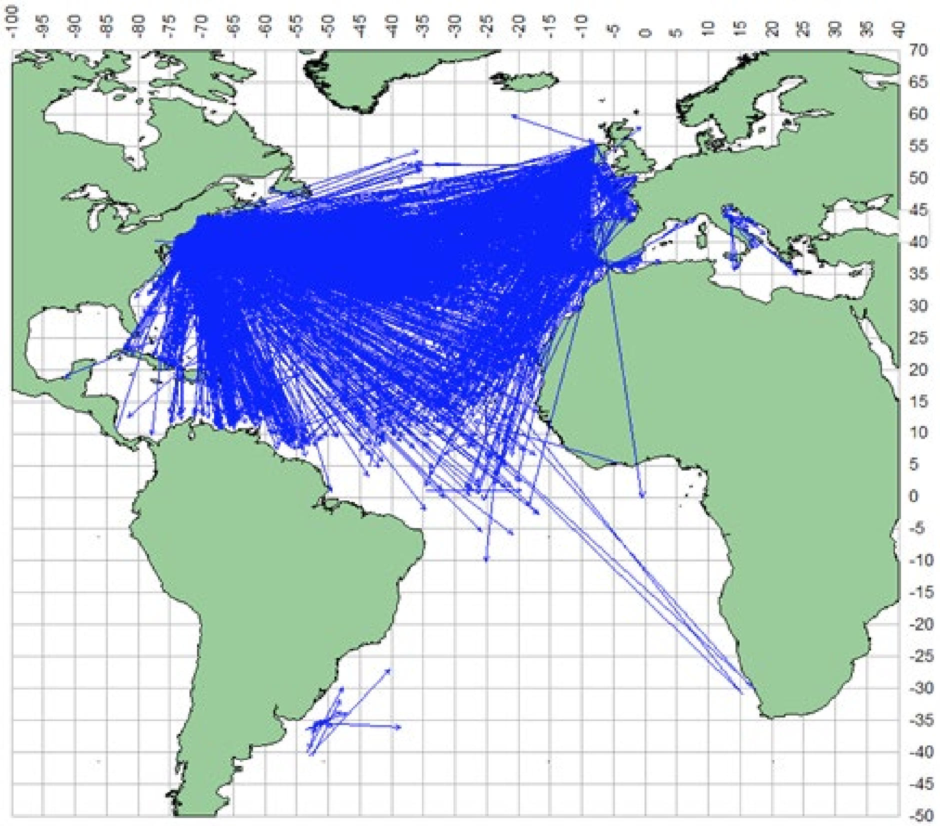

Figure 9.3. Tag and release distribution for Prionace glauca *(blue shark) in the Atlantic Ocean, lines describe straight displacement between release and recovery locations. Reproduced from ICCAT (2013).*

9.1.3.1.2 Isurus oxyrinchus (shortfin mako)

Isurus oxyrinchus also has a regional distribution which crosses the northern MAR (Figure 9.4), with previous studies suggesting that *I. oxyrinchus* in the North Atlantic is one population. However more recent studies suggest some differentiation among the northern, southwestern, and southcentral and southeastern areas (ICES, 2017). The North Atlantic *I. oxyrinchus* stock is both overfished and overfishing is occurring (ICCAT, 2017), with high exploitation rates leading to the species being listed as globally Endangered by the IUCN.

In 2012, the International Commission for the Conservation of Atlantic Tunas (ICCAT) collated 1203 tags recaptured since 1962 (largely from tags deployed off the northeast coast of the United States). The 2012 ICCAT report noted that most movement of *I. oxyrinchus* was between South and East within the Northwest Atlantic, with few individuals captured below 20˚N and none captured South of 5˚N. This is despite individuals being reported to travel considerable distances of up to 3400 km across the Atlantic (ICCAT, 2013). While their core distribution is over the continental shelf, *I. oxyrinchus* range across coastal and pelagic habitats and interact with the water column above a broad swath of the MAR (Queiroz *et al.,* 2016; Vaudo *et al.,* 2017). The western North Atlantic population is believed to migrate from the north-eastern United States and Canada (Grand Banks) South into the Gulf Stream and Sargasso Sea to over-winter.

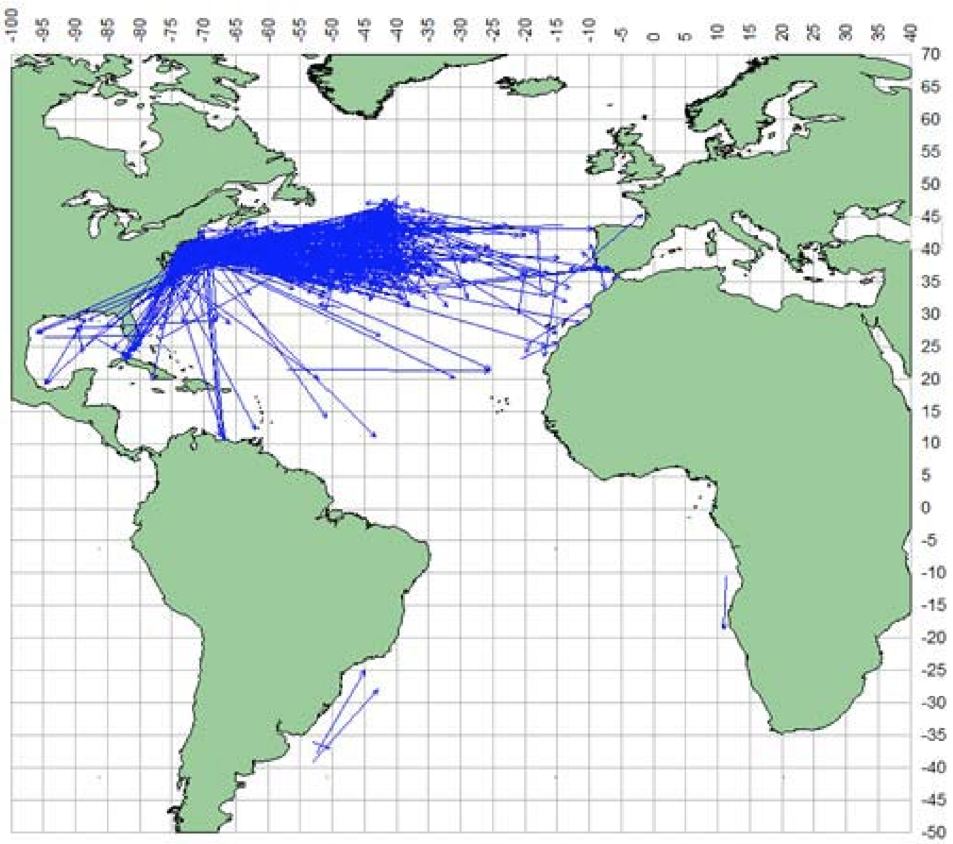

Figure 9.4. Tag and Release distributions for Isurus oxyrinchus *(Shortfin Mako) in the Atlantic Ocean, lines describe straight displacement between release and recovery locations. Reproduced from ICCAT (2013).*

9.1.3.1.3 Lamna nasus (Porbeagle shark)

Lamna nasus (Porbeagle shark) is a large pelagic shark found globally in temperate waters, with a distribution encompassing the high seas, coastal shelf, and inshore areas (Figure 9.5). *Lamna nasus* also has the potential for long-distance migrations, with studies demonstrating that *L. nasus* migrate widely across the northeast Atlantic but have limited exchange between eastern and western sub-populations (Cameron *et al.,* 2018; Bias *et al.,* 2017). Low reproductive capacity and high commercial exploitation has led to overfishing and the species is currently listed as globally Vulnerable, and Critically Endangered in the northeast Atlantic. Bias *et al.,* (2017) tracked multiple individuals swimming from the Bay of Biscay out past 30° W, North of the Azores. These tracks placed the individuals over the MAR and indicated that whilst *L. nasus* utilized depths down to 1600 m, they rarely occurred below 700 m.

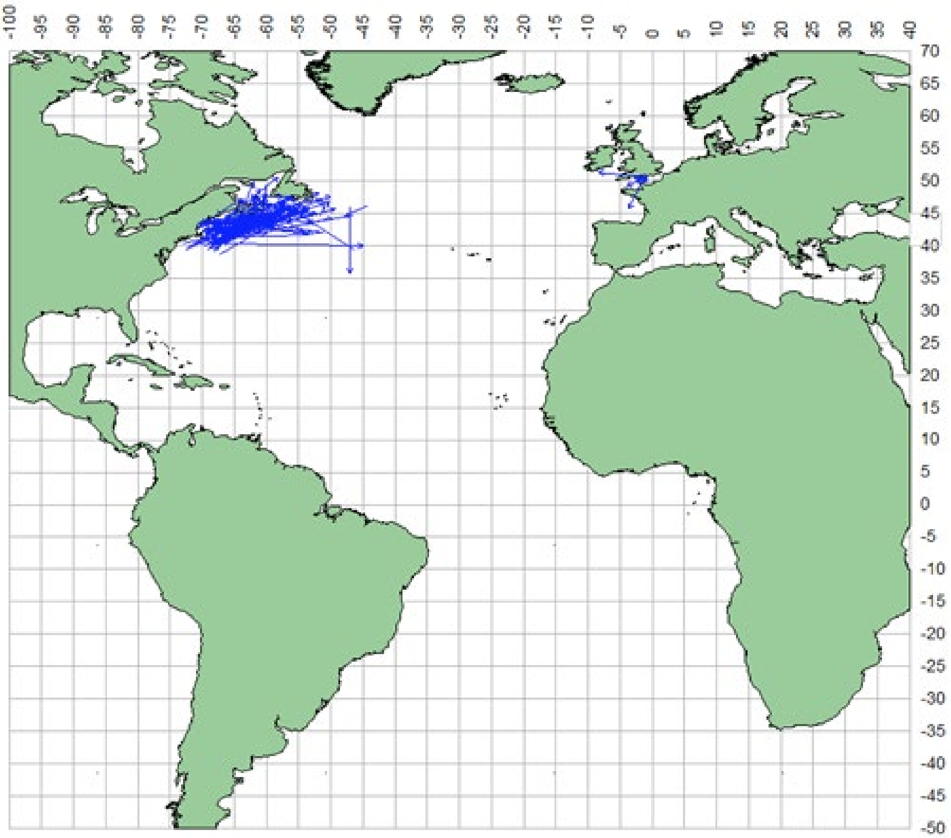

Figure 9.5. Tag and Release distributions Lamna nasus *(Porbeagle sharks) in the Atlantic Ocean, lines describe straight displacement between release and recovery locations. Reproduced from ICCAT (2013).*

9.1.3.1.4 Carcharodon carcharias (white shark)

Despite being one of the better known and charismatic shark species, and numerous studies in the Eastern Pacific Ocean, little is known about the distribution of *Carcharodon carcharias* (white shark) in the North Atlantic. Historically considered an epipelagic and neritic species with seasonal, coastal latitudinal migrations (Curtis *et al.,* 2014), new studies have shown a broader distribution and significant use of the mesopelagic zone (Skomal *et al.,* 2017). Specifically, Skomal *et al.*, (2017) described an ontogenetic shift from shelf waters to the open ocean with frequent excursions to mesopelagic depths. Sub-adult and adult sharks of both sexes utilized pelagic waters and ranged widely in the fall, winter, and spring from The Bahamas to an area on the MAR around 50° N, and as far East as the Azores (Figure 9.6). The tagged *C. carcharias* dove to 1128 m and appeared to target specific mesopelagic depths to forage. *Carcharodon carcharias* are globally considered Vulnerable by the IUCN, though this listing has not been updated in a decade (IUCN, 2017).

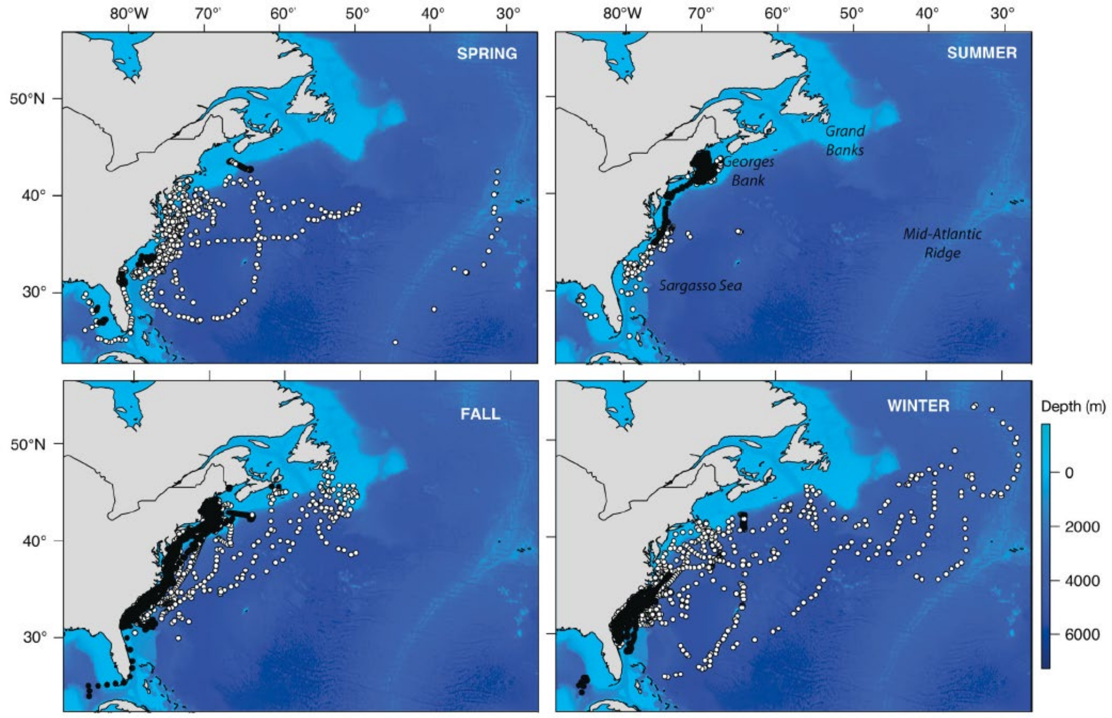

Figure 9.6. Seasonal movements of Carcharodon carcharias *(white sharks) tagged in the western North Atlantic, 2009−2014, generated from both SPOT (n = 5) and PSAT (n = 24) tags and broken down by individuals demonstrating coastal (black circles) vs. pelagic (white circles) behaviour with associated bathymetry. Seasons are based on the lunar calendar. Reproduced from Skomal* et al.*, (2017).*

9.1.3.1.5 Rhincodon typus (whale sharks)

Rhincodon typus (whale sharks) have also been recorded in the pelagic environment of the MAR, although many aspects of this species' biology and habitat remain poorly understood. What is known is that the species distribution spans warm and temperate waters between 30°N and 30°S, with tracking and mark-recapture studies showing aggregations of sharks, particularly juvenile males, where there are seasonal blooms of their planktonic prey. These studies also show very long, seasonal, largely longitudinal migratory movements. While long distance migrations from aggregation sites have been documented, return migration to the tagging site had not been demonstrated. During these horizontal travels, *R. typus* spend the majority of their time in the epipelagic zone but have irregular deep dives to >1000 m.

Sequeira *et al.,* (2012) modelled global *R. typus* habitat (Figure 9.7), showing extensive habitat is centred over the northern MAR as well as the Romanche Fracture Zone. This is not surprising given the records of aggregations at oceanic islands in the Atlantic including the Azores (Afonso *et al.,* 2014b), the Archipelago of São Pedro and São Paulo near the Equator (Macena & Hazin, 2016) and St. Helena (Clingham *et al.,* 2014). It has been suggested that the latter two locations may be mating sites for *R. typus* (Clingham *et al.,* 2014; Macena & Hazin, 2016). *Rhincodon typus* is considered Endangered and vulnerable to over-exploitation due to its slow growth, late maturation, extended longevity, slow swimming speed and docility at the surface, and highly migratory nature (IUCN, 2017).

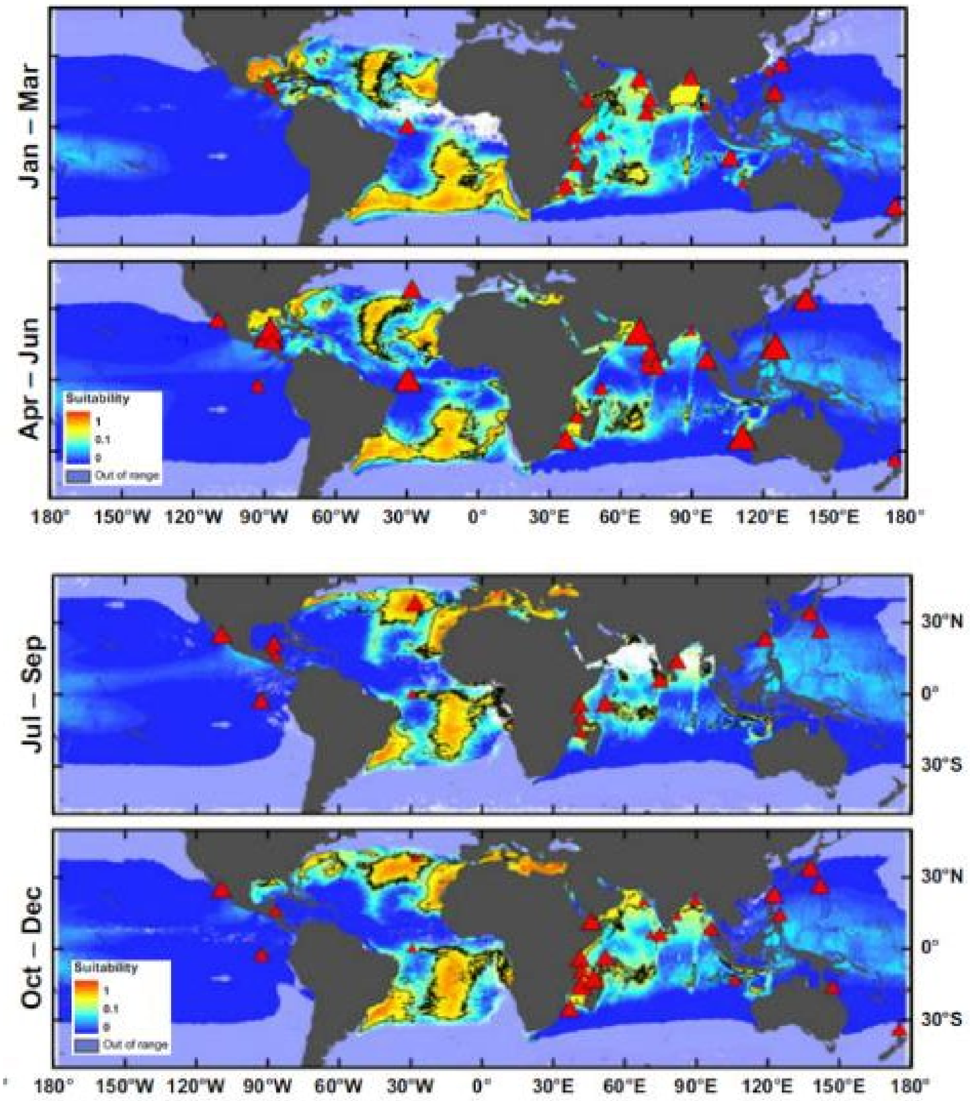

Figure 9.7. Global predictions of current seasonal habitat suitability for Rhincodon typus *(whale sharks). Prediction maps generated from generalized linear mixed-effects models fit with the sightings and effort data collected by tuna purse-seine fisheries. Where environmental inputs fell outside the environmental space used for the original statistical fit results are shown as 'out of range' in the map. Red triangles indicate known aggregation locations within the seasons represented in each map (symbol size proportional to relative size of aggregation). Areas where some environmental predictors were not available (e.g., due to cloud cover) are shown in white (no result). To aid visualization, solid line delineates areas where habitat suitability >0.1 was predicted. Adapted from Sequeira* et al.*, (2014).*

9.1.3.1.6 Cetorhinus maximus (basking sharks)

Cetorhinus maximus (basking sharks) can spend significant time in the pelagic environment of the MAR, yet little is known about their regional distribution. Recent tracking studies have shown extensive movements in both the eastern and western North Atlantic. Eastern Atlantic individuals displayed three migratory behaviours: remaining in waters of west of the United Kingdom and Ireland, migrating South to the Bay of Biscay, or migrating to an area West of the Strait of Gibraltar along routes that take some into international waters (Doherty *et al.,* 2017). These authors identified round-trip migrations to over-winter in these areas and then return to coastal UK and Irish water during the spring and summer. Previously, *C. maximus* have been assumed to remain in temperate continental shelf areas, but new evidence over the last decade indicates they undertake trans-ocean basin and trans-equatorial migrations. Gore *et al.,* (2008) tracked one *C. maximus* that crossed the North Atlantic, from the Isle of

Man to Newfoundland, traveling nearly 10 000 km. Individuals from the Western Atlantic population have also been tracked engaging in seasonal movements from coastal waters in high latitudes during the summer to overwintering areas as far as south as Brazil, with migrations extensively utilizing international waters and diving to depths greater than 1500 m. The utilization distributions in Braun *et al*., (2018) demonstrate that *C. maximus* spend significant time over the MAR from north of Vema Fracture Zone to South of the Romanche Fracture Zone (Figure 9.8). *Cetorhinus maximus* is listed as Vulnerable globally, and Endangered in the Northeast Atlantic (IUCN, 2017).

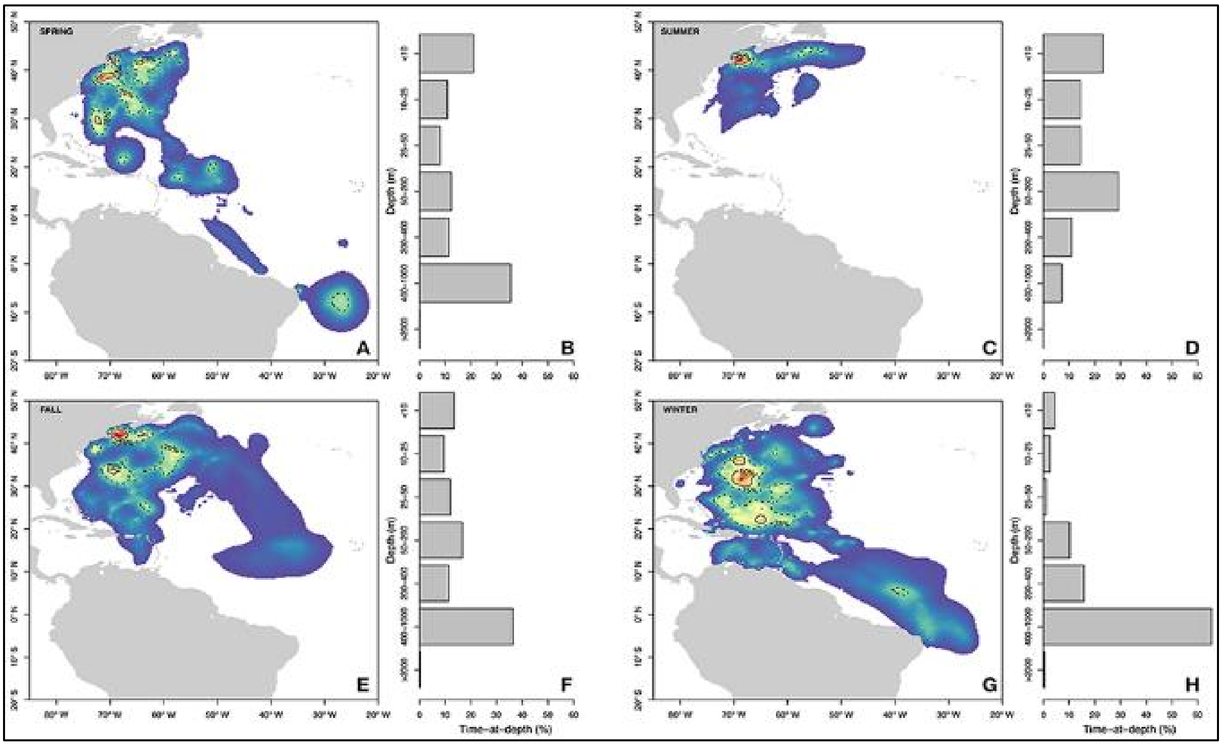

Figure 9.8. Seasonal residency distributions (A, C, E, G) and cumulative time-at-depth (B, D, F, H) for Cetorhinus maximus *(basking sharks) in spring (A, B), summer (C, D), fall (E, F), and winter (G, H). Contour lines represent 50 and 75% of occupation for a given season as depicted by solid and dashed contours, respectively. Reproduced from Braun* et al.*, (2018).*

9.1.3.2 *Tuna and swordfish*

The pelagic environment of the northern MAR provides habitat for multiple commercially important tuna species: *Katsuwonus pelamis* (skipjack tuna), *Thunnus albacares* (yellowfin tuna), *Thunnus obesus* (bigeye tuna), *Thunnus alalunga* (albacore), *Thunnus thynnus* (Atlantic bluefin tuna), alongside *Xiphias gladius* (swordfish). The following sections provide details about the regional distribution of these species.

9.1.3.2.1 *Katsuwonus pelamis* (skipjack tuna)

Katsuwonus pelamis (skipjack tuna) is a widely-distributed species occurring in tropical and subtropical areas of the Pacific, Atlantic and Indian oceans (ICCAT, 2015). *Katsuwonus pelamis* is considered the fastest growing tuna species reaching approximately 45 cm after the first year of age (Druon *et al.*, 2016) and approximately 120 cm at maximum size, with an estimated life span of 6–8 years. In the Atlantic Ocean, *K. pelamis* can be divided in two stocks including the western and the eastern stock, both of which are subjected to intensive fishing (ICCAT, 2006). *Katsuwonus pelamis* is the most caught tuna species in the Atlantic Ocean with an average annual catch (2010-2017) of about 240 000 tonnes (ICCAT, 2019). Most of the catch is distributed in the tropical East Atlantic, with only a small portion being caught along the MAR close to and South of the Azores. In the Azores region, *K. pelamis* is the most frequently caught tuna species. An analysis of *K. pelamis* movements based on present ICCAT data in the Atlantic showed quite limited horizontal movements (Figure 9.9) when compared to other ocean basins, with average travelled distances in the Atlantic of less than 500 nautical miles (Fonteneau, 2015). Data from the Western Pacific Ocean showed that *K. pelamis* displayed a distinct diurnal vertical movement pattern, from shallow at night to depths of about 250–350 m during the night (Schaefer *et al*., 2009), which may also occur in the North Atlantic.

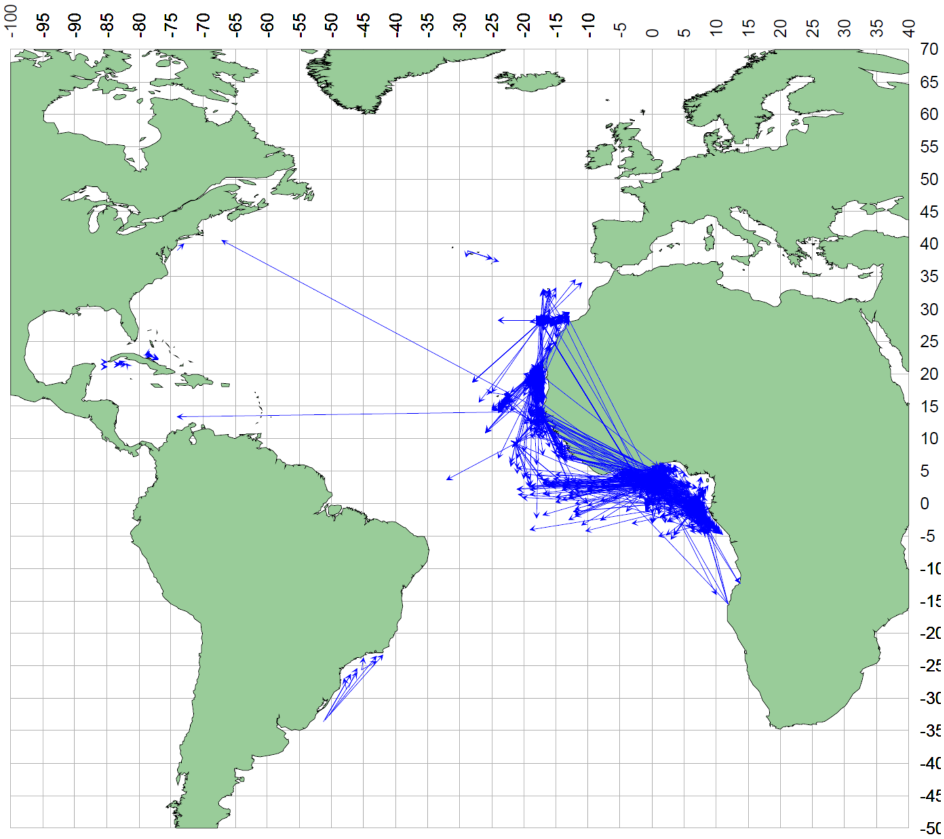

Figure 9.9. Horizontal movements of 5,990 tagged and recaptured Katsuwonus pelamis *(skipjack tuna) specimens. Direct trajectories between releases and recoveries. Reproduced from ICCAT (2006).*

9.1.3.2.2 *Thunnus albacares* (yellowfin tuna)

Thunnus albacares (yellowfin tuna) is a large and widely distributed tuna species, occurring predominantly in the tropical and subtropical regions of all oceans (Collette & Nauen, 1983). *Thunnus albacares* can attain a maximum size of more than 200 cm, with and a life span of approximately 7 years (Diaha *et al*., 2016; Lessa & Duarte-Neto, 2004). *Thunnus albacares* is the second most caught tuna species in the Atlantic Ocean with an average catch (2010-2017) of approximately 120 000 tonnes (ICCAT, 2019). Most of the catch is distributed in tropical Atlantic Ocean between 10°S and 20°N of latitude, with only a small portion of Yellowfin being caught along the tropical MAR. In the Atlantic Ocean, *T. albacares* may form a distinct stock, since this species has only one main spawning area in the eastern Atlantic and showed marked East to West transatlantic migrations (Fonteneau, 1994; Fonteneau & Soubrier, 1996). In general, juveniles fish move along the African coastal waters, preform transatlantic migration when pre-adults, and return to the eastern Atlantic at adult stage (Bard & Hervé, 1994; Fonteneau & Soubrier, 1996). Tag and release data shows marked migration routes across the Atlantic crossing the MAR (Figure 9.10), driven by temperature and salinity gradients (Maury *et al*., 2001). *Thunnus albacares* distribution seemed to be strongly associated with the Intertropical Convergence Zone (ITCZ) position and its temporal variability (Zagaglia *et al*., 2004).

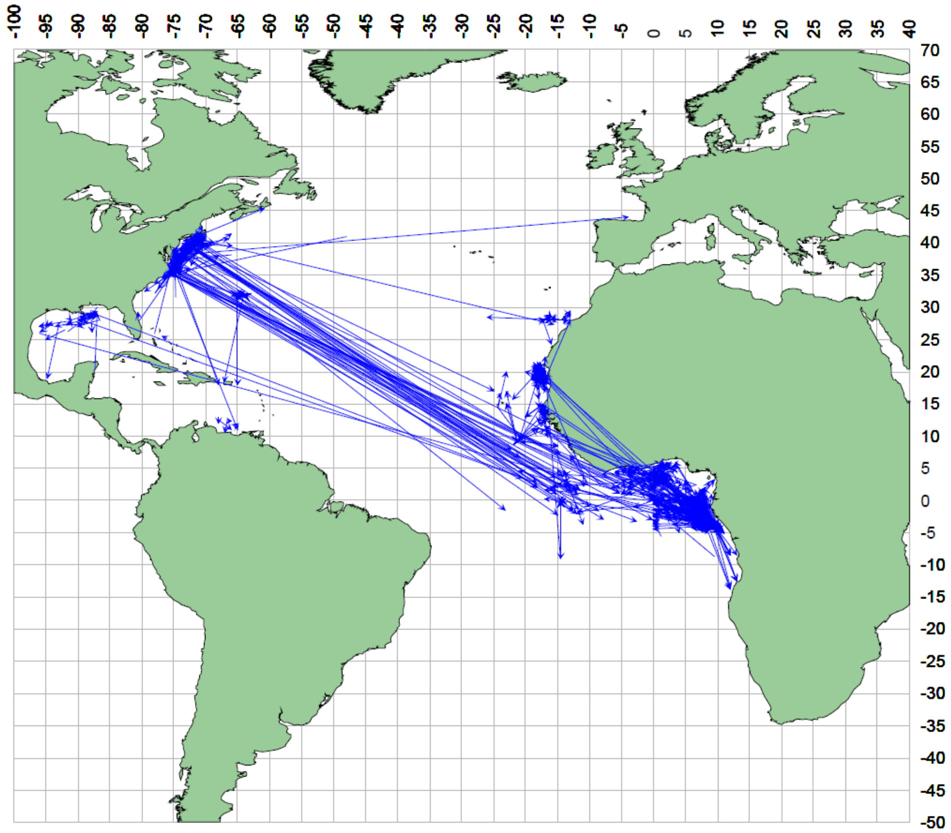

Figure 9.10. Horizontal movements of 1,711 tagged and recaptured Thunnus albacares *(yellowfin tuna). Direct trajectories between releases and recoveries. Reproduced from ICCAT (2006).*

9.1.3.2.3 *Thunnus obesus* (bigeye tuna)

Thunnus obesus (bigeye tuna) is also a widely-distributed tuna species, occurring in the tropical and subtropical waters of the Atlantic, Indian and Pacific Oceans (Collette & Nauen 1983). *Thunnus obesus* is one of the largest tuna species reaching a maximum size of approximately 250 cm, with a maximum longevity of 11 to 15 years (ICCAT, 2006). In the Atlantic Ocean, *T. obesus* may form a distinct stock, suggested by tagging studies which have showed transatlantic migrations from the Gulf of Guinea to the Central and eastern Atlantic (Pereira, 1995) and genetic studies supporting the homogeneity of the Atlantic *T. obesus* population (Chow *et al*., 2000). *Thunnus obesus* is the third most caught tuna species in the Atlantic Ocean with an average catch (2010-2017) of approximately 75 000 tonnes (ICCAT, 2019). Most of the catch is distributed in the tropical eastern Atlantic with an important portion of *T. obesus* being caught along the MAR close to the Azores. Tag and recapture studies (Figure 9.11) showed *T. obesus* undertake frequent migrations (ICCAT, 2006), which are dependent on age group (Bard *et al*., 1991). For example, juveniles are usually found in the eastern equatorial Atlantic where they migrate along the African coast towards the tropics and continuing to higher latitudes such as the Azores (Bard *et al*., 1991; Bard & Amon Kothias, 1986). Data from pop-up archival satellite tags suggest *T. obesus* can dive to forage on organisms from the deep scattering layer at around 200 m to 500 m depth (Dagorn *et al*., 2000; Musyl *et al*., 2003).

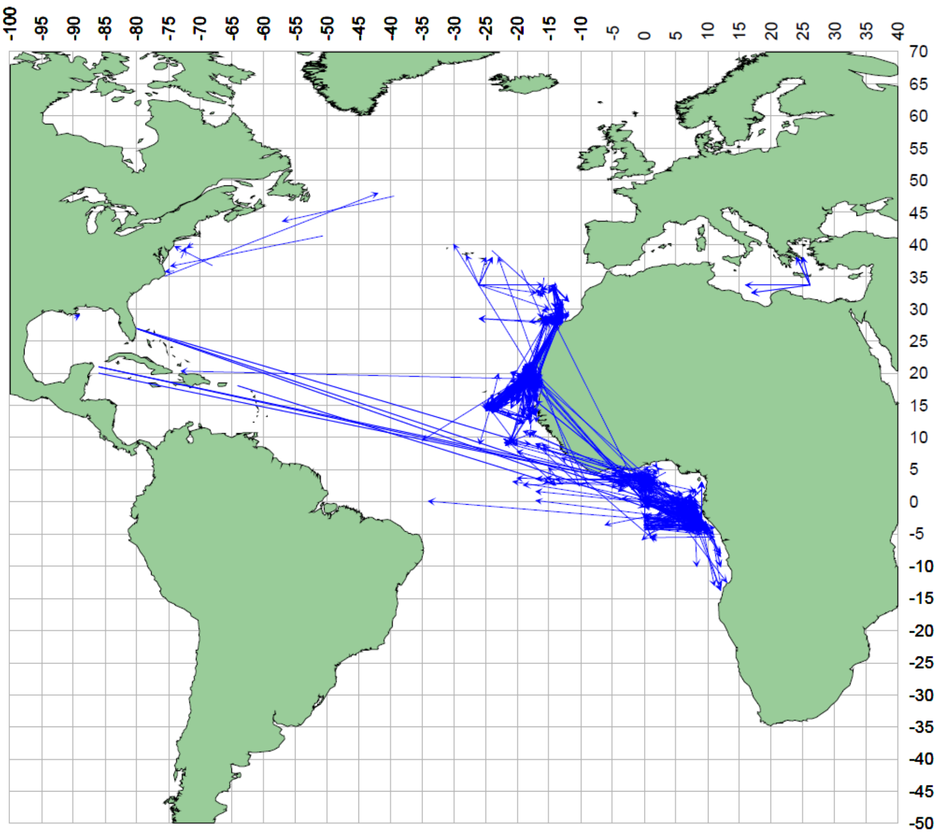

Figure 9.11. Horizontal movements of 3,021 tagged and recaptured Thunnus obesus *(bigeye tuna). Direct trajectories between releases and recoveries. Reproduced from ICCAT (2006).*

9.1.3.2.4 *Thunnus alalunga* (albacore)

Thunnus alalunga (albacore) is another widely-distributed species with adults usually associated with tropical or subtropical areas, and juveniles mostly found in temperate waters. *Thunnus alalunga* is a small tuna species attaining a maximum length of approximately 130 cm in the Atlantic, with a maximum age of approximately 15 years. In the Atlantic Ocean, *T. alalunga* can be divided into three different stocks, including northern and southern Atlantic stocks divided by the parallel 5°N, and the Mediterranean stock (ICCAT, 2001). *Thunnus alalunga* is the fourth most caught tuna species in the Atlantic Ocean with an average catch (2010-2017) of about 46 000 tonnes (ICCAT, 2019). Most of the catch is distributed in the Northeast and Southeast Atlantic, with only a small portion of *T. alalunga* being caught along the MAR close to and South of the Azores. Arrizabalaga *et al.,* (2002) conducted a tag release-recapture experiment and highlighted the long distance, transoceanic movements, and the possibility of an interchange of fish between the North Atlantic and the Mediterranean (Figure 9.12). Data from pop-up archival satellite tags suggest *T. alalunga* can dive to 200 m depth with consistently shallow nocturnal and deeper diurnal depth preferences (Cosgrove *et al.,* 2014).

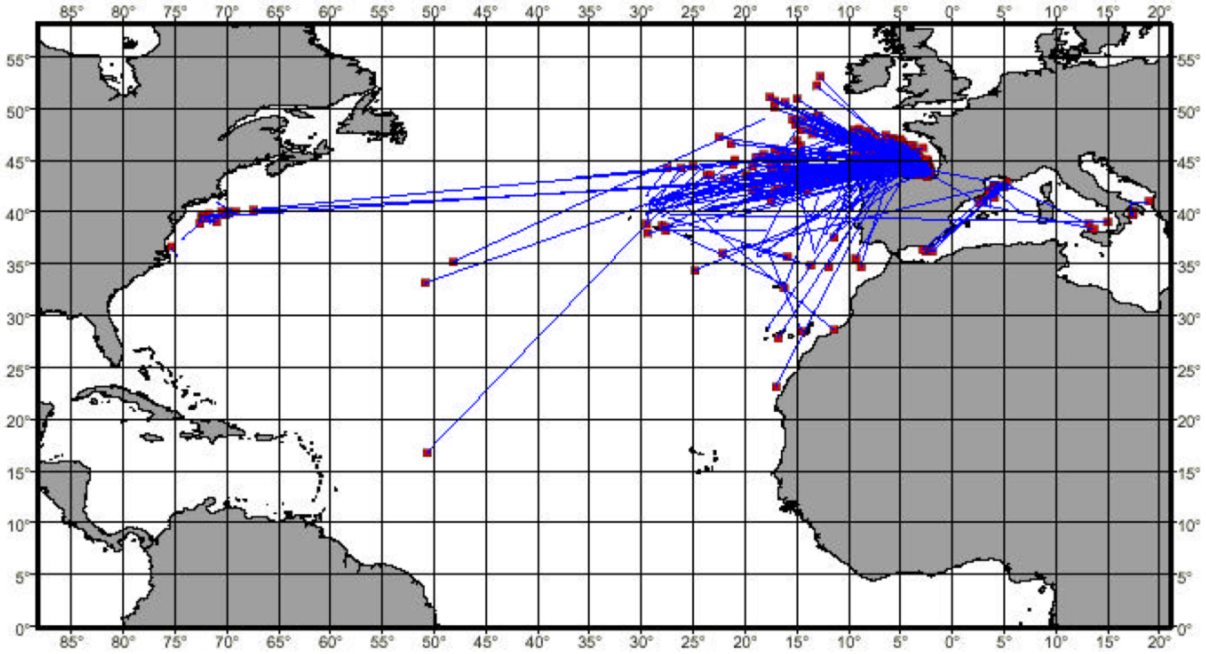

Figure 9.12. Thunnus alalunga *(albacore) tagging and recapture in the North Atlantic and Mediterranean (1968-1999). Reproduced from Arrizabalaga* et al.*, (2002).*

9.1.3.2.5 *Thunnus thynnus* (bluefin tuna)

Atlantic *Thunnus thynnus* (bluefin tuna) is the largest tuna species with a maximum weight exceeding 700 kg, and inhabits the entire Atlantic Ocean and the Mediterranean Sea. Archival tagging and tracking information demonstrate that *T. thynnus* can sustain cold (down to 3°C) as well as warm (up to 30°C) temperatures (Block *et al*., 2002), although juveniles spend the majority of their time in water warmer (Brill *et al*., 2002). ICCAT currently manages *Thunnus thynnus* as two distinct stocks, with the boundary between the two spatial units being the 45°W meridian (ICCAT, 2002). However, genetic studies showed complex population structure with genetic differences between the Mediterranean Sea and the central North Atlantic (Carlsson *et al*., 2004; Carlsson *et al*., 2006), while larval collections showed multiple spawning grounds in the western Atlantic (Richardson *et al*., 2016). Additionally, electronic tagging showed a high rate of transatlantic migration (Figure 9.13) with a large portion of the juveniles tagged in the Bay of Biscay overwintering near the MAR close to the Azores or Madeira (Arregui *et al*., 2018; Block *et al*., 2005; Rooker *et al*., 2007). *Thunnus thynnus* is the most commercially important tuna species, but is only the fifth most caught tuna species in the Atlantic Ocean with an average catch (2010-2017) of approximately 16 000 tonnes (ICCAT, 2019). Most of the catch is distributed in the Mediterranean Sea and in the North Atlantic, with only a small portion of *T. thynnus* being caught along the MAR close to Reykjanes Ridge, off Iceland. Data from pop-up archival satellite tags suggest that both juvenile and adult *T. thynnus* frequently dive to 500-1000m depth (Brill *et al*., 2001; Lutcavage *et al*., 1999), with such behaviour associated with foraging in the deep-scattering layers.

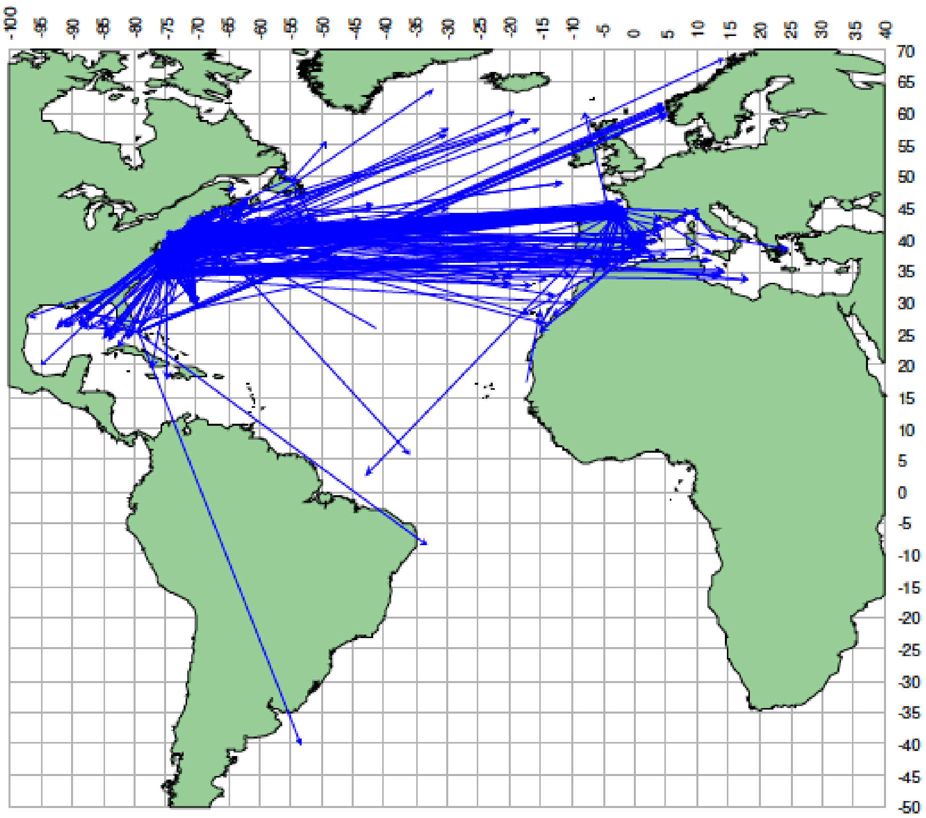

Figure 9.13. Horizontal movements of tagged and recaptured Thunnus thynnus *(Bluefin tuna). Direct trajectories between releases and recoveries. Reproduced from ICCAT (2006).*

9.1.3.2.6 *Xiphias gladius* (swordfish)

Xiphias gladius (swordfish) is a large epipelagic fish with a wide distribution across all the world's oceans and with a high tolerance to temperature ranges (Nakamura, 1985). *Xiphias gladius* can exceed 4 m total length and weight more than 400 kg. ICCAT considers *X. gladius* to be divided into three different stocks: North Atlantic, South Atlantic and Mediterranean (ICCAT, 2006). However, recent studies suggest that the assumption of a single homogeneous stock in the North Atlantic may be overly simplistic (Abascal *et al*., 2015). *Xiphias gladius* is an important commercial fish species, which is mainly fished with surface longlines. The average *X. gladius* catch in the Atlantic (2010-2017) was approximately 32 000 tonnes (ICCAT, 2019). In the North Atlantic, the distribution of fishing effort strongly overlaps with the MAR (Queiroz *et al*., 2016). *Xiphias gladius* is known to migrate between subtropical and temperate waters of the North and South Atlantic (Figure 9.14), although tag and recapture studies do not appear to demonstrate extensive transatlantic migrations (Brown, 1995; Garcia-Cortés *et al*., 2003; Sperling *et al*., 2005). *Xiphias gladius* display clear diel vertical patterns, feeding at 300–600 m during the day and staying in the mixed layer at night (Abascal *et al*., 2015).

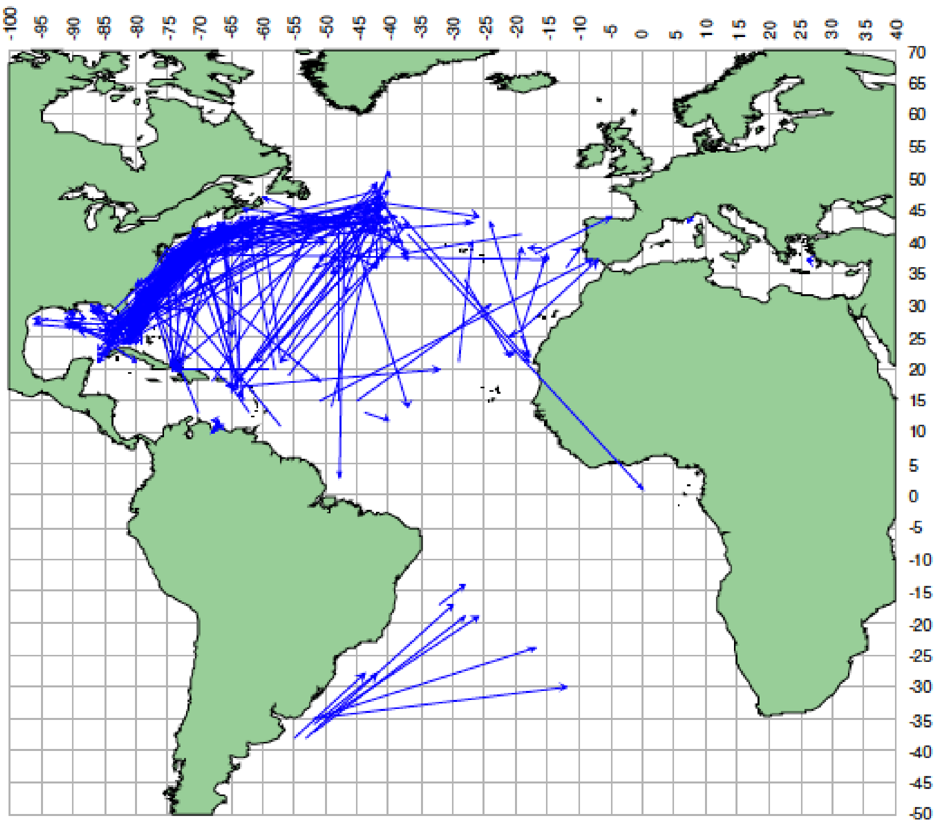

Figure 9.14. Horizontal movements of tagged and recaptured Xiphias gladius *(swordfish). Direct trajectories between releases and recoveries. Reproduced from ICCAT (2006).*

9.1.4 Air-breathing fauna

A diverse air-breathing fauna occurs in the pelagic environment overlying the MAR, including multiple seabird species, sea turtles, and cetaceans (whales and dolphins). The seabirds are constricted to the surface environment by their maximum diving depth, whilst the sea turtles and cetaceans can extend deep into the mid-water, with some cetacean species able to dive more than a kilometre to feed at the seafloor of the MAR flanks. Whilst sea turtles and cetaceans, as free-swimming animals, could also be considered as 'nekton', they are considered separately here to reflect their obligation to return to the surface to breathe, which may expose them to different stressors and impacts compared to nekton which are not air-breathing fauna. It is not possible within the scope of this document to review the regional distribution of all the air-breathing fauna occurring in the pelagic environment overlying the MAR, however, detailed accounts for common or important species are provided where possible.

9.1.4.1 Seabirds

A large number of seabird species have been recorded in the North Atlantic, with many of them feeding in the pelagic environment overlying the MAR. Whilst it is not an exhaustive list, Jungblut *et al.,* (2017) recorded a total of 79 seabird species during four latitudinal transects in the Atlantic Ocean, extending from approximately 55°N to 50°S. Of these species, 17 only occur in the North Atlantic and 36 occur in both the North and South Atlantic (Table 9.5). A further 26 species are known to only occur in the South Atlantic, according to the IUCN Red List of Threatened Species[1].

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[1] The IUCN Red List of Threatened Species: https://www.iucnredlist.org/

It is beyond the scope of this document to provide a detailed account of the regional distribution for all of these seabirds. Instead, the regional distributions of three species are discussed to illustrate the range of distribution patterns observed in North Atlantic seabirds: *Puffinus griseus* (Sooty shearwater), *Fratercula arctica* (Atlantic puffin), and *Pterodroma deserta* (Bugio petrel).

Table 9.5. Seabird species observed in the North Atlantic by Jungblut et al.*, (2017). Species distributions (North Atlantic only or North and South Atlantic) were determined using the IUCN Red List of Threatened Species.*

Seabird species occurring in the North Atlantic	**Seabird species occurring in both the North and South Atlantic**
Fulmarus glacialis (Northern fulmar)	*Pterodroma arminjoniana* (Trinidade petrel)
Pterodroma feae (Fea's petrel)	*Bulweria bulwerii* (Bulwer's petrel)
Puffinus mauretanicus (Balearic shearwater)	*Calonectris diomedea* (Cory's shearwater)
Puffinus baroli (Macaronesian shearwater)	*Calonectris edwardsii* (Cabo Verde shearwater)
Morus bassanus (Northern gannet)	*Puffinus gravis* (Great shearwater)
Catharacta skua (Great skua)	*Puffinus griseus* (Sooty shearwater)
Gavia arctica (Black-throated diver)	*Puffinus puffinus* (Manx shearwater)
Larus canus (Common gull)	*Puffinus lherminieri* (Audubon's shearwater)
Larus melanocephalus (Mediteranean gull)	*Oceanites oceanicus* (Wilson's storm-petrel)
Larus argentatus (Herring gull)	*Pelagodroma marina* (White-faced storm-petrel)
Larus michahellis (Yellow-legged gull)	*Oceanodroma castro* (Madeiran storm-petrel)
Larus marinus (Great black-backed)	*Oceanodroma leucorhoa* (Leach's storm-petrel)
Chroicocephalus ridibundus (Black-headed gull)	*Hydrobates pelagicus* (European storm-petrel)
Larus minutus (Little gull)	*Phaethon aethereus* (Red-billed tropicbird)
Rissa tridactyla (Black-legged kittiwake)	*Phaethon lepturus* (White-tailed tropicbird)
Uria aalge (Common guillemot)	*Fregata magnificens* (Magnificent frigatebird)
Alca torda (Razorbill)	*Sula capensis* (Cape gannet)
	Sula sula (Red-footed booby)
	Sula leucogaster (Brown booby)
	Catharacta maccormicki (South polar skua)
	Stercorarius pomarinus (Pomarine skua)
	Stercorarius parasiticus (Arctic skua)
	Stercorarius longicaudus (Long-tailed skua)
	Phalacrocorax carbo (Great cormorant)
	Phalaropus fulicarius (Red phalarope)
	Larus fuscus (Lesser Black-backed gull)
	Xema sabini (Sabine's gull)
	Sterna hirundo (Common tern)
	Sterna paradisaea (Arctic tern)
	Onychoprion anaethetus (Bridled tern)
	Sterna dougallii (Roseate tern)
	Sterna fuscata (Sooty tern)
	Sterna sandvicensis (Sandwich tern)

	Thalasseus maximus (Royal tern)
	Chlidonias niger (Black tern)
	Anous stolidus (Brown noddy)

9.1.4.1.1 *Puffinus griseus* (sooty shearwater)

Puffinus griseus (sooty shearwater) is a highly migratory species, moving between hemispheres to breed in the Southwest Atlantic and to forage in overwintering grounds in the Central North Atlantic, generally north of 40°N, where they reside from mid-April to early September (Hedd *et al.,* 2012). Residence in the North Atlantic is broken up between staging grounds above the Charlie Gibbs Fracture Zone (and southwest), and overwintering grounds in more coastal waters off of the Grand Bank and Newfoundland and Labrador shelves (Hedd *et al.,* 2012; Figure 9.15). The migration pattern of *P. griseus* is similar to some *Sterna paradisaeal* (Arctic terns) migrating between Greenland and the Brazilian coast (Egevang *et al.,* 2010). The clockwise migration pattern of *P. griseus* corresponding to the circulation of the North Atlantic gyre (leading to a counter-clockwise migration in the South Atlantic) places *P. griseus* directly above the MAR for much of its northward migration (red lines in Figure 9.15). Whilst *P. griseus* and many migratory seabirds do not exhibit foraging behaviour while migrating, light pollution from any vessels involved in mining activities in the region could impact on their navigational abilities. Globally, *P. griseus* is listed as near threatened with a declining population (IUCN, 2017).

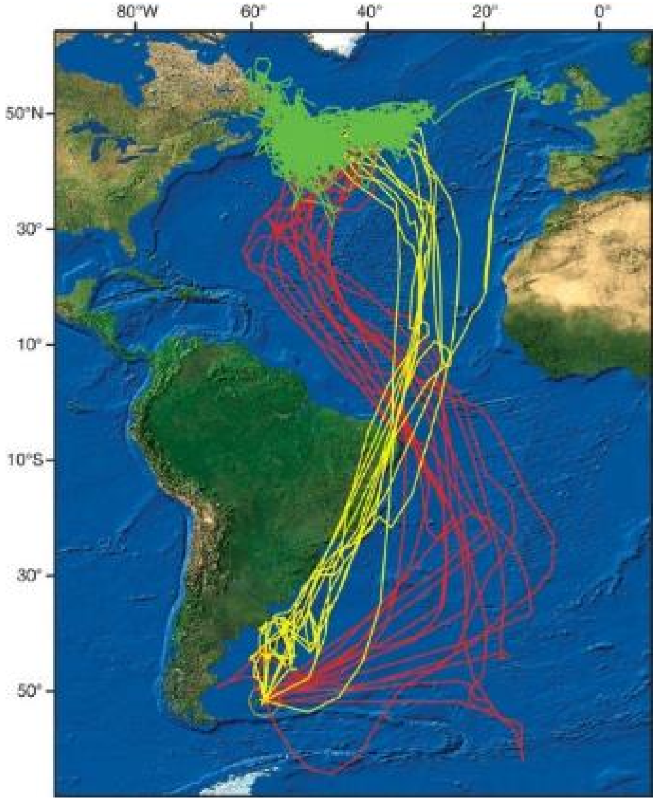

Figure 9.15. Trans-equatorial migration and nonbreeding distribution of Puffinus griseus *(sooty shearwaters) from Kidney Island, Falklands Islands, South Atlantic in 2008 and 2009. Red depicts the northward migration, green the main staging and nonbreeding areas and yellow depicts the southward migration. Reproduced from Hedd* et al.*, (2012).*

9.1.4.1.2 *Fratercula arctica* (Atlantic puffin)

Fratercula arctica (Atlantic puffin) is one of the most common seabirds in the northern North Atlantic, with breeding colonies on both sides of the Atlantic and a species distribution which extends from ~45°N to polar regions. *Fratercula arctica* is entirely pelagic during the non-breeding period and only visits land to breed and to rear its chicks. Different colonies of *F. arctica* in the Northeast Atlantic exhibit varied use of the Central North Atlantic. While *F. arctica* from colonies on the East coast of the UK spend the winter largely within the North Sea (Harris *et al.,* 2010), individuals tracked from the

West coast of Wales utilized the North Sea, coastal western Europe, and the North Central Atlantic (Guilford *et al.,* 2011; Figure 9.16), and birds tracked from western Ireland uniformly migrated West, travelling as far as the Newfoundland-Labrador shelf (Jessopp *et al.,* 2013). For the colony in western Ireland, two key non-breeding destinations for migrating *P. deserta* were identified, the Newfoundland-Labrador shelf immediately post-breeding and the Central North Atlantic from October to early spring (Jessopp *et al.,* 2013). *Fratercula arctica* from the Northwest Atlantic have not been shown to exhibit migrations to non-breeding areas that may interact with the MAR, except potentially through eastward extensions of the foraging area off Labrador (Hedd *et al.,* 2010). Despite being common in the northern North Atlantic, *F. arctica* is Vulnerable globally and endangered in the Northeast Atlantic (IUCN, 2017).

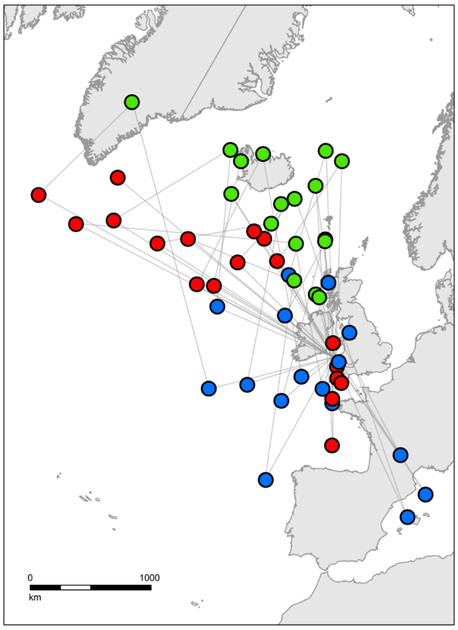

Figure 9.16. Dispersive migration in Fratercula arctica *(Atlantic Puffic). Patterns of migratory movements for 18* F. arctica *tracked using geolocators are shown as median individual position estimates during three months outside the breeding season: August (red); October (green); and February (blue). Lines join each individual bird's successive positions but do not indicate the path travelled. Reproduced from Guilford* et al., *(2011).*

9.1.4.1.3 *Pterodroma deserta* (Bugio petrel)

Pterodroma deserta (Bugio petrel) is a highly pelagic gadfly petrel species. During pre-laying and incubation (between mid-July and the end of August), the species utilizes waters above the MAR North and West of the Azores to 50°N and 47°W (Ramírez *et al.,* 2016). Chick-rearing occurs between September and November and results in a more restricted distribution around Madeira. In late November, *P. deserta* migrates to one of five overwintering areas either in the Northwest Atlantic, or Southwest Atlantic, beginning the return trip in May. Migration to overwintering areas in the South Atlantic takes *P. deserta* across the MAR with stopovers around Cabo Verde and the Northeast Brazil shelf (Ramírez *et al.,* 2013; Ramírez *et al.,* 2016; Ramos *et al.,* 2016). *Pterodroma deserta* is one of the rarest Pterodroma species, with fewer than 1000 individuals, and it only breeds on Bugio Island (Madeira). The population of *P. deserta* is stable but listed as Vulnerable (IUCN, 2017).

9.1.4.2 Sea turtles

Three sea turtle species were recorded by Jungblut *et al.,* (2017) during four latitudinal transects in the Atlantic Ocean, extending from approximately 55°N to 50°S: *Dermochelys coriacea* (leatherback turtle), *Chelonia mydas* (green turtle) and *Caretta caretta* (loggerhead turtle). All these species occur in both the North and South Atlantic Oceans, according to species ranges within the IUCN Red List of Threatened Species[3]. The regional distributions of *D. coriacea* and *C. caretta* are considered in more detail below.

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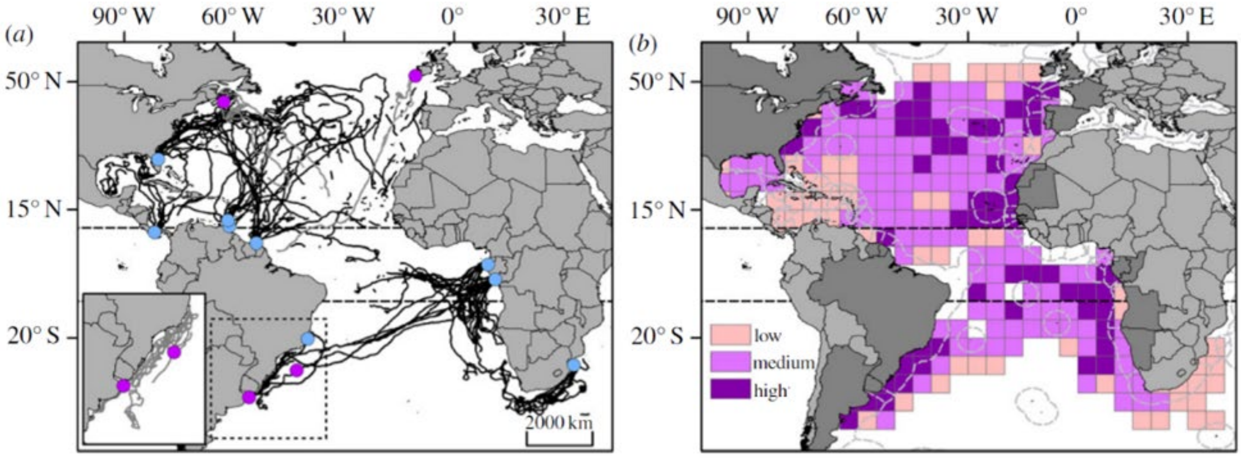
[3] The IUCN Red List of Threatened Species: https://www.iucnredlist.org/

9.1.4.2.1 *Dermochelys coriacea* (Leatherback sea turtles)

Dermochelys coriacea (Leatherback turtles) are oceanic, highly migratory, marine predators distributed circumglobally between sub-arctic and tropical environments. *Dermochelys coriacea* can undertake extensive migrations, swimming thousands of kilometres between foraging grounds and nesting beaches. In the North Atlantic, most *D. coriacea* remain in cold, northern (temperate or subarctic) latitudes in the summer and early autumn and migrate to mate and nest in subtropical and tropical habitat in the late autumn, winter and spring. Diving behaviour recorded with tracking studies indicates that migrations generally occur in epipelagic (surface) waters, whilst foraging dives can reach 1300 m. The foraging behaviour of *D. coriacea* has been linked to the location of fronts, upwelling and downwelling zones, and mesoscale features.

Dermochelys coriacea in the North Atlantic heavily utilize international waters, with more than 50 % of daily positions occurring in international waters for the 65 turtles in a study by Fossette *et al.,* (2014). The same study demonstrated that the turtles connect the waters beyond national jurisdiction with the Exclusive Economic Zones (EEZs) of 46 out of the 97 countries with Atlantic coastlines. Fossette *et al.,* (2014) also describe high-use areas for *D. coriacea*, which intersect the MAR Southwest of the Azores from October to March and East of the Romanche Fracture Zone from April to September. Additional high-use areas for *D. coriacea* occur year-round to the West of Cabo Verde, with a diffuse migratory corridor connecting French Guiana/Suriname/Grenada/Trinidad and eastern Canada (Figure 9.18). An additional study described the trajectories of a further 20 *D. coriacea* individuals tagged with satellite transmitters near Massachusetts (Dodge *et al.,* 2014). Many of these individuals showed return migrations heading Southeast to the MAR before curving back towards the eastern Caribbean and finally returning North, clearly indicating that the northern MAR falls within a migratory corridor for that *D. coriacea* population (Figure 9.17). Although the North Atlantic populations are increasing, *D. coriacea* is listed as globally Vulnerable (IUCN, 2017).



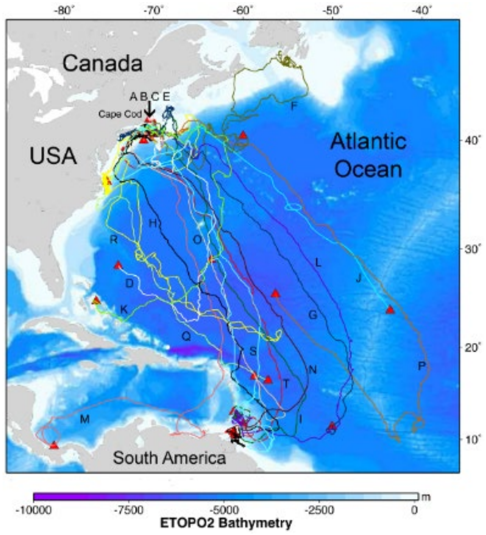


Figure 9.17. Top left: Movements of 106 satellite-tracked Dermochelys coriacea *(Leatherback turtle) during their migration in the Atlantic Ocean, between 1995 and 2010 tagged on nesting beaches (blue dots) or at sea (purple dots). Top right: Density of* D. coriacea *daily locations (locations were time-weighted and population-size normalized). Three density classes were defined: low, medium and high use. Bottom: Reconstructed movements of 20 satellite-tagged* D. coriacea *in the North Atlantic Ocean, 2007–2010. Tracks show turtle movements from point of release (Cape Cod) to point of last Argos transmission (red triangles). Adapted from Fossette* et al.*, (2014) (top) and Dodge* et al.*, (2014) (bottom).*

9.1.4.2.2 Caretta caretta (Loggerhead sea turtles)

Caretta caretta (Loggerhead sea turtles) are found throughout the temperate and tropical regions of the Atlantic. *Caretta caretta* have a complex life history which is not yet fully understood. Hatchlings from nesting beaches in the West Atlantic have been shown to migrate into the North Atlantic following magnetic cues, which enable them to stay them in the North Atlantic Gyre. Mansfield *et al.,* (2014) demonstrate that, as predicted by laboratory experiments (Lohmann & Lohmann, 1996) and models (Putman *et al.,* 2012), *C. caretta* individuals do not travel beyond the constraints of the outer Gyre boundaries. Some individuals do travel into the Sargasso Sea, likely due to the protective and foraging environment provided by Sargassum mats (Figure 9.18). Use of the Azores and Madeira as juvenile habitat for *C. caretta* is well known (Brongersma, 1972), but movements across the North Atlantic have only more recently been detailed. Juveniles have been described as ‘ranging’ on both sides of the Atlantic, and not necessarily settling in neritic habitats as previously assumed. Data from McClellan & Read (2007) describe broad use of the Northeast Atlantic (out to just West of the Azores) by juvenile *C. caretta*, while Freitas *et al.,* (2019) show movements of juveniles from Madeira both East to the coast of Africa and West across the MAR. Migrations by large juveniles from the West Mediterranean across the North Atlantic have also been described (Figure 9.19), with movement of individuals towards both the East Coast of the United States and towards the Caribbean (Eckert *et al.,* 2008). Seasonal migrations of adult *C. caretta* along coastal zones (particularly the East Coast of the United States) have also been documented, but adult use of ocean habitats is currently unknown. The Northwest Atlantic sub-population of *C. caretta* is listed as Least Concern on the IUCN Red List, although the global population is listed as Vulnerable (IUCN, 2017).

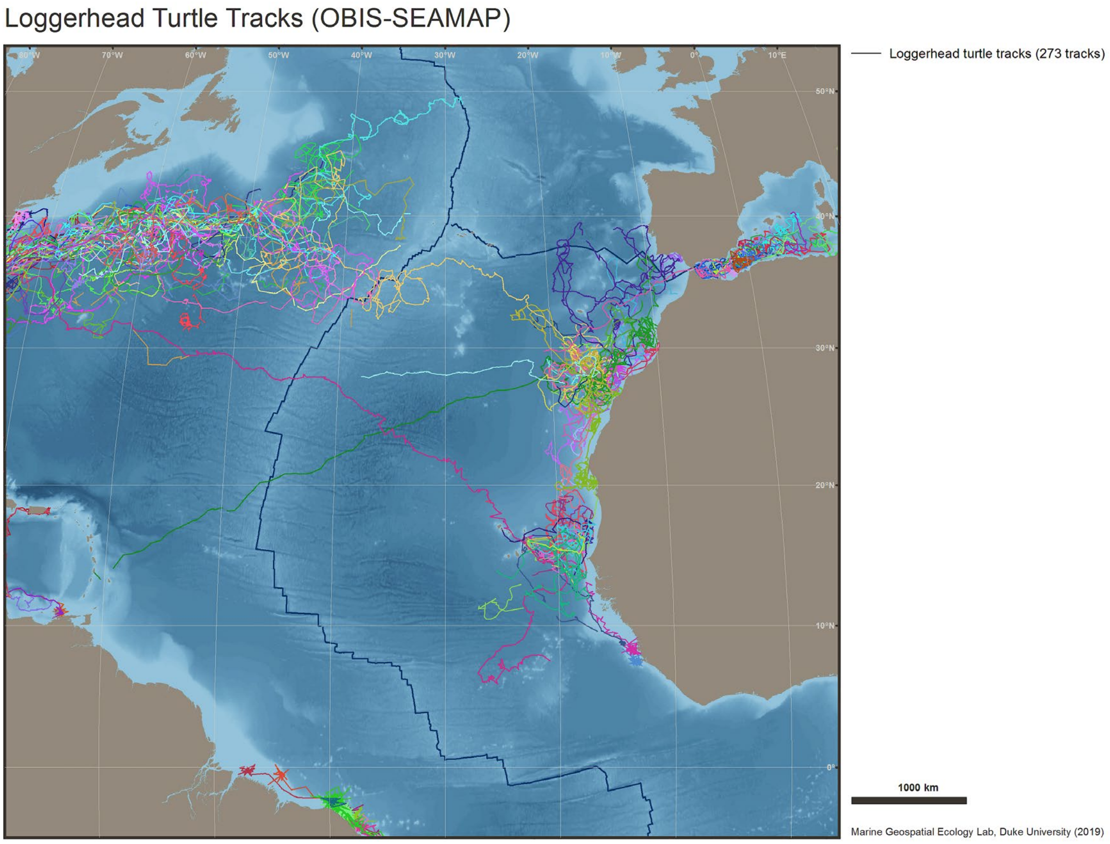


Figure 9.18. Caretta caretta (loggerhead turtle) tracks of 273 individuals. Map reproduced with permission from Cleary et al.*, 2019. Data taken from OBIS-SEAMAP. Map available: https://ran-s3.s3.amazonaws.com/isa.org.jm/s3fs-public/files/documents/datareport-19nov-lowres.pdf.*

9.1.4.3 Cetaceans (whales and dolphins)

Whilst not an exhaustive list, Jungblut *et al.*, (2017) recorded a total of 21 cetaceans (whales and dolphins) during four latitudinal transects in the Atlantic Ocean, extending from approximately 55°N to 50°S. Of these species, 19 occur in both the North and South Atlantic, and one only occurs solely in the North Atlantic (Table 9.6). One additional species only occurs in the South Atlantic (*Lagenorhynchus australis*: Peale's dolphin), according to species ranges within the IUCN Red List of Threatened Species[4], and is excluded from Table 9.6. It is beyond the scope of this document to describe the regional distribution for all of the 20 North Atlantic cetacean species recorded by Jungblut *et al.*, (2017). Instead, the regional distributions of select Odontoceti (toothed-whales and dolphins) species are discussed below.

Table 9.6. Cetacean species observed in the North Atlantic by Jungblut et al.*, (2017). All species occur in both the North and South Atlantic, except Lagenorhynchus albirostris (White-beaked dolphin), which only occurs in the North Atlantic. Species names were updated using the World Register of Marine Species, and species distributions were determined using the IUCN Red List of Threatened Species.*

Odontoceti (toothed whales and dolphins)	**Mysticeti (baleen whales)**
Lagenorhynchus albirostris (White-beaked dolphin)*	*Megaptera novaeangliae* (Humpback whale)
Physeter macrocephalus (Sperm whale)	*Balaenoptera physalus* (Fin whale)

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[4] The IUCN Red List of Threatened Species: https://www.iucnredlist.org/

Globicephala melas (Long-finned pilot whale)	*Balaenoptera borealis* (Sei whale)
Globicephala macrorhynchus (Short-finned pilot whale)	*Balaenoptera acutorostrata* (Minke whale)
Ziphius cavirostris (Cuvier´s beaked whale)	*Balaenoptera edeni* (Bryde´s whale)
Orcinus orca (Killer whale)	
Delphinus delphis (Common dolphin)	
Stenella frontalis (Atlantic spotted dolphin)	
Stenella coeruleoalba (Striped dolphin)	
Stenella clymene (Clymene dolphin)	
Tursiops truncatus (Bottlenose dolphin)	
Grampus griseus (Risso´s dolphin)	
Steno bredanensis (Rough-toothed dolphin)	
Stenella longirostris (Spinner dolphin)	
Phocoena phocoena (Harbour porpoise)	

9.1.4.3.1 Ziphiidae (beaked whales)

Within the Odontoceti (toothed whales and dolphins), the Ziphiidae (beaked whales) is one of the least known families, with very little known about the distribution of species within this family due to historically very low sampling effort. Recent efforts to integrate data from various sources and develop robust methods to interpolate models beyond the area sampled have allowed better insight into their potential distribution. Due to difficulty in identifying these animals to species level and the rarity of sightings, they have generally been grouped in distribution models.

A recent study grouping *Ziphius cavirostris* (Cuvier's beaked whales), *Hyperoodon ampullatus* (Northern bottlenose whales), and *Mesoplodon* spp. sightings in the North Atlantic found the highest relative densities of Ziphiidae to occur at approximately 1500 m depth in locations characterised by intermediate net primary production and high values for slope and sea surface temperature (Virgil *et al.,* 2019). As a result, steep slope areas associated with greater depths and high temperature gradients had high predicted relative densities of Ziphiid whales, particularly in the West Atlantic. Along with identifying areas of high predicted densities in the western North Atlantic, the models also predicted increased abundance around the MAR, due to its steep slopes. Areas of increased abundance appeared to be associated with the Faraday and Charlie Gibbs Fracture Zones, and to some degree around Kane Fracture Zone (Virgili *et al.,* 2019; Figure 9.19).

Ziphius cavirostris has a very broad distribution, occurring in offshore waters of all oceans, from the tropics to the polar regions in both hemispheres. Tagging studies of *Z. cavirostris* off Southern California established *Z. cavirostris* as the world's deepest diving mammal, diving as deep as 2992 m, with a maximum dive time of 137.5 minutes (Schorr *et al.,* 2014). The same study also demonstrated diel patterns in diving behaviour, with individuals spending significantly more time in waters above 50 m at night that they do during the day. This sort of deep-diving behaviour could bring *Z. cavirostris* into contact with mining activities at the seafloor, whilst prolonged resting near the surface overnight may increase the likelihood of encounters with vessels.

A separate study addressing *H. ampullatus* in the Northwest Atlantic during summer (June-August) also found that depth and sea surface temperature were the main drivers of whale distribution, with these environmental factors thought be determining the distribution of prey species, such as the deep-water squid *Gonatus* spp. (Gomez *et al.,* 2017). Deep-diving whales more broadly are known to feed on mesopelagic/bathypelagic cephalopods and benthic fishes that utilize strong temperature gradients along high-slope areas (Spitz *et al.,* 2011), which would support the identification of the shelf break and similar areas of high slope by the model as being important habitat for *H. ampullatus*.

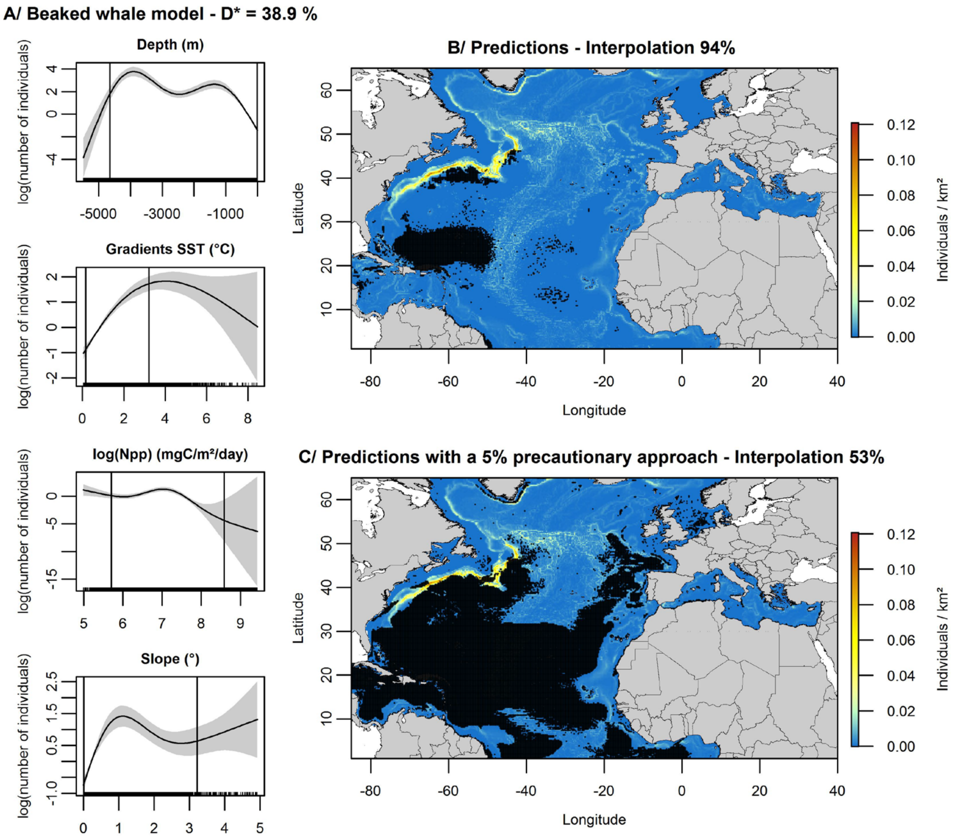

Figure 9.19. Functional relationships for the selected variable (A) and the predicted relative densities of individuals per km^2 of Ziphius cavirostris *(Cuvier's beaked whales),* Hyperoodon ampullatus *(Northern bottlenose whales), and* Mesoplodon *spp. combined (B, C). A: Solid lines are the estimated smooth functions, and the shaded areas represent the approximate 95 % confidence intervals. The y-axes indicate the number of individuals on a log scale, where zero indicates no effect of the covariate. The vertical lines indicate the 2.5th and 97.5th quantiles of the data. B, C: Black areas on prediction maps (B: without precautionary approach and C: with a 5 % precautionary approach) represent zones where predictions were not extrapolated. Reproduced from Virgil (2018).*

9.1.4.3.2 Kogiidae

The Kogiidae is one of the smallest families within the Odontoceti, with only two extant species, *Kogia breviceps* (Pygmy sperm whale) and *Kogia sima* (Dwarf sperm whale). Due to very limited sightings at sea, both species are listed as Data Deficient under the IUCN Red List (IUCN, 2017). *Kogia breviceps* and *K. sima* are believed to dive to depths below 300 m and are most frequently sighted in deep waters ranging from 400 to 1000 m. Results from a recent study that aggregated and modelled known observations of Kogiidae in the North Atlantic indicated that the highest density of individuals was related to fronts, canyons and seamounts in deep waters (Virgili *et al.,* 2019). The shelf break along the Gulf Stream in the western North Atlantic was identified as the highest density area, whilst increased densities were also predicted for the slopes of the MAR, particularly in conjunction with seamounts (Figure 9.20). It is important to note that deeper areas of the North Atlantic Gyre are particularly poorly sampled and required extrapolation of the model beyond the sampled environment, further sampling would considerably improve these basin-scale models.

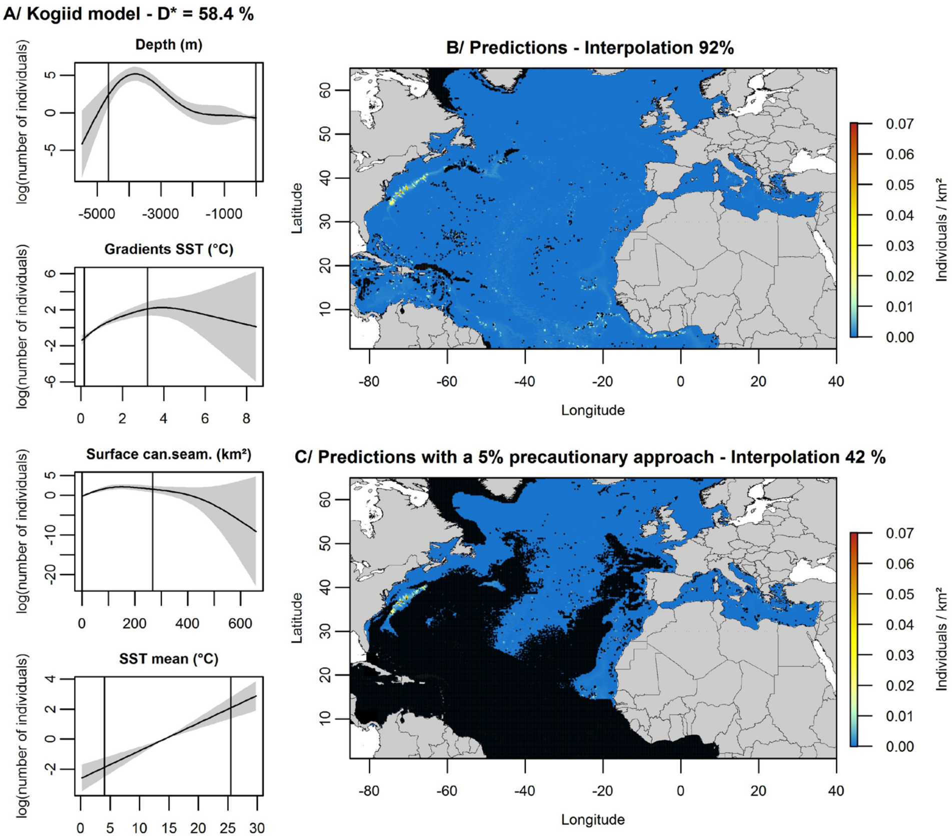

Figure 9.20. Functional relationships for the selected variable (A) and the predicted relative densities of individuals per km^2 of Kogia breviceps *(Pygmy sperm whale) and* Kogia sima *(Dwarf sperm whale) combined (B, C). Percentages represent the proportion of the study area defined as interpolation with the gap analysis. Reproduced from Virgili (2018).*

9.1.4.3.3 Other Odontoceti (toothed whales and dolphins)

Heightened densities for the Odontoceti guilds Delphinidae and Globicephalinae have also been predicted along the MAR, in particular North and Northwest of the Romanche Fracture Zone (Mannocci *et al*., 2015). The MAR axis South of 40° N was also predicted to be an area of increased density of *Physeter macrocephalus* (true sperm whales), although the area between 40° N and 50° N both on and off the ridge axis, was predicted to have lower densities (Virgil *et al.,* 2019). These patterns reflect the finding that deep waters (> 2000 m) associated with high gradients of sea-surface temperature and net primary production were particularly important for *P. macrocephalus* (Virgil *et al.,* 2019). Predicted higher densities of *P. macrocephalus* were broadly distributed across the North Atlantic with maxima located along the Gulf Stream (Figure 9.21). This broader predicted distribution could be due to the fact that the distribution of prey targeted by *P. macrocephalus* is more driven by dynamic variables than by static features, or by the greater diversity of prey size and type consumed by *P. macrocephalus* (Spitz *et al.,* 2011; Virgili *et al.,* 2019).

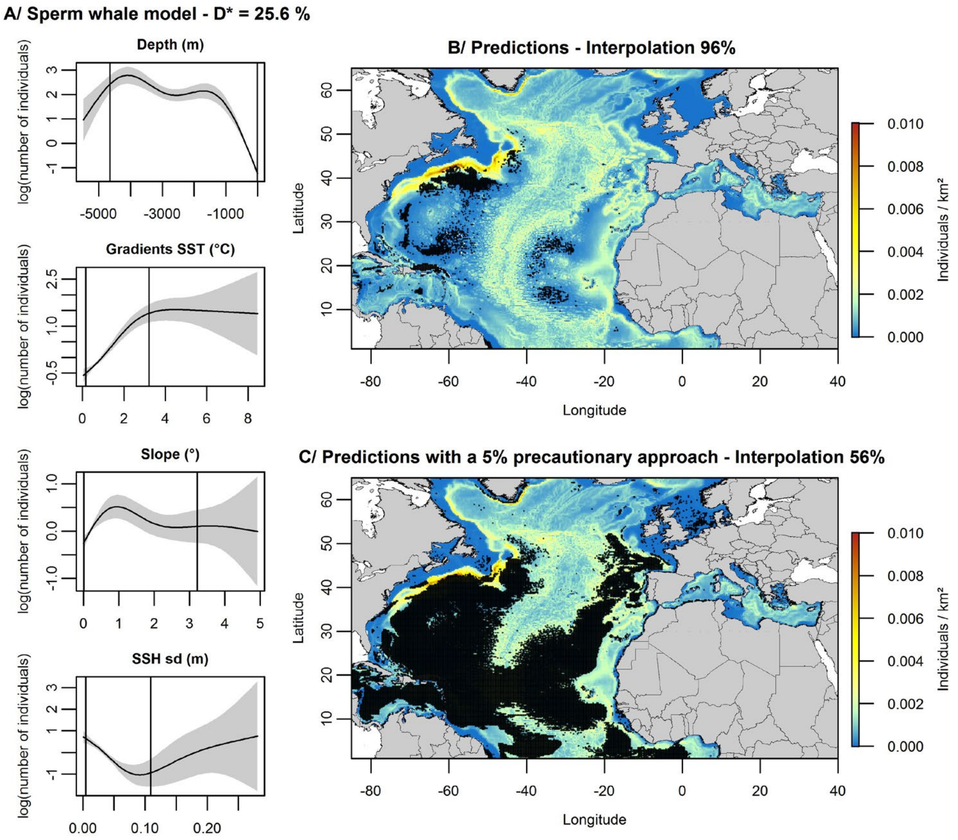

Figure 9.21. Functional relationships for the selected variable (A) and the predicted relative densities of individuals per km^2 *of* Physeter macrocephalus *(true sperm whales) (B, C). Percentages represent the proportion of the study area defined as interpolation with the gap analysis. Reproduced from Virgili (2018).*

9.2 Temporal variability

Temporal variation in the surface and mid-water fauna can occur on daily (e.g. diurnal migration and response to tidal cycles), monthly (e.g. lunar cycles), seasonal (e.g. migration between feeding and breeding grounds), or interannual timescales (e.g. fish stock movement in response to shifting ocean climate). Far less is known about temporal variability compared to the information available on regional distribution of the surface and mid-water fauna. Geographically, the majority of information is available from South of Iceland to North of the Azores, with far less information available for South of the Azores to the equator.

In the following section, the information available on the temporal variability of mid-water nekton along the northern MAR is presented. It was not possible within the scope of this version of the document to provide information on the temporal variation of sharks and commercially valuable species, such as tuna; or air-breathing fauna, such as seabirds, sea turtles and cetaceans. Future versions of this document may consider the temporal variation of these biological components in more detail.

9.2.1 Daily vertical migration

The most important temporal variation in the mid-water nekton is the diel vertical migrations (DVM) displayed by many species (Pearcy & Brodeur, 2009). There is a general movement of fishes and other fauna towards the surface at night where they can feed on plankton in the productive surface layers, safe from visual predators, before descending to the safety of greater depths at dawn. It is important to note that different species show different patterns of movement. For example, the myctophid *Lobianchia dofleini,* which is abundant over the MAR, moves between 500 m depth and the surface whereas other species may move from 2000 m to the surface (Figure 9.22). Also, not all individuals of a species move, with several species having a non-migratory component. The predatory dragonfishes, *Chauliodus* spp. move relatively little, intercepting their prey during the upward and downward migration. These patterns of mass vertical migration are evident in echograms recorded from ship-board sonars (Figure 9.23).

The important contributors to acoustic backscatter around the northern MAR were considered by Opdal *et al.,* (2008) to be:

- *Maurolicus muelleri* (lightfish) – vertical migrator 100-500 m
- *Benthosema glaciale* (lanternfish) – vertical migrator 100-500 m
- *Notoscopelus kroyeri* and *N. bolini* (lanternfish) – vertical migrators 150-700 m
- *Lampanyctus macdonaldi* (lanternfish) – vertical migrator 200-1000m
- *Scopelogadus beanii* (Melamphaidae) – deep non-migrating mesopelagic <1000 m
- *Serrivomer beanii* (sawtooth eel) – deep non-migrating mesopelagic <1000 m
- *Cyclothone microdon* (bristlemouth) – non-migrator at 500–2700 m
- *Bathylagus euryops* (deep-sea smelt) – weak migrator at 500–1500 m
- *Maulisia microlepis* (tubeshoulder) – non-migrator at 700–2000 m

In a global study, Aksnes *et al.*, (2017) showed that the structure of deep acoustic scattering layers is largely determined by light penetration so that the DSLs are shallower when light penetration is reduced and deeper when light penetration is greatest. This is explained by mesopelagic fishes seeking their optimum ‘Light Comfort Zone’ depth (Røstad *et al.,* 2016). On the MAR from approximately 60°N to 40°N, Opdal *et al.,* (2008) found that in optically clear waters to the South (Central North Atlantic) with good light penetration, the amplitude and intensity of DVM was greatest. In more phytoplankton-rich waters in the vicinity of the Sub-Polar Front, although acoustic backscatter and estimated biomass were higher, DVM was less pronounced.

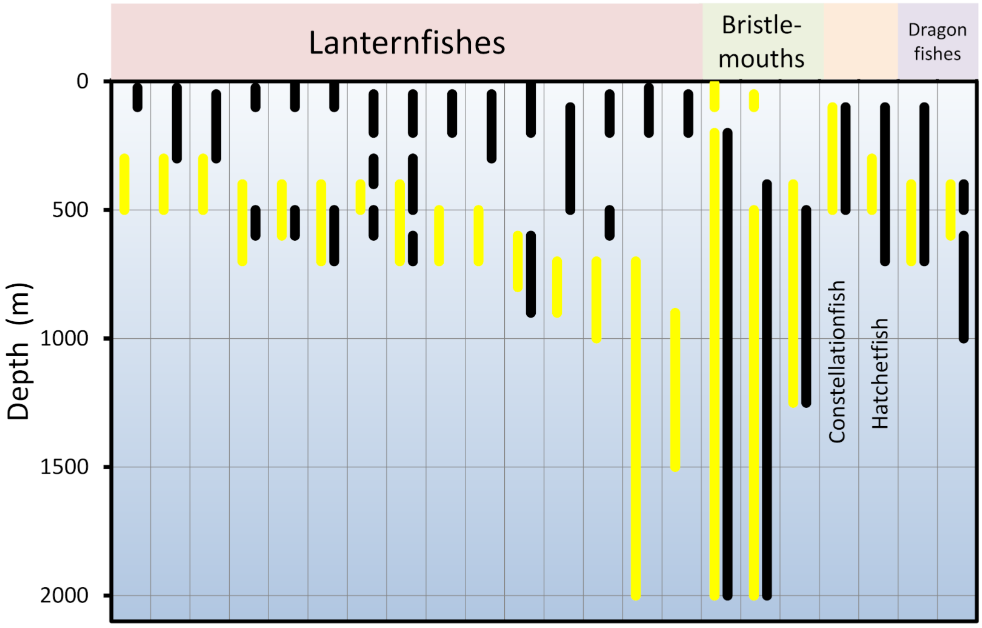

Figure 9.22. The day (yellow) and night (black) vertical distribution of different species of mid-water fishes, at 30°N 23°W in the Central North Atlantic ecoregion to the East of the Mid-Atlantic Ridge. Based on data from Badcock & Merrett, (1976). Figure courtesy of Monty Priede.

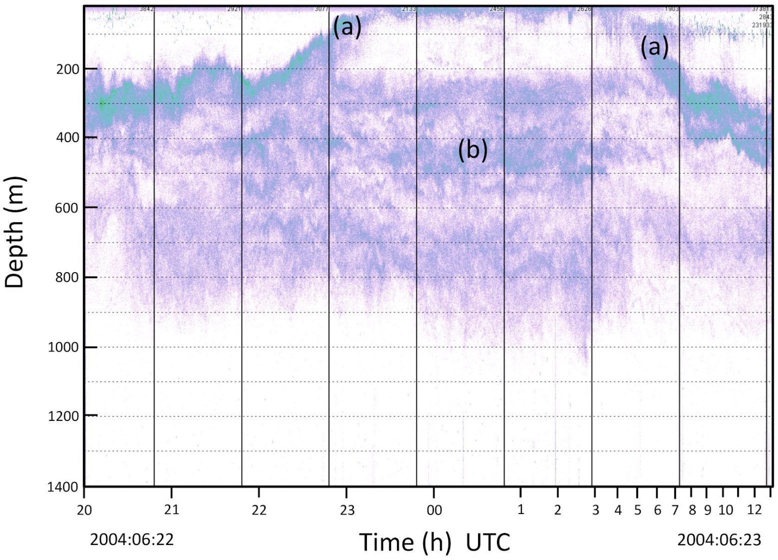

Figure 9.23. Daily Vertical Migration (DVM) of mid-water animals over the Mid-Atlantic Ridge. 18 kHz echogram taken between 2000h and 1300h by the RV GO Sars MAR-ECO voyage in 2004. Discrete deep-scattering layers move towards the surface at night (a), but important components do not move (b). Courtesy of Odd Aksel Bergstad and Åge Høines, IMR Norway.

One effect of the DVM over the MAR is that organisms transported over the ridge by prevailing currents find their descent impeded, resulting in concentration of biomass over the summits (Figure 9.24). This effect can vary in intensity according to phases of the moon and has been found to influence the behaviour of predators feeding on the scattering layers (Afonso *et al.*, 2014a). The trapping of downward migrants may partially explain the high near-bottom biomass over the ridge shown in Figure 9.24.

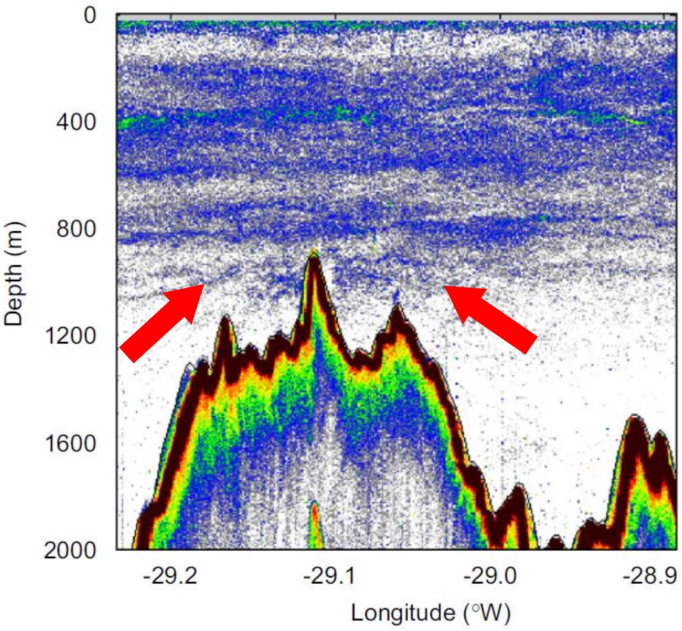

Figure 9.24. 18 kHz acoustic backscatter over the Mid-Atlantic Ridge around 48°N 28.5°W in the Azores region. Arrows indicate regions with enhanced near-ridge backscatter. Detail from Sutton et al., *(2008).*

9.2.2 Seasonal variation

The North Atlantic Drift Area ecoregion is notable for the greatest seasonal changes in surface chlorophyll of any region of the world's oceans (Longhurst 1998) driving a highly seasonal cycle of production. How this seasonal signal is transmitted to the mid-water assemblage of the DSLs is not well documented. Invoking the Light Comfort Zone hypothesis, it is reasonable to assume that depth and movements of the DSL will be influenced by changes in water transparency with seasons. For example, it has been shown that changing weather, in the form of passing rainstorms can influence behaviour of mid-water fauna as deep as 700 m (Kaartvedt *et al.,* 2017). The intensity of moonlight and starlight also have important influences (Kaartvedt *et al.,* 2019) and there is evidence of this occurring on the MAR (Afonso *et al.,* 2014a).

9.2.3 Inter- and intra-species interactions

In addition to responding to the surrounding environment, mid-water animals respond to each other. Benoit-Bird *et al*., (2017) found that different species or taxa do not mix randomly, nor do they form single-species layers. Rather they are organised into mono-specific schools or aggregations composed of a narrow size class, horizontally adjacent to other discrete schools of other taxa together forming a heterogeneous layer. The structure of the DSL is therefore maintained by social interactions.

In schools of crustacea the inter-individual distance is 5 – 60 cm, in fishes 5 – 120 cm and for squid 5 – 260 cm. These schools can respond rapidly to presence of a predator, squid respond by compression reducing the average inter-individual spacing from approximately 110 to 50 cm and they are capable of a rapid 'flash' compression within 4 – 5 seconds. Adjacent schools within the layer then expand to fill the available space. Thus, on a very short time scales of seconds, the structure of the mid-water layers is constantly changing and responding to disturbances. When a net is towed through the deep-scattering layer animals such as the myctophid *Benthosema glaciale* are remarkably adept at moving out of the path of the net so that only a small percentage is captured (Kaartvedt *et al.,* 2012; Figure 9.25). This further complicates study of the mid-water fauna, as many species are capable of highly successful net-avoidance behaviours, which introduces bias when comparing net samples with other sampling methods, such as through imagery.

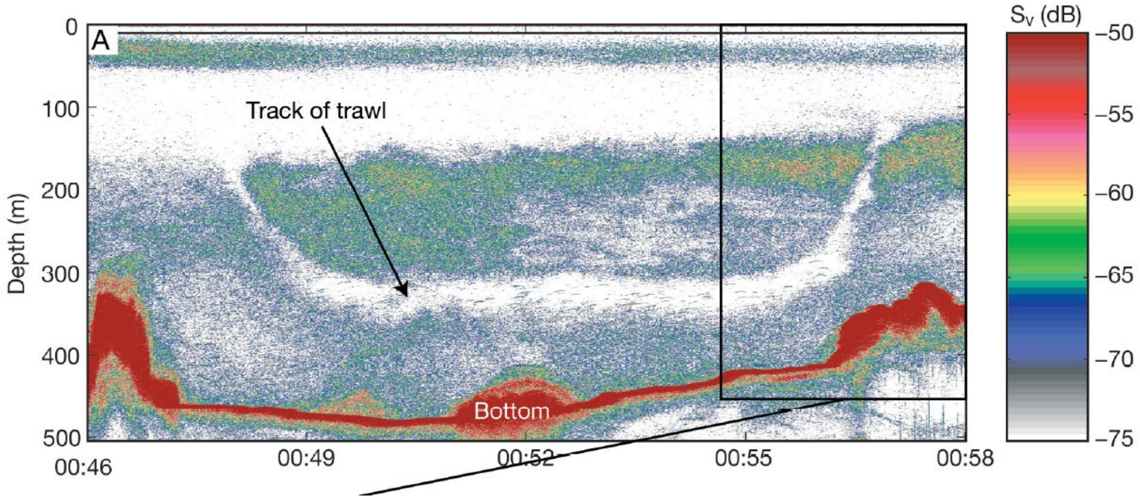

Figure 9.25. Avoidance of trawl by mid-water fishes. Echogram of the path of a trawl towed through the deep-sea scattering layer. The trawl had free through flow and was not sampling, so the void in the acoustic records cannot be explained by removal of fish. Reproduced from Kaartvedt et al., *(2012)*

9.2.4 Life history and ontogenetic descent

A common driver of temporal variation is the reproductive cycle of animals which is often tied to an annual migration cycle. In pelagic squids, there is evidence of seasonal migrations and changes in depth distribution (Roper & Young, 1975) but sampling over the MAR is insufficient to provide definitive information on the species occurring there. The myctophid, *Benthosema glaciale* in the North-East Atlantic begins spawning in late March and larvae are found in the upper 75 m of the ocean during April to July. As the larvae grow, they move deeper metamorphosing into juveniles at > 500 m depth during June to August so that by the end of September there are no larvae in the surface layers. *Benthosema glaciale* take two to three years to grow to sexual maturity, with slower growth during the winter than in summer (Kawaguchi & Mauchline, 1982). Each species within the mid-water nekton assemblage has its own life cycle usually with ontogenetic descent during development from early life-history stages that generally occur in the surface layers. The reproductive cycle may drive annual changes in distribution within the mid-water.

9.2.5 Multidecadal variability

Considering long term change over multidecadal time scales it is known that the North Atlantic region has been warming for the past 100 years. Superimposed on this trend there is variability known as the Atlantic Multidecadal Variability (AMV) which may be coupled to changes in ocean circulation, particularly the Atlantic Meridional Overturning Circulation (AMOC) whereby warm water flows northwards at the surface, is cooled in the Arctic and returns as a cold bottom water moving southwards at depth thus ventilating the deep sea. The AMOC itself in turn has a periodicity imposed upon it by the North Atlantic Oscillation (NAO) (Robson *et al*., 2018). Recent studies suggest that the AMOC is also slowing down, thought to be a result of global climate change (Thornalley *et al.,* 2018). Changes in Atlantic circulation have resulted in long-term changes in phytoplankton, zooplankton and fisheries leading to large scale biogeographic shifts in the North-East Atlantic Ocean (Beaugard & Reid, 2003; Hátún *et al.,* 2009).

For the mid-water nekton of the MAR there are insufficient data to determine whether there has been climate change-associated long term changes in the fish, shrimp and cephalopod assemblages. The study by Sutton *et al.,* (2008) during the Census or Marine Life (COML) programme 2000-2010 was the first targeted systematic sampling effort on the MAR. Earlier data from the Woodshole Oceanographic Institution from 1963 to 1974 were not targeted at the MAR and did not use comparable quantitative opening and closing net systems (Judkins & Haedrich 2018). Time series sampling in the future will be necessary to resolve these issues.

9.3 Trophic relationships

The food-web in the mid-water environment overlying the MAR is reliant on the food derived in surface waters, with photosynthesising phytoplankton most commonly at the base of the food chain. Complex linkages between phytoplankton, zooplankton, bacteria, shrimps, fishes, sharks, seabirds, cephalopods, sea turtles and cetaceans facilitate transfer of energy between trophic levels and support nutrient recycling. Nutrients and energy are transferred horizontally and vertically through the mid-water environment via movement of the mid-water fauna and the rain of particulate organic material and flocculates (marine snow), which descends from the surface and sinks towards the seafloor.

In general, less is known about MAR mid-water trophic relationships than for the regional distribution or temporal variation of MAR mid-water fauna. In the following section, the available information on trophic relationships for the pelagic environment is provided. Given the interconnected nature of biological components in the MAR pelagic food web, this section is not broken down into separate biological components but considered as a whole.

Much attention has been directed to the trophic role of mid-water fishes in the global open ocean following publication estimates of global biomass of 10 000 million tonnes (Kaartvedt *et al.,* 2012), ten times higher than previously assumed. These estimates suggest remarkably high trophic efficiency, with these fishes potentially respiring approximately 10% of the primary production in deep waters (Irigoien *et al.,* 2014). At a regional level, Morato *et al.,* (2016) produced a food-web model of the open-ocean and deep-sea environments of the Azores. This identifies the mesopelagic and bathypelagic compartments as two of the largest components of the food-web at trophic levels three to four. The same study suggests high keystoneness index for small-size pelagic fishes and bathypelagic fish, indicating their important role as prey in the food-web.

Using stable isotope analysis of carbon (C) and nitrogen (N) Hoffman & Sutton (2010) determined the trophic levels of mid-water fauna on the MAR and showed that trophic level varied between 1.8 and 5.7 increasing with depth. More than half of zooplankton and micronekton were at trophic level 3, nearly half of the meso-pelagic fishes were at level 4.

Most fishes were at trophic level approximately 4.5 and the deepest living bathypelagic fishes were at 4.8 or higher. It is concluded that there is widespread opportunistic feeding in the mid-water with many species sharing similar trophic levels because omnivory seems to be common. This is at variance with the conclusion of Morato *et al*., (2016) that omnivory indices in the Azores system are generally low indicating prey specialisation for the majority of groups. Within the mid-water environment compartment it appears that there is a distinctive food-web that differs from the higher-level analysis for the total MAR ecosystem.

The mesopelagic is one of the least well-known parts of the global marine ecosystem (St John *et al.,* 2016) and attempting a detailed trophic analysis may be premature. However, Anderson *et al*., (2019) have applied a simplified food-web model to the quantify carbon fluxes to mesopelagic fishes at latitudes 40°N to 40°S which should be applicable to much of the Central North Atlantic and southwards. They identify three main pathways for transfer of primary production from the epipelagic zone (surface waters) to the mid-water food-web, mediated by copepod grazing on phytoplankton (Figure 9.26). These are:

1. Resident epipelagic zooplankton – consumed near the surface by mesopelagic fish at night during daily vertical migration
2. Migrating epipelagic zooplankton – intercepted by mesopelagic fish waiting in the deep layers
3. Detritivore zooplankton – zooplankton feeding on sinking particulate organic matter, including bacteria growing on the detritus.

These components together act as a 'biological pump' combining the vertical movements of the copepods with vertical movements of mesopelagic fishes supplementing the gravity-driven sinking of particulate organic matter to sustain the deep-sea pelagic and benthic biomass. One conclusion from the model is that very high estimates of global mesopelagic fish biomass in excess of 10 Gigatonnes are very unlikely unless very high levels of efficiency are assumed in the pelagic food chain (Anderson *et al.,* 2019).

Inspecting Figure 9.26 it is clear that all of the mid-water nekton must be at trophic level 3 (secondary consumer/carnivore) or higher. Carnivorous plankton including some copepods are likely present in the epipelagic so it cannot be assumed that all prey consumed will be from trophic level 2 (primary consumer/herbivore). The abundant small mid-water fishes, Myctophidae, Gonostomatidae, Sternoptychidae and Phosichthyidae consume herbivorous, omnivorous and carnivorous copepods that they encounter during their daily vertical migration. The shrimps show similar feeding behaviour together with the smaller cephalopods and their early life-history stages. There is considerable predation activity within the mid-water nekton. The Paralepididae (barracudinas) are probably agile swift swimmers and able to pursue prey which they capture in their large jaws. In the sparse deep-pelagic environment where nearest-neighbour distances are long, sit-and-wait foraging is used by long-bodied fishes with well-developed lateral line sense organs such as the Nemichthyid and Serrivomerid eels that can detect the slightest vibration of moving prey. Many fishes have bioluminescent lures to attract prey such as in the Stomiidae (barbeled dragon fishes) and Ceratioid anglerfishes. Large teeth are characteristic as in the Evermannellidae (sabretooth fishes). The effectiveness of these feeding specialisations is exemplified by the fact that dragonfishes can consume 53 – 230% of the standing stock of their fish prey per year (Clarke, 1982; Davison *et al.,* 2013; Sutton & Hopkins 1996).

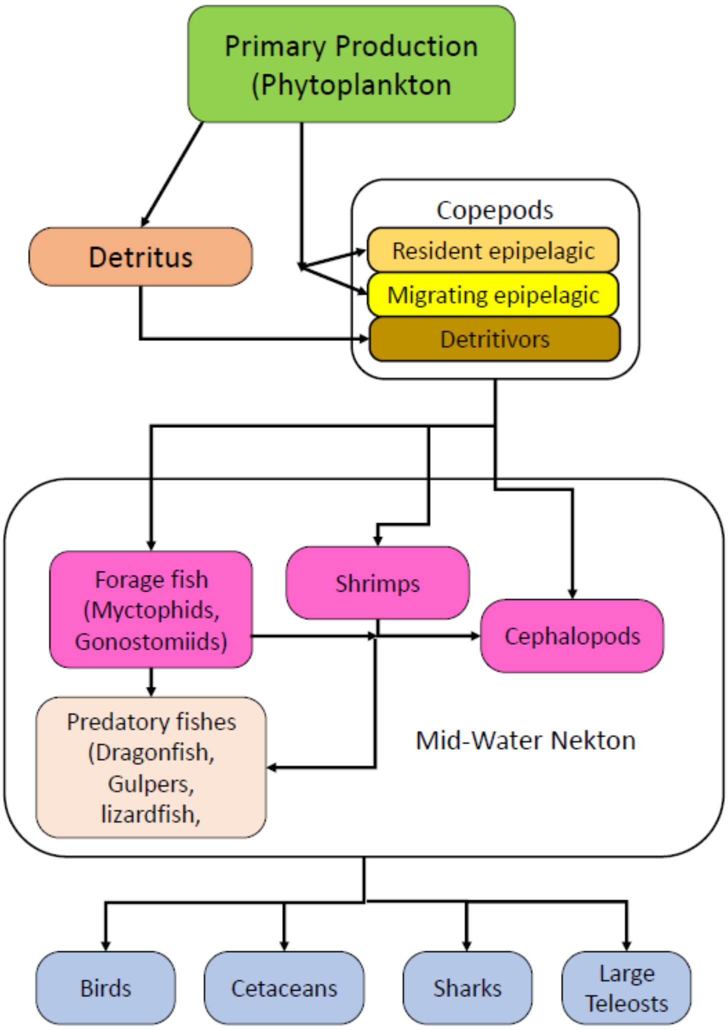

Figure 9.26. A simplified mid-water nekton food web, showing transfer of energy from primary production of phytoplankton. Reproduced from Anderson et al.*, (2019).*

Micromesistius poutassou (Blue whiting) is a mesopelagic gadoid fish that is widely distributed in Northeast Atlantic from the Canary Islands to Spitsbergen, with scattered observations showing that the species occurs along the MAR from the Azores in the South to the Reykjanes Ridge in the North. Where present, *M. poutassou* is often highly abundant, and plays an important role in pelagic ecosystems, both as a consumer of zooplankton and small mesopelagic fishes, and as prey for larger fish and cetaceans (Heino & Godø, 2002).

Deep-sea cephalopods along the MAR have a variety of feeding strategies. The octopus *Japetella diaphana* feeds on euphausiids and copepods, several species of squid are recorded as feeding on copepods including *Abraliopsis* sp., *Histiotuethis corona*, and Pyrotheuthidae. Many species feed on small crustacea such as euphausiids (krill and shrimps) and consumption of fish is important in the Gonatidae, Histiotheuthidae, Ommastrephidae and Onychoteuthidae. Feeding behaviour varies from active predation to 'sit-and-wait' predators that use bioluminescence to lure their prey. The long-armed squids (Chiroteuthidae) for example have long retractable arms with photophores on a club-like ending. The Mastigoteuthidae have whiplash tentacles with minute suckers capable of capturing copepods. The vampire squid has been observed to scavenge off detritus composed of gelatinous plankton, copepods, amphipods and squid. The range of feeding adaptations and strategies in deep-sea cephalopods is only beginning to be understood (Hoving *et al.*, 2014).

In turn, the mid-water cephalopods, such as Ommastrephid squids, octopods, hisoteuthids and architeuthids are important prey items for large pelagic fishes, such as tuna, shark, and billfish species (Logan *et al.,* 2013). Within the Central North Atlantic, mesopelagic fishes and Sargassum-associated fishes were also identified as important prey for these large predators, with diet composition varying spatially and prey size increasing with predator size (Logan *et al.,* 2013).

The mid-water nekton is one of the main mechanisms transferring organic carbon or food energy into the deep-sea where it is utilised within the mid-water food web and by benthic fauna intercepting mid-water animals that impinge on the slopes, including the MAR (Mauchline & Gordon, 1991). Myctophid fishes alone along the MAR, through their diel vertical migrations, can transport up to 8 % of the sinking particulate organic carbon in the North Atlantic (Hudson *et al.,* 2014).

The biomass transferred through the mid-water nekton is so great that even air breathing animals find it worthwhile to descend to great depths to forage. Diving by sperm whales to feed on deep-sea squid is very well documented (Clarke *et al.,* 1993), with stomach contents showing that in the Azores region, squid such as Histioteuthidae are by far the most important prey with significant quantities of Octopoteuthidae, Cyclotheuthidae and Cranchidae. *Mesoplodon bidens* (Sowerby's beaked whale) occurring in the North Atlantic also feeds on cephalopods, although the main dietary component is small mesopelagic and benthopelagic fishes (Pereira *et al.,* 2011; Wenzel *et al.,* 2013). In addition to *M. bidens*, many other species of cetacean occur in the North Atlantic, feeding on fishes and cephalopods within the pelagic environment and potentially interacting with topographic features, such as the MAR. These species include, but are not limited to, *Globicephala melas*, (Long-finned pilot whales), *Grampus griseus* (Risso's dolphins), *Peponocephala electra* (Melon-headed whales), *Ziphius cavirostris* (Cuvier's beaked whales), *Hyperoodon ampullatus* (Northern bottlenose whales), *Physeter macrocephalus* (true sperm whales), *Kogia sima* (Dwarf sperm whales) and *Kogia breviceps* (Pygmy sperm whales) (Spitz *et al.,* 2011). *Ziphius cavirostris* are the deepest-diving animals on the planet, being able to dive to 2992 m deep and stay at depth for up to 137 minutes (Schorr *et al.,* 2014), thus facilitating the transfer of material between different levels of the water column. *Ziphius cavirostris* also exhibit significant diel behavioral variation, presumably to forage at depth, where they are feed on a number of oceanic cephalopod species (Santos *et al.,* 2001). The range of species found in the diet of *Z. cavirostris* is greater than that reported for either sperm whales or bottlenosed whales in the Northeast Atlantic (Santos *et al.,* 2001), suggesting a wider range of food-web connections for this species.

Elucidating deep-sea food-webs in still in the very early stages, with many unknowns, including for the MAR mid-water fauna. Further studies, including *in situ* observation of feeding events from Remotely Operated Vehicles (ROVs) or other submersibles, will be required to develop the understanding of trophic relationships. As databases of undersea imagery become sufficiently large that significant information can be extracted (Choy *et al.,* 2017), underwater imagery may prove an important new source of information on mid-water trophic relationships along the MAR.

9.4 Ecosystem function

Information is scarce on the role of individual species in the ecosystem functions provided by the pelagic fauna. As a result, the ecosystem function of the pelagic as a whole is considered here, without sub-dividing into the different components of the pelagic fauna.

The mid-water zone of the ocean is too deep for photosynthesis and is hence a net consumer of oxygen and producer of carbon dioxide. The mesopelagic zone (200-1000 m depth) occupies a large percentage of the global ocean volume and intercepts approximately 90% of the downward flux of organic carbon from the surface waters before it can be sequestered into the deep-sea sediments. Through interception by the mid-water fauna, this carbon is released in the form of carbon dioxide back into the water column, contributing possibly 30% of total ocean carbon dioxide production (Costello & Breyer, 2017; Robinson *et al*., 2010). An important feature of this in global ecosystem function is the role of daily vertical migration in downward transport of organic carbon through the water column. Studies by Kelly *et al*., (2019) and Anderson *et al*., (2019) indicate the importance of daily vertical migration by plankton but the role that larger nekton remains to be determined.

Irigoien *et al*., (2014) suggest that mesopelagic fishes alone may be responsible for respiring 10% of primary production in the open ocean. This is based on a major upward revision of estimated total global mesopelagic fish biomass, mainly myctophids, which is controversial. Estimating the fish biomass and trophic efficiencies in the relevant food chains remains a major challenge in understanding ecosystem function in the mid-water environment. Very little is known about the specific contributions of MAR mid-water fauna to marine carbon cycling.

Marine mammals are considered important in the transfer of nutrients from deep water to surface water by releasing faecal plumes at the surface, after feeding in deeper waters (ICES, 2019a). Cetaceans can also sequester carbon to the deep sea, with whale falls thought to transfer an estimated 190 000 tonnes of carbon per year from the atmosphere to deeper waters (Pershing *et al.,* 2010). As a result, it has been suggested that declining populations of larger cetaceans, such as some baleen whale species, reduces the potential for marine ecosystems to retain carbon (Pershing *et al.,* 2019). Whilst not yet investigated for the pelagic environment of the MAR, in the Southern Ocean it was demonstrated that baleen whales may also influence biogeochemical cycles by releasing nutrients such as nitrogen through their urine and faeces (Lavery *et al.,* 2010; Nicol *et al.,* 2010). Migration patterns of marine mammals may also move nutrients from highly productive feeding grounds, to (otherwise) relatively unproductive breeding grounds (ICES, 2019a).

9.5 Connectivity

The mid-water environment over the MAR is part of the continuous global mesopelagic and bathypelagic zone and hence there is high connectivity with the surrounding Atlantic Ocean and other regions of the world. One of the simplest measures of connectivity is species distributions, with connectivity between locations being implied if the same species occur in both places. For species distributions to be maintained, there need to be connections between populations in different regions, through the exchange of adults or young; this type of population connectivity is often assessed using genetic markers.

More information is available regarding species distributions of pelagic fauna along the MAR than population connectivity, with genetic analyses only available for a few species. This section discusses the information available on connectivity of mid-water fauna along the northern MAR, with a focus on the mid-water nekton, alongside some examples from the air-breathing fauna.

9.5.1 Mid-water nekton

Many of the mid-water nekton species that occur along the MAR are also found in other regions, with some being considered circumglobal. Briggs (1960) first published a checklist of circumglobal fishes occurring in all three major ocean basins at low latitudes and found only 107 species, a miniscule proportion of the global fish fauna. Gaither *et al*., (2016) updated this to 284 circumglobal species. Examining the species list in Table 9.1 of mid-water fishes occurring on the MAR we find that 72 of the 229 species recorded by Sutton *et al*., (2008) are listed by Gaither *et al.,* (2016) as circumglobal. This means that 31% of the fishes found over the MAR are circumglobal (Table 9.7).

Amongst the shrimps (Table 9.3) 40 out of 64 species listed (62%) occur in more than one major ocean. These numbers are indicative of the remarkably high connectivity found in deep-sea pelagic environments and how the northern MAR is linked to global oceanic ecosystem. There are caveats, discussed by Gaither *et al*., (2016), as to the amount of gene flow between different ocean regions and whether there are subspecies or cryptic speciation. Nevertheless, by this index of connectivity, mid-water species are much better connected than bathyal demersal species (Priede *et al*., 2017).

An alternative approach to connectivity, is to consider the transfer of material or trophic resources between the ecosystem and contiguous systems. Zuercher & Galloway (2019) consider the relationship between the pelagic ocean and kelp forests and invoke the concept of trophic subsidies that originate in one ecosystem and are moved to another. They define a subsidised ecosystem as "*a geographic area whose boundaries do not encompass the entire area of production that supports it*". Under this definition, the mid-water ecosystem is a subsidised system since it is entirely dependent on import of material from the overlying photic zone mediated by daily vertical migration as discussed previously.

The pelagic environment is unbounded; animals can freely move horizontally across the MAR virtually unimpeded, and the MAR system exchanges nekton, eggs and larval stages with the surrounding ocean. In practice, there are biogeographic limits delineated by different water masses and thermal optima, which shape the regional distribution of these species, as discussed in section 9.1 Regional Distribution. Given the vastness of the mid-water environment and general lack of information regarding its fauna, measuring population connectivity through genetic markers may not be possible for the majority of species. Species distribution information may facilitate an initial view of connectivity for the mid-water fauna.

Table 9.7. Circumglobal mid-water fishes of the northern Mid-Atlantic Ridge. Based on data from Gaither et al.*, (2016) and Sutton* et al.*, (2008).*

Order	Family	Species
Anguilliformes	Derichthyidae (longneck eels)	*Derichthys serpentinus*
	Nemichthyidae (snipe eels)	*Nemichthys scolopaceus*
Saccopharyngiform	Eurypharyngidae (gulper eels)	*Eurypharynx pelecanoides*
Argentiniformes	Microstomatidae (pencil smelts)	*Melanolagus bericoides, Microstoma microstoma*
	Platytroctidae (tubeshoulders)	*Maulisia mauli*
	Alepocephalidae (slickheads)	*Bajacalifornia megalops, Photostylus pycnopterus, Rouleina attrita*
Stomiiformes	Gonostomatidae (bristlemouths)	*Cyclothone microdon, Sigmops bathyphilum, Sigmops elongatus, Cyclothone braueri, Cyclothone pallida, Cyclothone pseudopallida*
	Sternoptychidae (hatchetfish & pearlsides)	*Argyropelecus hemigymnus, Argyropelecus aculeatus, Argyropelecus olfersii, Sternoptyx pseudobscura, Valenciennellus tripunctulatus* *Argyropelecus gigas*
	Phosichthyidae (lightfishes)	*Ichthyococcus ovatus*
	Stomiidae (barbeled dragonfishes)	*Chauliodus sloani, Stomias boa ferox, Pachystomias microdon, Aristostomias tittmanni, Photonectes margarita*
Aulopiformes	Paralepididae (barracudinas)	*Arctozenus risso*
Myctophiformes	Myctophidae (lantern fishes)	*Benthosema suborbital, Ceratoscopelus warmingii, Diaphus effulgens, Diaphus mollis, Diogenichthys atlanticus, Electrona risso, Hygophum hygomii, Hygophum reinhardtii, Lampadena chavesi, Lampadena speculigera, Lampanyctus festivus, Lampanyctus pusillus, Lobianchia dofleini, Lobianchia gemellarii, Loweina interrupta, Notolychnus valdiviae, Taaningichthys bathyphilus*
Gadiformes	Moridae (deep-sea cods)	*Halargyreus johnsonii*
	Melanonidae (pelagic cods)	*Melanonus zugmayeri*
Lophiiformes	Melanocetidae (black sea devils)	*Melanocetus johnsonii*

(anglerfishes)	Oneirodidae (dreamers)	*Chaenophryne draco, Dolopichthys longicornis, Microlophichthys microlophus*
	Ceratiidae (seadevils)	*Ceratias holboelli, Cryptopsaras couesii*
	Gigantactinidae (whipnose anglers)	*Gigantactis vanhoeffeni*
Stephanoberyciformes	Melamphaidae (bigscale fishes)	*Scopeloberyx opisthopterus*
	Rondeletiidae (redmouth whalefishes)	*Rondeletia loricata*
	Cetomimidae (flabby whalefishes)	*Cetostoma regani*
Beryciformes	Anoplogastridae (fangtooth)	*Anoplogaster cornuta*
	Diretmidae (spinyfins)	*Diretmus argenteus*
Perciformes	Chiasmodontidae (swallowers)	*Pseudoscopelus altipinnis, Kali indica*
	Gempylidae (snake mackerels)	*Diplospinus multistriatus*
	Tetragonuridae (squaretails)	*Tetragonurus cuvieri*

9.5.2 Air-breathing fauna

Connectivity of the air-breathing fauna can be considered and respectively measured in multiple ways. Many of the air-breathing species utilising the pelagic environment over the MAR are migratory, and depend upon critical habitats for breeding and foraging, as well as the migratory corridors or pathways connecting these habitats (Dunn & Harrison *et al.,* 2019). According to Dunn & Harrison *et al.,* (2019), many of the migratory species recorded in the pelagic environment of the MAR will exhibit at least one of the three forms of connectivity described by Webster *et al.,* (2002):

- Migratory connectivity: the seasonal movement of individuals between breeding and post-breeding foraging sites;
- Seascape connectivity: the regional movement of individuals amongst habitat patches;
- Natal dispersal: the spread of individuals from birth sites to breeding sites.

Migratory species, both at an individual and population level, encounter a variety of stressors, both natural and anthropogenic (Halpern *et al.,* 2008; Maxwell *et al.,* 2013). Migratory connectivity, defined as the geographical linking of individuals and populations through their migratory cycles (Marra *et al.,* 2006) will affect how natural and anthropogenic stressors impact both individuals and populations. In the case of individuals, migratory connectivity will influence how stressors impact at each crucial life-history stage. Migratory connectivity will subsequently influence how effects at the individual level may scale up to effects on population abundance and distribution, and ultimately species persistence (Dunn & Harrison *et al.,* 2019). Understanding how populations are connected and how connectivity influences demographic rates is an important prerequisite to designing effective environmental management measures for the conservation and sustainable use of migratory species.

It is beyond the scope of this document to review the connectivity of all the migratory air-breathing species which have been recorded in the pelagic environment overlying the MAR. However, to illustrate the importance of connectivity for the air-breathing fauna, two example species are considered in detail below, *Calonectris borealis* (Cory’s shearwater) and *Megaptera novaeangliae* (Humpback whales).

9.5.2.1 Calonectris borealis *(Cory’s shearwater)*

Calonectris borealis (Cory’s shearwater) is an elusive species of nocturnal seabird that nests in underground burrows and on remote islands in the Mediterranean and eastern Atlantic. During their breeding season, the seabirds remain close to the colony to feed and care for their chicks. However, once the chicks are independent, the adults migrate thousands of kilometres across the ocean to warmer climates to feed during the winter. Some individuals return to the same winter foraging sites each year, others shift their wintering destinations from year to year.

The information for two populations of *C. borealis* (Selvagens and Berlagens) has been aggregated in the Migratory Connectivity in the Ocean (MiCO) System[5] (Dunn & Harrison *et al.,* 2019) based on existing data (Dias *et al.,* 2011; Dias *et al.,* 2013; Catry *et al.,* 2013). These two populations of *C. borealis* have up to six overwintering grounds (Dias *et al.,* 2011) including: The Southwest Atlantic off of Brazil, the Northwest Atlantic, off of Northwest Africa, the Southeast Atlantic, and around South Africa into the Southwest Indian Ocean (Figure 9.27, Panel C). The outbound and inbound migration routes to the Northwest Atlantic overwintering ground overlap the MAR, but in different locations (Figure 9.27, Panels A & B). On the outward journey (Figure 9.27, Panel A) *C. borealis* generally travel North of the Azores in October and November and interact with the MAR between 37°N and 50°N. *Calonectris borealis* overwinter in the Northwest Atlantic, just West of the Azores EEZ and the MAR, between October and February. On the return migration (January – February), individuals travel South of the Azores and cross the MAR between 30°N and 40°N. Only individuals from Selvagens have been tracked overwintering in the Northwest Atlantic, although birds from both colonies use the area as a staging ground.

The migratory connectivity generated by these populations means that any impacts resulting from activities in the Northwest Atlantic could be felt 1000s of kilometres away in overwintering grounds off of Brazil or South Africa. The same principle would apply to many other seabird species in the North Atlantic including, but not limited to: *Sterna paradisaea* (Arctic tern), *Puffinus puffinus* (Manx shearwater), *Catharacta maccormicki* (South polar skua), *Stercorarius longicaudus* (Long-tailed jaeger), *Catharacta skua* (Great skua), *Oceanodroma leucorhoa* (Leach's storm-petrel), *Fulmarus glacialis* (Northern fulmar), *Morus bassanus* (Northern gannet), *Pterodroma madeira* (Zino's petrel), *Pterodroma deserta* (Desertas petrel), *Pterodroma cahow* (Bermuda petrel), *Pterodroma hasitata* (Black-capped petrel), *Pterodroma feae* (Cabo Verde/Fea's petrel), *Pterodroma arminjoniana* (Trinidade petrel), *Pterodroma incerta* (Atlantic petrel), *Pterodroma mollis* (Soft-plumaged petrel), *Bulweria bulwerii* (Bulwer's petrel), *Xema sabini* (Sabine's gull), *Uria aalge* (Common murre), *Uria lomvia* (thick-billed murre), *Alle alle* (Little auk), and *Alca torda* (Razorbill).

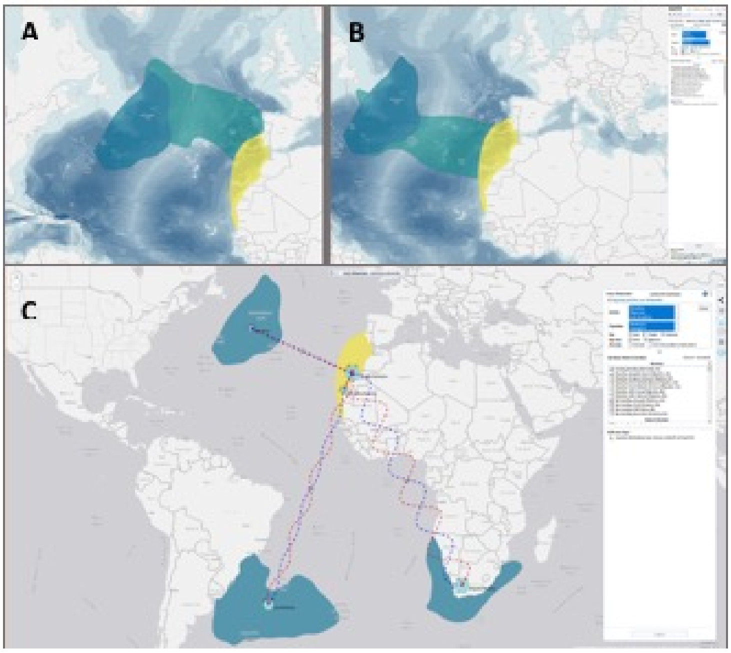

Figure 9.27. Migratory information for two populations of Calonectris borealis *(Cory's shearwater: Selvagens and Berlagens populations) as aggregated in the Migratory Connectivity in the Ocean (MiCO) System*[6]

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[5] Migratory Connectivity in the Ocean (MiCO) System: https:/mico.eco/system

[6] Migratory Connectivity in the Ocean (MiCO) System: https:/mico.eco/system

(Reproduced from Dunn et al.*, 2019). Panels A & B: outbound and inbound migration routes; Panel C: overwintering grounds.*

9.5.2.2 Megaptera novaeangliae *(Humpback whale)*

Megaptera novaeangliae (Humpback whales) undertake extensive migrations on an annual basis; understanding this migratory connectivity requires knowledge of the population structure of *M. novaeangliae* within a region. *Megaptera novaeangliae* in the North Atlantic have traditionally been thought to be one population, breeding in the Caribbean and dispersing to four northern foraging areas (the Northeast United States, Nova Scotia/Newfoundland, Greenland, Iceland and Norway) in the summer months (Figure 9.28), although the connection to Norway was only identified detailed recently (Stevick *et al*., 2018). Tracking studies describe highly directed migration routes toward these breeding and foraging destinations (Kennedy *et al.,* 2014).

However, the migrations described in Figure 9.29, are temporally offset and there is mounting evidence that the breeding population in the southeastern Caribbean may be separate. *Megaptera novaeangliae* on Silver and Navidad Banks in the Dominican Republic arrive in early January and return North by early April (Whitehead, 1982). This contrasts with the southeastern Caribbean where few *M. novaeangliae* are seen before February, and densities peak in March and April, declining rapidly until no individuals are present by July (Stevick *et al.,* 2018). Alongside the disparity in migration timing are strong differences in scarring of *M. novaeangliae* individuals from interaction with killer whales, which typically happens in Norway and Iceland (Stevick *et al.,* 2018). The quantity of scarring and other evidence strongly suggests that *M. novaeangliae* from Norway are disproportionately represented in the southeastern Caribbean breeding ground (Figure 9.29), indicating strong differences in the distribution of where *M. novaeangliae* are arriving from, when comparing *M. novaeangliae* occurring in the Dominican Republic to those observed in the southeastern Caribbean. The potential for two populations to exist in the North Atlantic, with each population having different migratory connectivity, has important management and conservation implications, not the least of which is a need to understand population trends at a finer resolution.

The potential for the occurrence of two North Atlantic *M. novaeangliae* populations may also have implications for activities along the MAR, as *M. novaeangliae* migrating towards the southeastern Caribbean interact with the MAR, whereas individuals migrating towards Silver Bank from the Northeast US or Canada do not. Some individuals travelling from the southeastern Caribbean heading North also travel straight to Cabo Verde before continuing North, which would bring them into contact with the MAR. If these two potential North Atlantic populations of *M. novaeangliae* do not mix, then the smaller southeastern Caribbean population, some of which interacts with the MAR during migration, may be more vulnerable than the larger Silver Banks population.

Megaptera novaeangliae globally and in Northeast Atlantic Ocean are listed as least concern by the IUCN and their populations are growing (IUCN, 2017), although many States have stringent national laws to protect this species.

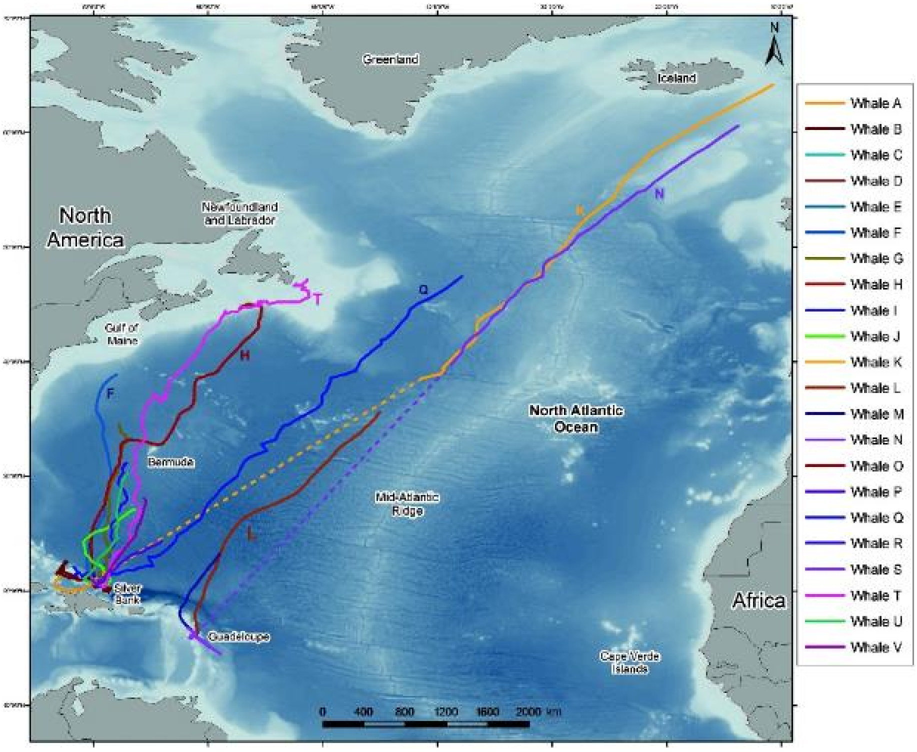

Figure 9.28. Movement of 22 tracked M. novaeangliae. Track locations were estimated at 12 h intervals using a Bayesian switching state–space model (SSSM). Broken lines indicate distance between tagging location and first transmission. Some longer tracks are labelled for clarity. Reproduced with permission from Kennedy et al.*, (2014).*

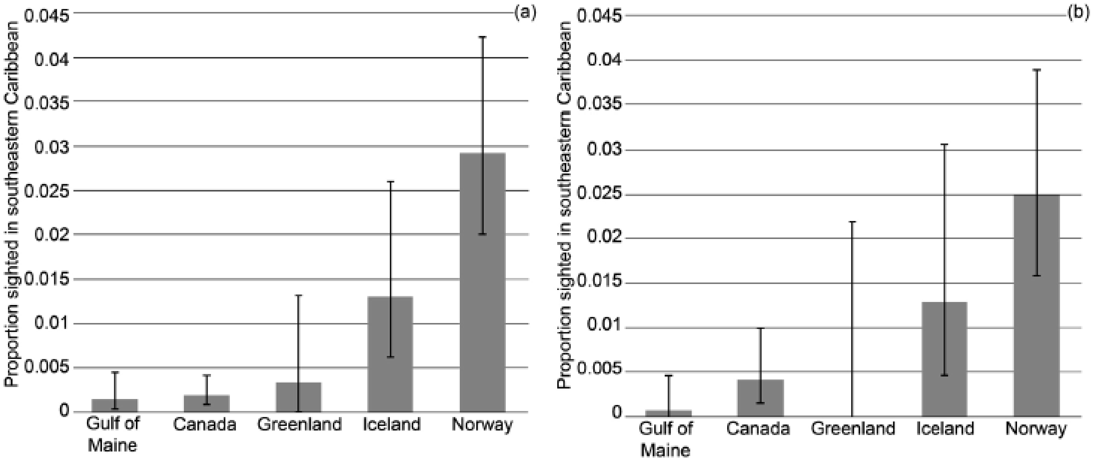

Figure 9.29. The proportion of Megaptera novaeangliae *(Humpback whales) (with 95% Confidence Intervals) from each of the high latitude feeding areas that also have been sighted in the southeastern Caribbean. Left: all individuals identified in the high latitude feeding areas; Right: only those records from the high latitude feeding areas that are more recent than year 2000. Adapted from Stevick* et al.*, (2018).*

9.6 Resilience and recovery

Resilience in marine ecosystems refers to persistence of a system in the face of catastrophes or external changes through two mechanisms resistance and recovery. Resistance is the ability of components of the system to survive stress and recovery, whilst recovery is the ability of the system to regrow or replace itself after varying degrees of destruction (O'Leary *et al*., 2017).

There have not been any studies to date assessing the ability of northern MAR pelagic fauna to either resist or recover from environmental stressors resulting from deep-sea mining. To date, most studies on the resilience of marine organisms have focussed on static entities, such as coral reefs (Darling & Côté, 2018). In this section, the principles of resistance and recovery as expressed by O'Leary *et al.,* (2017) are considered for a few of the biological components within the mid-water nekton (small fishes, shrimp and cephalopods). These are high-level, generalised considerations and do not attempt to take the place of detailed, site-specific risk assessments to determine the resilience of pelagic fauna to any future mining operations. It is beyond the scope of this document to address the potential resilience and recovery of other components of the mid-water fauna, such as sharks, commercially important fishes, and air-breathing animals, such as seabirds, sea turtles and cetaceans, all of which are expected to exhibit different resilience. Future versions of this document may consider the resilience and recovery of these biological components in more detail.

9.6.1 Mid-water nekton

Resilience and stability have not been formally assessed for the northern MAR mid-water nekton. However, they have been considered for other oceans, such as the Southern California Current System which is the best-sampled pelagic ecosystem in the world with 60 years of annual sampling. Lindegren *et al*., (2016) considered the resilience and stability of the Southern California Current System by examining functional changes in relation to the El Nino southern oscillation (ENSO), Pacific decadal oscillation (PDO) and North Pacific Gyre Oscillation. Lindegren *et al*., (2016) show that functional complementarity, adaptive prey preference and omnivory all contribute to increased food-web stability. This study does not consider the deep pelagic food-web, but these results suggest that functional complementarity, adaptive prey preference and omnivory in the mid-water nekton may increase stability in the northern MAR mid-water food-web and so promote resilience.

Six factors were considered by O'Leary *et al.,* (2017) to promote resilience: recruitment or connectivity; remaining biogenic habitat; functional diversity; genetic diversity; species interactions; and remoteness. These factors are considered for mid-water nekton in Table 9.8. This cursory analysis suggests that the mid-water nekton of the MAR should show high resilience to disturbance in general, however analysis of resilience in pelagic systems is at very early stages, data are generally deficient, and studies specific to the MAR mid-water nekton have not been attempted. It should also be noted that the deep-sea environment generally exhibits great stability in terms of temperature and salinity and that deep-sea fauna may be unable to adapt to major global stressors such as ocean acidification, global warming or deoxygenation. Deep-sea mining could potentially act as an additional stressor, with the potential that mid-water nekton in deeper portions of the water column may have a lower resilience to such cumulative impacts but see Chapter 7.0 Cumulative Impacts.

Table 9.8. Potential resilience of the Mid-Atlantic Ridge mid-water nekton to disturbance

Factor contributing to resilience	**Status for mid-water nekton**
Recruitment or connectivity	Connectivity is very high in the mid-water nekton. The age to first maturity in the main species (for example 3 years in myctophids) is generally low so population intrinsic growth rate can be high.
Remaining biogenic habitat	The mid-water habitat is the largest biological habitat in the world, although biogeographic

	boundaries occur as a result of different water masses. Extensive habitat availability would confer high resilience.
Functional diversity	Analysis of the fauna shows high species diversity with corresponding high functional diversity. For example, 44 different species of myctophid each have different functional characteristics, implying low functional redundancy.
Genetic diversity	Insufficient information is available for mid-water nekton.
Species interactions	Mid-water nekton typically have a complex web of species interactions.
Remoteness	Large areas of the northern Mid-Atlantic Ridge have little anthropogenic disturbance.

Although the mid-water nekton may appear to have high resilience to disturbance as a whole, different species could have different levels of resilience and individual impairment or mortality as a result of deep-sea mining activities may still be high. Over the MAR, a large proportion of the mid-water abundance and biomass is concentrated within 200 m vertical height above the sea floor (Sutton *et al.*, 2008), which would result in disproportionate exposure of the mid-water fauna to near-floor mining activity.

Some of the mid-water fauna may not have adaptations to cope with the anticipated mining impacts, such as generation of sediment plumes. For example, shallow water and bottom-living fishes have a coughing reflex which enables them to reverse water flow over the gills to clear them of particulate material (Hughes & Adeney, 1977). Mid-water fishes do not naturally encounter high concentrations of suspended particulate matter and have no coughing ability, making them vulnerable to damage to their respiratory system by suspended particulate matter. Suspended particulate matter from mining activities, if it is released in the mid-water, may have the effect of attenuating the intensity of downwelling light (sunlight, moonlight, starlight) in the ocean. Mid-water animals use this light as a cue for their behaviour as they seek to remain at the depth of their ‘Light Comfort Zone’ (Langbehn *et al.,* 2019). If this occurred, then some mid-water animals could be expected to modify their behaviour by swimming much nearer the surface than they would naturally, which would bring them within the range of surface-dwelling predators. If these plumes have a toxic component, as toxins dissolved in seawater or carried on fine particulate matter, then mid-water fauna may absorb these through their gills, skin or via ingestion.

Mid-water fishes are also known to be very sensitive to the light and noise of ships, particularly at night (Peña, 2019), which may lead to avoidance behaviour. Mid-water fishes also demonstrate avoidance behaviours to towed equipment in the water column (Kaartvedt *et al.,* 2012), and may attempt to avoid Remotely Operated Vehicles, sampling equipment, or the mining vehicles themselves. Despite attempted avoidance behaviours it is likely that some mid-water nekton may be sucked through thrusters and seawater pumping systems, resulting in mortality.

In summary, whilst the mid-water nekton may appear to have high resilience generally, the resilience of the northern MAR mid-water nekton to deep-sea mining impacts is unknown. More information would be needed on the nature and extent of deep-sea mining impacts along the MAR, and the biology of the mid-water nekton, to conduct a robust assessment of the resilience of this fauna.

10. Benthic Biology

The benthic environment of the northern Mid-Atlantic Ridge (MAR) is a complex patchwork of habitats spanning thousands of metres depth range and encompassing varied seabed geomorphologies. The MAR incorporates not only the rocky ridge, but also rift valleys, fracture zones, seamounts, underwater volcanoes, hydrothermal vents, sedimented slopes, sedimented plains and oceanic core complexes (Harris *et al.,* 2014). The ridge itself has an active spreading centre, with a pronounced central rift valley, whilst the flanks of the MAR are made up of mainly (> 95 %) gentle slopes and discontinuous flat plains, which are largely sedimented. The flat plains are generally aligned parallel with the axis of the ridge (Priede *et al*., 2013a). Steep (mainly hard substrate) slopes comprise only about 5 % of the area (Niedzielski *et al*., 2013), although in the context of a largely sedimented Atlantic Ocean basin, the MAR provides a large proportion of hard substrata habitat.

The MAR is a slow spreading ridge system, and the active volcanism associated with spreading centres along the MAR has created a series of hydrothermal vent sites. The hydrothermal activity at these sites and resulting precipitation of sulphide minerals has formed hard substrate sulphide habitat, and in some places, metal-rich sediments. In some locations, sulphide habitat remains hydrothermally active, whilst in other locations, hydrothermal activity has ceased rendering the sulphides hydrothermally inactive. Hard sulphide substrata (both hydrothermally active and inactive) can also be buried by sediment, and in the case of continued hydrothermal activity, hydrothermally active sediment habitat may occur. As well as the seafloor itself, the water column immediately above the seafloor (here only 50 m above seabed is considered) provides important habitat for a range of organisms who are generally more mobile than the species found inhabiting the seafloor. Although not considered in detail within this document, buoyant and neutrally buoyant hydrothermal plumes are also habitat for microorganisms and some consumers, acting as a link between the benthic and pelagic environments.

The diverse range of benthic habitats along the MAR can be broadly grouped into four types: 1) hydrothermal hard substrata habitat (subdivided into hydrothermally active and inactive sulphide habitat); 2) exposed non-sulphide hard substrate (such as basalt); 3) soft sediment (including pelagic sediment and hydrothermally active sediment); and 4) the water column 50 m above the seafloor (benthopelagic). These broad habitat groups are not necessarily all-encompassing but form the structure for the Biology section. The divisions between these four broad habitat types can also be unclear, and it is important to consider that deep-sea benthic habitats are dynamically connected over a range of spatial scales through dispersal processes and interactions with the pelagic ecosystem (Snelgrove, 2010).

Distinguishing between exposed hard substrate (either sulphide or non-sulphide) and soft sediment habitat is generally straightforward, although there are locations where a thin layer of sediment can overlay hard substrata, supporting an apparent mix of biological communities. The distinction between pelagic sediment and hydrothermally active sediment habitat is generally clear, with visual differences in surface sediment colouration reflecting differences in chemical composition. In some areas, hydrothermal fluids can escape through cracks in basalt or amongst pillow lava, meaning that hydrothermal vent communities can occur on both hydrothermally active sulphide habitat and hydrothermally-influenced non-sulphide hard substrata. The distinction between active and inactive sulphide habitat is often less clear, as hydrothermal activity in an area can change over multiple time scales, rendering active sulphide habitat inactive, and inactive sulphide habitat active (Van Dover, 2019). In some locations, active and inactive sulphide habitats can occur in close proximity; there can also be activity gradients across sulphide habitat, with the boundary between active and inactive being sometimes unclear. Distinguishing between active and inactive sulphide habitat can be challenging, but is essential, because active and inactive habitats support very different biological communities, which are ultimately expected to demonstrate different resilience and recovery potential to future mining impacts.

The need to distinguish between hydrothermally active and inactive sulphide habitat is reflected in Recommendations issued by the Legal and Technical Commission (LTC) of the International Seabed Authority (ISA) (ISBA/25/LTC/6), which recommends that as part of the baseline environmental assessment, hydrothermal vent areas (often active sulphide habitat, but also on occasion basalt bathed in hydrothermal fluid) should be classified as either active vent sites or inactive/extinct sites. This document identifies three hydrothermal activity scenarios which vent areas should be attributed to: case 1 – active hydrothermal vents; case 2 – inactive vents that may restart due to mining activity; case 3 – extinct vents that will remain hydrothermally inactive even when disturbed by test-mining. The same document also goes on to define what is meant by 'active' and 'inactive'[1]. For the purpose of the Regional Environmental Assessment, reference to active, inactive and extinct sulphide or hydrothermally influenced basalt habitat will be in the context of the definitions within ISBA/25/LTC/6, acknowledging the complex nature of hydrothermal activity of sulphide habitats discussed by Van Dover (2019).

Different biological communities will occur at hydrothermal habitat (active and inactive); exposed non-hydrothermal hard substrate; soft sediment; and the water column 50 m above the seafloor, which will be important to consider in the context of regional environmental planning. This section of the REA brings together the available information on the regional distribution, temporal variability, ecosystem function, connectivity, and resilience and recovery of each of these broad benthic habitat types, and their respective biological components. Some of these habitats are better characterised than others, with studies along the MAR historically focussing on active vents or seamounts. More recent campaigns have focussed on the largely sedimented ridge flanks and other habitats (Census of Marine Life MAR-ECO: Bergstad *et al.*, 2008 and Bergstad & Gebruk, 2008; UK-led ECOMAR: Priede *et al.* 2013b). Ongoing underwater surveys within the ongoing European Union Horizon 2020 ATLAS[2] and SponGES[3] projects are revealing important aspects of the benthic communities inhabiting different habitats of the northern MAR, highlighting the biological diversity and ecological importance of the MAR. A common finding of many of these studies is the high heterogeneity of habitats along the MAR. Many of these studies also consider biodiversity to be greatly underestimated as a result of under-sampling.

The lower water column (50 m above bottom, also known as the benthopelagic environment), provides an important connection between the benthic and pelagic biota, although very little is known about the benthopelagic biota. Aas this habitat connects the benthic and mid-water environments, it is likely that the benthopelagic biota will be a mix of taxa found from these environments. It is not clear if there are taxa who are truly restricted to this habitat, *i.e.* spend their entire lives in the benthopelagic. Mobile benthic invertebrates, especially those that can swim, may spend prolonged periods in the benthopelagic and use the currents in the Benthic Boundary Layer (BBL) to move to new areas, either to find food or to escape predators.
Some micronekton species occur only in the BBL, but others may descend to the sediment surface to feed (Miller & Pawson, 1990; Rogacheva *et al.,* 2019). Swimming holothurians are generally found drifting in the water column just above the seabed, although they do need to descend periodically to feed at the sediment surface (Barnes *et al*., 1976; Billett *et al.*, 1985; Miller & Pawson, 1990; Rogacheva *et al.,* 2012). In some locations of the northern MAR deep pelagic fish abundance peaks within the

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[1] *ISBA/25/LTC/6*: Definitions of active and inactive sulphides.

Active sulphides: Polymetallic sulphides through which warm or hot water is flowing. Active sulphides (also called hydrothermal vents) deliver reduced compounds (e.g. sulphide) to the sea floor-seawater interface where they can be oxidized or otherwise autotrophically metabolized by free-living or symbiotic organisms.

Inactive (or dormant) sulphides: Polymetallic sulphides through which warm water is no longer flowing into the overlying seawater (i.e. they are "cold"). Disturbance of these sulphides may result in renewal of hydrothermal fluxes into the water column, turning inactive sulphides into active sulphides (hence the concept of "dormant" sulphides).

[2] A transatlantic assessment and deep-water ecosystem-based spatial management plan for Europe (EU-ATLAS Project): https://www.eu-atlas.org/

[3] Deep-sea sponge grounds ecosystems of the North Atlantic (SponGES): http://www.deepseasponges.org/

BBL, suggesting predator-prey relationships between demersal fish and migrating pelagic fish as a mechanism underlying enhanced demersal fish biomass over the MAR (Sutton *et al.,* 2008; Bergstad *et al.,* 2008).

Vertical migration of zooplankton within the water column overlying the MAR may bring some of these zooplankton into the benthopelagic environment. Appendicularian zooplankton were observed in slightly higher abundance within the BBL over the MAR compared to the deep-overlying water column (Craig *et al.,* 2015). Some of the benthopelagic micronekton also have the capacity, through migrations, to link the seabed environment with higher levels within the water column (Billett *et al*., 1985; Angel, 1990; Roe *et al*., 1990). The abundance of zooplankton in deep-water BBLs is regulated by a number of complex factors, including current flow patterns, particle resuspension, trophic dynamics, geomorphology, hydrodynamic conditions, the quality of organic particles reaching the seafloor and community composition. These combine to create site and season specific conditions for benthopelagic organisms (Craig *et al.,* 2015).

The Benthic environment section of this Regional Environmental Assessment (REA) focuses on the seabed beyond national jurisdiction (the Area) from South of the Iceland Extended Continental Shelf (ECS) Submission to the Romanche Fracture Zone near the equator. However, the biota found in this area is probably not constrained by jurisdictional boundaries. Understanding the benthic environment, especially the regional distribution and connectivity of benthic biota on the MAR, may require reference to similar habitat in the broader region, which is provided where appropriate in the text. In general, very little published information is available for the Benthic environment being described within the geographic extent of the REA. To try to address this, where appropriate the document refers to occurrences of the same habitat in adjacent sections of the ridge, or other occurrences within the region, to provide a regional context for the biota within the area of interest.

10.1 Regional distribution

Models of the regional distribution of benthic fauna along the MAR are intimately linked to the physical and chemical oceanography, and seafloor bathymetry, of the MAR (see Chapter 6: Physical Oceanography). In particular, water depth is a well-established environmental driver of benthic faunal distributions. Depth is often considered a proxy for other environmental gradients which correlate with water depth, such as temperature, pressure, and food availability. Different benthic species have different physiological tolerances to these gradients, resulting in changes in faunal composition with depth. Major changes occur in the composition of the deep-sea benthic fauna on continental slopes with increasing depth (Billett, 1991; Carney, 2005) and similar zonation also occurs on the northern MAR (Alt *et al.,* 2013). The majority of the MAR lies within the lower bathyal (800 – 3500 m depth: Watling *et al.,* 2013; Niedzielski *et al.,* 2013), with large portions of the continental slopes and some seamounts also featuring benthic habitat within this depth range (Figure 10.1). The MAR lower bathyal habitat has been considered both part of the Northern Atlantic Boreal and North Atlantic GOODS lower bathyal provinces (Watling *et al.,* 2013) and as its own province, the Extended Mid-Atlantic Ridge Lower Bathyal Province (EMARLBP: Niedzielski *et al.,* 2013).

Where locations along the MAR are of a similar depth to the continental slope or seamounts in the region, there is the potential that some species could be shared between these seabed areas. In this context, studies on the benthic biota on the continental slopes to either side of the MAR, and seamounts to the south of Reykjanes Ridge, may be pertinent to the wider biogeography of the MAR.

Based on survey data, the Charlie-Gibbs Fracture Zone between 51° N and 53° N is considered a biogeographic boundary for multiple benthic faunal groups at both soft sediment and non-hydrothermal hard substrata habitats (Gebruk *et al.,* 2010). Trawls taken during the MAR-ECO Project, North of the Azores (42° N) and in two areas around the CGFZ (51° N and 53° N) at depths 1237 – 3527 m, revealed differences in fauna between stations from the CGFZ and the Azores regions (Gebruk *et al.,* 2010). Benthic fauna from the Azores was different to benthic fauna from the CGFZ, and within the CGFZ, the taxonomic structure was different in benthic samples from 1263 – 1916 m depth and in samples from 23350 – 3512 m depth. This biogeographic boundary was thought to relate to both seabed depth and the presence of the Sub-Polar Front, rather than to the physical structure of the fracture zone itself (Gebruk *et al.,* 2010). Similar faunal changes related to depth, and zonation within the bathyal zone, have also been noted for holothurians, asteroids and bivalves on continental margins (Billett, 1991; Howell *et al.*, 2002; Olabarria, 2005).

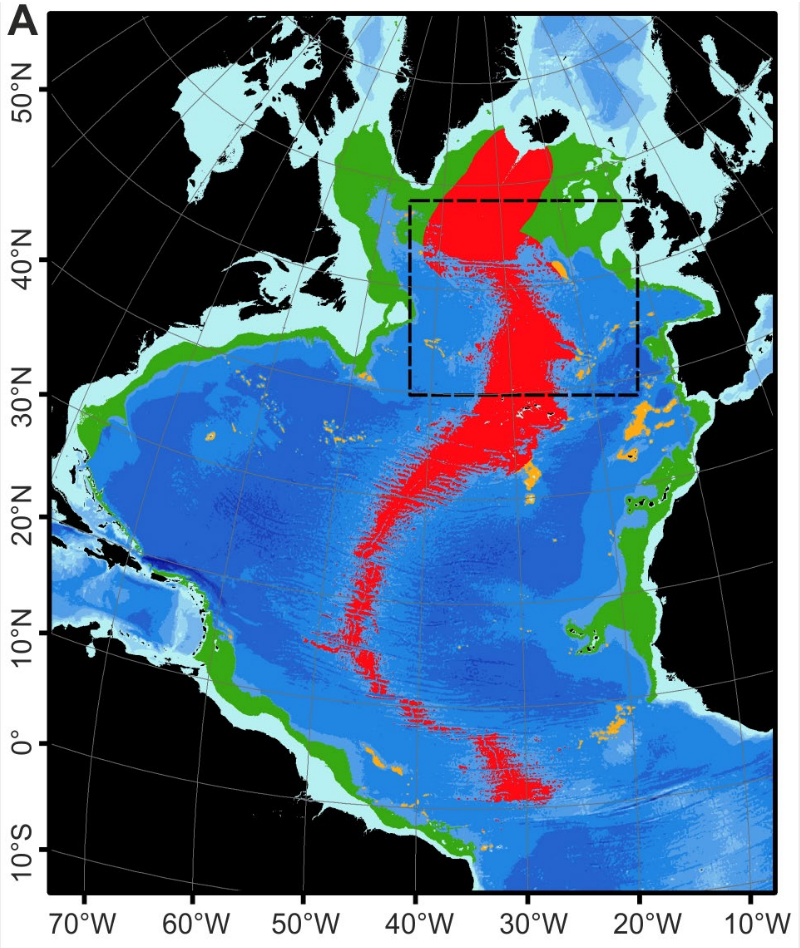

Figure 10.1. Bathymetry map of the North Atlantic Ocean, based on the GEBCO 30° grid, showing the extent of the lower bathyal (depth 800 – 3500 m) area on the Mid-Atlantic Ridge (red), the ocean margins (green) and seamounts (orange). The area in red corresponds to the Extended Mid-Atlantic Ridge Lower Bathyal Province (EMARLBP). Reproduced from Priede et al. *(2013a)*

Not all faunal groups are restricted to just one of the four broad habitat types considered here. For example, mobile scavengers, such as hermit crabs, are also likely to occur within multiple habitat types along the MAR and may exhibit widespread distributions. For example, the hermit crab species *Parapagurus abyssorum, Parapagurus nudus* and *Parapagurus pilosimanus* were reported in the South Atlantic MAR but are also known to occur in deep areas of the North Atlantic (Perez *et al.,* 2012). These three hermit crabs live in gastropod shells with anthozoans (Actiniaria) attached to the hermit crabs' gastropod shell. *Parapagurus nudus* was also one of the most abundant crustaceans collected in benthic samples within the Russian Exploration Area along the northern MAR (Galkin *et al.,* 2019).

Certain rhodaliid (semi)benthic siphonophores (sea dandelions) can anchor themselves to a variety of substrata with their long tentacles, and are also found on both hard substrate and soft sediments. Two different rhodaliids were observed on the northern MAR at 3500 m in the outer zone of hydrothermal vent habitats, where there is no hydrogen sulphide in the water (Mapstone *et al.*, 2017, Figure 10.2). Rhodaliids generally occur individually but have been found in groupings of up to 11 m^{-2}. Only a few rhodaliid species are known from the Atlantic Ocean, all previously recorded from continental margin settings.

Figure 10.2. Morpho-species of rhodaliid from the Mid-Atlantic Ridge in the vicinity of hydrothermal vent fields. Left: Orange rhodaliid from Snake Pit, Mid-Atlantic Ridge. Right: White rhodaliid from TAG vent. Reproduced with permission: © Ifremer, Bicose (2014).

Where possible, information on the apparent endemicity of species is provided. However, it is beyond the scope of this version of the document to provide an exhaustive account of endemicity of all species. Providing a robust view of endemicity is particularly challenging, given that some parts of the MAR have higher spatial and temporal survey resolution than others. This means that if a species has not yet been recorded from a site, it may reflect differences in sampling effort and may not be a true absence, which complicates the view of endemicity. Future versions of this document could be supported by in-depth assessments of endemicity by phylum along the MAR.

It should also be considered that the sampling methods employed can influence the view of regional distribution obtained from these samples. Different locations along the MAR have been sampled using different techniques, with different resolutions, which may introduce sampling bias and skew the views which can be obtained from these samples. Providing a detailed review of the sampling techniques used along the MAR, and the sample bias these may introduce, is beyond the scope of the current document. However, dedicated studies assessing sampling bias could inform future versions of this document. Developing standardised sampling methodology, such as the use of a global standardised marine taxon reference image database to support image-based analysis of benthic biota (Howell *et al.,* 2019), may help to ensure that futre data collections are more readily comparable.

The general patters in regional distribution of hard non-hydrothermal substrata, sulphide substrata (active and inactive), soft sediment, and benthopelagic habitat and their associated benthic biota are considered below. This is followed by a more detailed account of the regional distribution of microorganisms, benthic invertebrates and benthic and demersal nekton found at each of these broad habitat types.

10.1.1 Hard non-hydrothermal substrata

Given that exposed hard substrata make up < 5% of the MAR, the biota associated with hard substrata is likely to have a patchy distribution focussed on the exposed hard substrata at the ridge axis where sediment cover is lowest. As well as hydrothermal hard substrata habitat (both active and inactive sulphides), the MAR also features a suite of non-hydrothermal hard substrata habitats. The seabed surface at five out of eight explored locations north of the Azores and north and south of the CGFZ consisted of more that 20 % non-hydrothermal hard substrata (stones and outcropping basaltic rock), indicating that these substrata can provide large contributions to the local habitat provision (Mortensen *et al.,* 2008).

Non-hydrothermal hard substrata occurrences along the MAR constitute an important habitat for the benthic species which would otherwise be confined to narrow strips of appropriate depth around the Atlantic Ocean margins (Bergstad *et al.,* 2012). The topography of the MAR promotes strong near-bed currents and enhanced food supply, providing favourable conditions for the colonisation of suspension-feeding fauna, such as cold-water corals and sponges (Mortensen *et al.,* 2008). These habitats can occur in high density, such as within the Azores Triple Junction area (Braga-Henriques *et al*., 2013, Tempera *et al*., 2013). The relative rarity of hard non-hydrothermal substrata on the MAR may need to be considered when determining environmental management measures for the MAR.

10.1.2 Hydrothermally active hard substrata

At least 41 active fields are known along the northern MAR, with an average spacing of one active vent field every 153 km of ridge axis (Beaulieu *et al.,* 2015, supplementary information). In reality, spacing of known active vent fields is more variable, with known active vent fields along the MAR being generally widely separated by 100 – 350 km (Murton *et al.,* 1994; German *et al.,* 1996). More active vent fields are predicted to occur than have been discovered along the northern MAR, with an anticipated total 86 vent fields and an average of 73 km distance between active vent fields (Beaulieu *et al.,* 2015, supplementary information). However, the remaining 45 predicted active vent fields have yet to be discovered, and in some cases, the spacing between these may be greater than the predicted average. Most, but not necessarily all, active vent fields support thriving biological communities. Large distances between active vent fields may act as a biogeographic filter along the MAR, where dispersal of some species may be inhibited (Van Dover, 1995). On a global scale, hydrothermally active habitat is very rare, with active vent ecosystems estimated to cover only 50 km^2, which is less than 0.00001% of the surface area of the planet (Van Dover *et al.,* 2018).

The benthic biota at hydrothermally active habitat is evolutionarily adapted to the hydrothermal ecosystem, with many highly-specialised organisms that are endemic to the habitat. Hydrothermally active habitat is variable within and amongst sites, with the environmental gradients and patchwork of microhabitats they exhibit resulting in different biotic compositions between sites. This may present difficulties for developing networks of representative hydrothermally active habitat, as finding examples of similar habitat with similar benthic communities is challenging (Van Dover *et al*., 2018).

10.1.3 Hydrothermally inactive sulphide substrata

Whilst hydrothermally inactive sulphide habitat has been reported from multiple locations along the MAR, these sites were largely discovered through detection of hydrothermal activity nearby. It is likely that the distribution of inactive sulphide habitat along the MAR has been under reported to date, with more occurrences waiting to be discovered in off-axis locations or along the ridge axis at sites more distal from active venting (Hannington *et al.,* 2011). According to the InterRidge database, there are 14 inactive vent fields along the northern MAR (Table 10.1). However, it is not always clear whether these are truly inactive vent fields, or locations where both active and inactive sulphide habitat occurs within the same field. The InterRidge database considers a vent field to be an "assemblage of vent sites[1]. These known inactive vent fields occur beyond national jurisdiction between the equator and 25°N.

Table 10.1. Inactive vent fields along the northern Mid-Atlantic Ridge, InterRidge Vents Database Ver.3.4

Vent field	Latitude	Longitude	Maximum depth (m)	Discovery References
Ashadze 4	12.97	-44.85	4530	Fouquet *et al*., (2007)

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[1] InterRidge Vents Database Ver.3.4: About the Database. https://vents-data.interridge.org/about_the_database. Accessed: 18 September 2019.

Krasnov	16.64	-46.475	3900	Bel'tenev *et al*., (2004); Fouquet *et al.,* (2007)
Logatchev 4	14.7063	-44.9083	2000	Kuhn *et al*., (2004)
Logatchev 5	14.75	-44.97	3100	Fouquet *et al.,* (2008)
MAR, 12° 48'N	12.8	-44.7883	2400	Rona *et al*., (1982)
MAR, 15° 50'N	15.8667	-46.6667	3000	Akimtsev *et al.,* (1991)
MAR, 16° 46'N	16.795	-46.38	3300	Eberhart *et al.,* (1988)
MAR, 22° 30'N	22.5	-45.005	2800	Rona *et al*., (1982)
MAR, 23° 35'N	23.5833	-45	3500	Delaney *et al*., 1987; Kelley & Delaney (1987)
MAR, 24° 20'N	24.35	-46.2	3200	Rona *et al*., (1980)
MAR, 24° 30'N	24.5	-46.1533	3900	Sudarikov *et al*., (1990), Krasnov *et al*., (1995)
MAR, 25° 50'N	25.8083	-44.9833	3000	Rona *et al*., (1982)
Vema Fracture Zone	10.85	-41.8	3600	Bonatti *et al*., (1976); Rona *et al*., (1976)
Zenith-Victory	20.1292	-45.6225	2390	Silantyev (2008)

Whilst hydrothermally inactive vent fields have the potential to provide hydrothermally inactive sulphide habitat, the occurrence of hydrothermally inactive vent fields does not guarantee this. There are very few instances, both along the MAR and globally, where hydrothermally inactive sulphide habitat has been confirmed and or where any associated biological communities have been quantitatively assessed or even qualitatively described (Van Dover, 2019). Not all inactive sulphide habitats support biological communities visible in seafloor survey imagery, however, there may be diverse microbial communities, which could provide a food source for other biota (Van Dover, 2019).

There are few occurrences of specific inactive sulphide habitat along the northern Mid-Atlantic Ridge where the scientific literature has reported associated biological communities. Some of these occurrences are at a scale smaller than whole vent fields, and so may not be recorded in the InterRidge Database. Occurrences include Mag Mell in the Moytirra vent field between the Azores and Iceland (Wheeler *et al.,* 2013); and some chimneys within the Eiffel Tower sulphide complex in the Lucky Strike vent field near the Azores (Cuvelier *et al*., 2009). Whilst there are additional hydrothermally inactive sulphide occurrences along the northern MAR, such as the Mir and Alvin zones of the TAG vent field (Rona *et al*., 1993; Krasnov *et al*., 1995; Lalou *et al*., 1998) and the Yubileinoe and Surprise vent fields (Bel'tenev *et al*., 2017), these commonly have little or no record of any associated biological communities.

10.1.4 Soft sediment substrata

The amount of pelagic sediment cover, and so the distribution of pelagic soft sediment habitat along the MAR, depends on the distance from the mid axial valley where new rock is formed. The thickness of the pelagic sediment layer is dependent to a certain extent on 1) the geomorphology of the seabed and 2) surface primary productivity, which influences the flux of organic matter and sediment to the seabed. Areas within a few tens of metres of hydrothermally active vents are covered discontinuously in pelagic sediments (Fabri *et al.,* 2011; Figure 10.3), which can be several metres thick within 1.5 km of the vent locality (Murton *et al*., 2019). Hydrothermal sediments on the seafloor surface can be either hydrothermally active or inactive and tend to occur within a few hundred metres of active hydrothermal venting (Fabri *et al.,* 2011). Little is known about the distribution of sub-surface hydrothermal sediments and any associated biological communities.

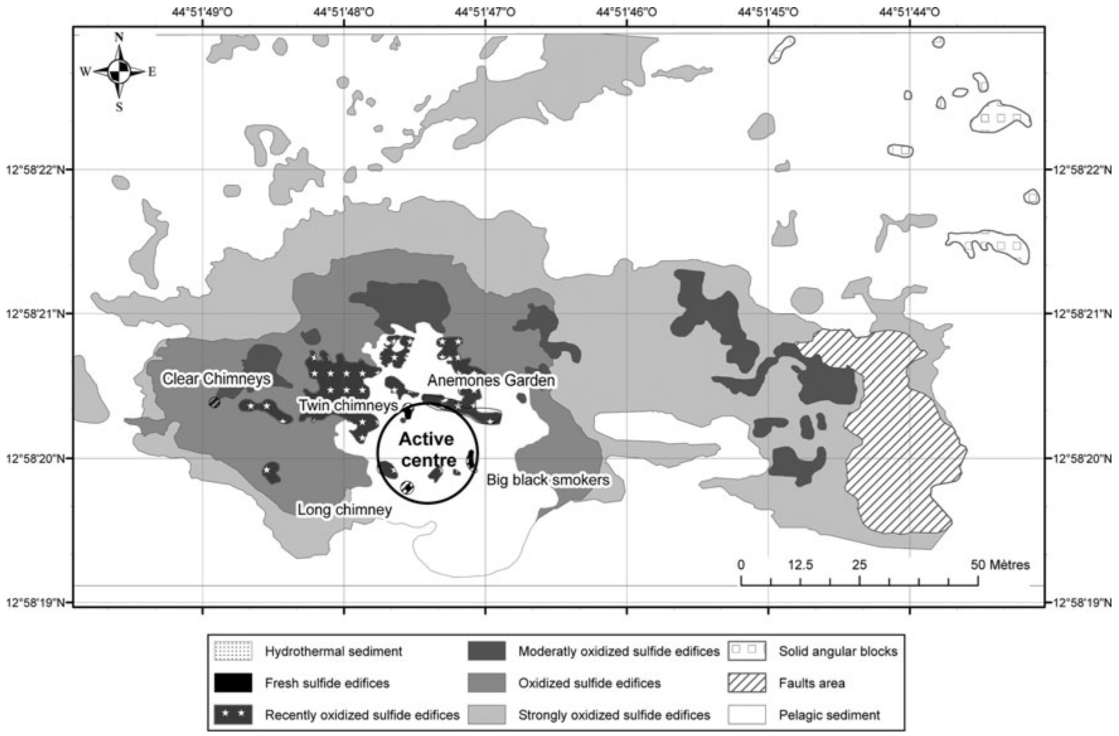

Figure 10.3. Ashadze-1 substrata divided into nine classes. The active centre is located in the south-western part, where the fresh sulphide edifices are in the middle of hydrothermal sediment area. The dark grey to light grey areas represent sulphide edifices ranging from fresh to oxidized stages. In the eastern part, several faults and angular blocks are present, with no specific hydrothermal activity. Reproduced with permission from Fabri et al.*, 2011.*

Most of the soft-bottom areas along the MAR have substantial sediment thicknesses (See Chapter 4: Geological Overview). Given that sedimented gentle slopes and discontinuous flat plains make up > 95% of the MAR, the areas over which sediment biota might be distributed are likely to be extremely large, depending on latitude, upper-ocean productivity biogeographic zones, depth of the seabed, geomorphology and the interactions of the latter with the local physical oceanography (such as near-seabed currents and internal tides) (See Chapter 6: Physical Oceanography). In some locations, the distribution of MAR soft-sediment epifauna appears to be clumped (i.e. not random) however it was not clear which environmental factors were driving the distribution of the soft sediment epifauna (Felley *et al.,* 2008). The majority of sedimented areas along the northern MAR are at abyssal depths (3500 – 6500 m) and are all contained in the North Atlantic GOODS Abyssal Province (Figure 10.4), which extends considerably beyond the MAR across the eastern and western North Atlantic Ocean basins. A small proportion of sedimented areas along the MAR occur at hadal depths (> 6500 m), such as base of the trench occurring at Romanche Fracture Zone.

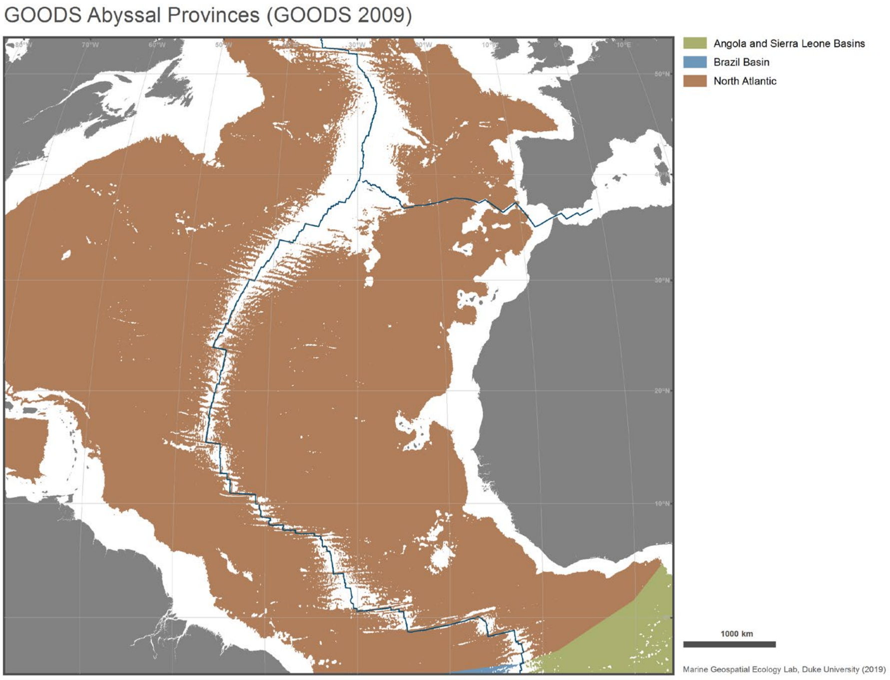

Figure 10.4. GOODS abyssal provinces, depth range 3500 – 6500 m. Map reproduced with permission from Cleary et al.*, 2019. Data taken from Watling* et al.*, (2013). Map available: https://ran-s3.s3.amazonaws.com/isa.org.jm/s3fs-public/files/documents/datareport-19nov-lowres.pdf.*

Sedimented areas on the MAR have received little attention and consequently faunal distribution knowledge is poor. Most studies on soft-bottom fauna on the MAR to date have focused on the larger invertebrates (megafauna) and fish to date (Vecchione *et al.*, 2010b). Concerted studies of the sedimented areas of the MAR did not take place until the late 20th century with a number of Russian studies (Mironov & Gebruk, 2006a) and later with the Census of Marine Life MAR-ECO project (Bergstad & Godø, 2003; Bergstad & Gebruk, 2008; Vecchione *et al.,* 2010b), and the UK ECOMAR project (Priede *et al.,* 2013b), mainly to the north of the Azores archipelago. To the South of the Azores the data on sediment fauna is scarce, although some preliminary data on sediment fauna was collected in the equatorial southern MAR by the MAR-ECO project (Perez *et al.,* 2012).

10.1.5 Lower water column (50 m above bottom)

The lower water column, considered here to be the 50 m of water column overlying the seafloor included within the ISA definition of the benthic environment, is largely equivalent of the benthopelagic. The lower water column is generally dominated by benthic and demersal nekton, such as fishes, cephalopods and some crustaceans. Being mobile, the taxa inhabiting the lower water column often occur overlying more than one seafloor habitat type along the MAR. Some of these species (generally the best swimmers) are particularly widespread, others may have a relatively localised distribution. As previously noted, the lower water column may also be visited by deep pelagic fish and cephalopods (Sutton *et al.,* 2008). 'Swimming' holothurians can also occur within the lower water column but are considered in detail under benthic invertebrates found on soft sediments.

There are very few studies addressing the regional distribution of benthopelagic nekton along the MAR. Most of these studies focus on the fishes and cephalopods from the North of the Azores to the South of Iceland during MAR-ECO (Felley *et al.,* 2008; Bergstad *et al.,* 2010; Vecchione *et al.,* 2010a), or the fishes to the North and South of the Charlie-Gibbs Fracture Zone during ECOMAR (Cousins *et al.,* 2013a; Cousins *et al.,* 2013; Dinley *et al.,* 2013). There are no published studies addressing the benthopelagic nekton South of the Azores to the equator. Video observations suggested that fish distribution patterns were related to depth (Felley *et al.,* 2008), a pattern also seen in trawl collections of some cephalopod species (Vecchione *et al.,* 2010a). collections, baited camera observations, and video surveys indicated that different fish assemblages occur North and South of the CGFZ (Cousins *et al.,* 2013a; Cousins *et al.,* 2013b; Linley *et al.,* 2013), whilst the Sub-Polar Front around the CGFZ was thought to represent the southern extent of some cephalopod species' distributions (Vecchione *et al.,* 2010a). Cousins *et al.,* (2013b) concluded that whilst all of the fish species observed along the MAR have been observed elsewhere in the Atlantic, the MAR provided important habitat for species which would otherwise be confined to narrow strips of appropriate depth band around the North Atlantic Ocean margins.

10.1.6 Microorganisms

Microorganisms (Bacteria, Archaea, Protista and Fungi) have been poorly studied to date in the marine environment generally, including the deep-sea benthic environment. The free-living bacteria found in active sulphide habitats, and the chemoautotrophic bacteria occurring in symbiosis with some hydrothermal vent fauna, have received more research attention but very little is known about the regional distribution of these along the MAR. Whilst some insightful studies have been conducted on bacteria at hydrothermally inactive sulphides in recent years, very few of these studies occurred along the MAR and little is known about the microorganisms at hydrothermally inactive sulphides generally (Van Dover, 2019). Next to nothing is known about the regional distribution of other microorganisms along the MAR, such as Protista, Archaea and Fungi. Growing interest in the biotechnology applications for microorganisms from extreme environments (such as the deep sea) may see an increase in the research attention these are afforded in future (Poli *et al.,* 2017).

10.1.6.1 Hard non-hydrothermal substrata

Very little is known about the regional diversity of microscopic Protista at of non-hydrothermal hard substrata, in part due to the difficulty of sampling them. No published information was available on the regional distribution of microscopic protists at non-hydrothermal hard substrata along the northern MAR. There is no published information available regarding the regional distribution of free-living Archaea or Bacteria at the surface of non-hydrothermal hard substrata along the northern MAR. Recent work at North Pond on the western flank of the northern MAR suggests that the non-hydrothermal seafloor sub-surface environment may support a distinct and active bacterial community (Meyer *et al.,* 2016) but the regional distribution of this community is not known.

Microorganisms can also occur in association with hard substrata megafauna, such as sponges, along the MAR. Some sponges even host specific assemblages of microorganisms. These microorganisms can be inter- or intra-cellular and occur on either the surface of the sponge (epibionts) or within the structure of the sponge (endosymbionts). Microorganisms, such as Archaea, Bacteria and Fungi, can make up to 40 % of the sponge's volume (Osinga *et al.,* 2001) and may play an important role in sponge metabolism and carbon fixing. They can also produce secondary metabolites, such as antibiotics, antifungals, and deterrent compounds, which can provide the sponge host with protection from predation and spatial competition (Osinga *et al.,* 2001). Some deep-water sponges, and their associated microorganisms, can also be important centres of chemosynthetic activity (Hentschel *et al.,* 2002). Whilst there have been studies investigating the regional distribution patterns of the sponge hosts, the regional distribution of associated microorganisms along the MAR is not known.

10.1.6.2 Hydrothermally active hard substrata

Hydrothermally active substrata habitat hosts an array of microorganisms, either free-living on the substrata (Figure 10.5), within hydrothermal vent plumes, or in symbiosis with hydrothermal vent fauna (Figure 10.6) (Dick *et al.,* 2019). Some of these microorganisms are chemoautolithotrophic (metabolise inorganic carbon sources) or methanotrophic and may be endemic to hydrothermally active habitat. The local distribution patterns of methanotrophic and chemoautolithotrophic microorganisms on the MAR depend on the chemistry of the hydrothermal fluids, including the relative abundance of methane and sulphide, and the geological setting, such as basalt or ultra-maphic rocks (Perner *et al.,* 2007). Comparisons between the microbial communities of the basalt-hosted Lucky Strike and ultra-maphic-hosted Rainbow vent fields determined that different archaeal and bacterial communities are associated with the different geological settings of these vent fields (Flores *et al.,* 2011). The regional distribution of these microorganisms will be restricted by the distribution of hydrothermally active habitat (either basalt or ultra-maphic) along the MAR. Other microorganisms found at hydrothermally active habitat are heterotrophic (metabolise organic carbon sources) and may occur in other deep-sea habitats along the MAR.

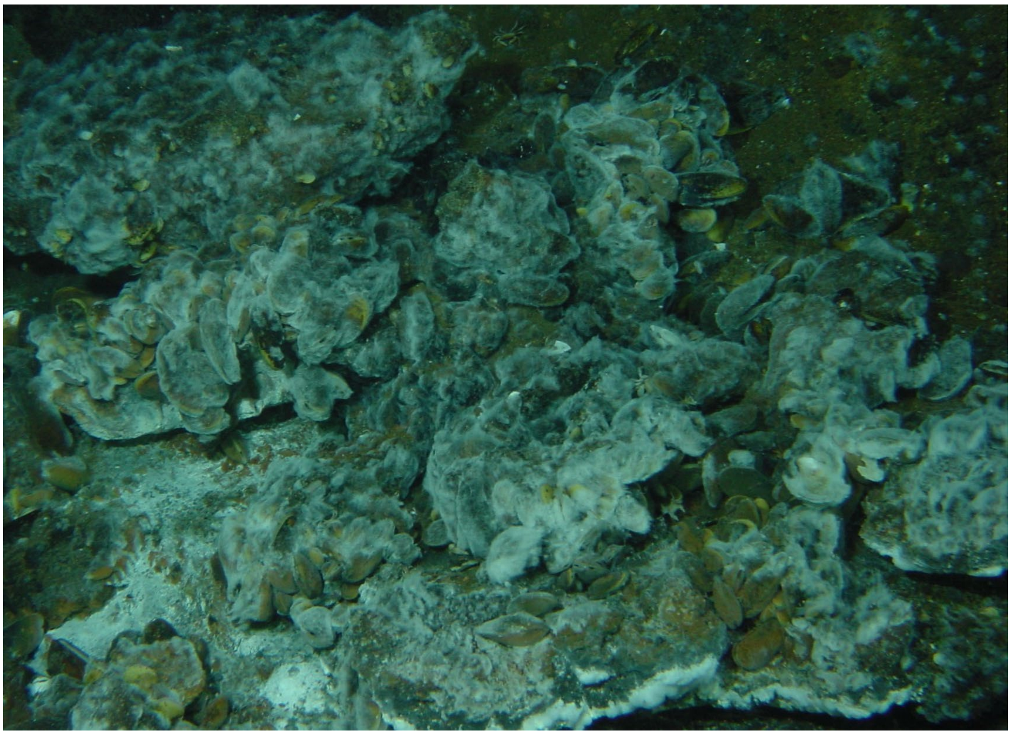

Figure 10.5. White filamentous bacteria on Bathymodiolus azoricus *mussels from the Lucky Strike vent field. Reproduced with permission: © SEAHMA - PDCTM/MAR/15281/1999.*

There are few studies on the biodiversity or functional biodiversity of microorganisms at hydrothermal habitat along the MAR. An assessment of diversity and function of microbial mats from Lucky Strike hydrothermal vent field (Crepeau *et al.,* 2011) indicated very low diversity of archaeal genetic sequences (just a single group), whilst bacterial sequences demonstrated considerably higher diversity. Functional gene libraries revealed a diverse and active chemoautolithotrophic community, including methanotrophic and thiotrophic bacterial symbionts associated with bathymodiolid vent mussels (Crepeau *et al.,* 2011). Comparisons between three ultra-maphic-hosted vent fields (Rainbow, Ashadze-1 and Lost City) indicated that the overall acrchaeal community was diverse and heterogeneously distributed between the hydrothermal sites and types of samples analysed (seawater, hydrothermal fluid, chimney and sediment) (Roussel *et al.,* 2011). Lost City hosted a distinct microbial diversity, which was thought to reflect the highly alkaline warm fluids unique to this location (Roussel *et al.,* 2011).

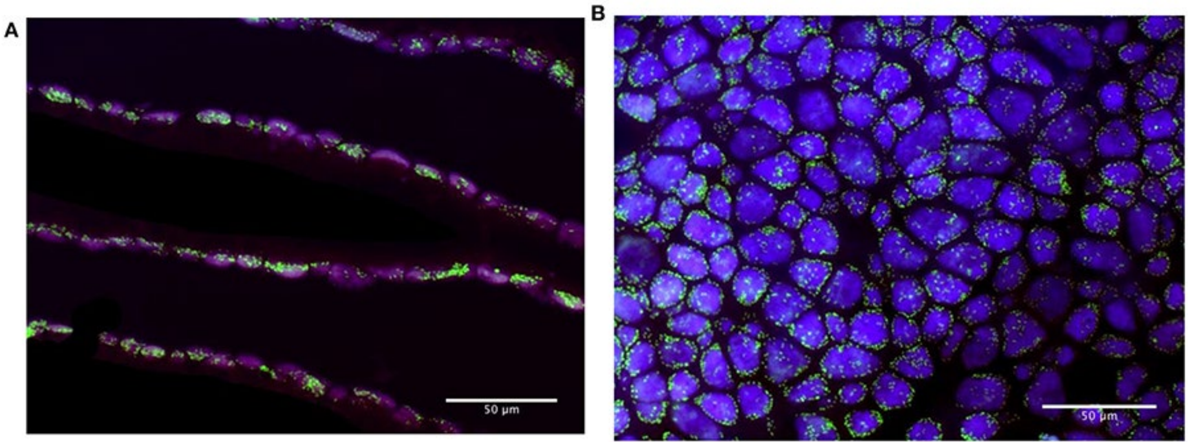

Figure 10.6. Symbiotic bacteria within bacteriocytes in the gills of the vent mussel Bathymodiolus puteoserpentis*, as visualised by fluorescence in situ hybridization (FISH). Sulphur-oxidizing bacteria, labelled with the BangT-642 probe, appear in purple. Methane-oxidizing bacteria, labelled with probe ImedM-138, appear in green. A: Transverse sections of gill filaments used for estimation of symbiont relative abundances. Reproduced from Duperron* et al.*, (2016).*

The regional distribution of symbiotic bacteria is very little known. Bacterial symbionts do not always share the same regional distribution as their hosts, for example the genealogies of chemoautotrophic and methanotrophic symbionts of *Bathymodiolus* spp. located on the MAR North and South of the equator were inconsistent, and different from their mussel hosts, indicating disconnected biogeography patterns (van der Heijden *et al.,* 2012).

There are few studies of microscopic Protista at hydrothermally active hard substrata in any region. Microcoloniser experimental systems deployed on the active Eiffel Tower chimney in Lucky Strike for 15 days were predominantly colonised by bodonid and ciliate protists, indicating that these may be pioneers in the colonization process of bare hydrothermally-active substrata (Lopez-Garcia *et al.,* 2003).

The regional distribution of microbial eukaryotes, such as Protista, along the MAR is not known. Whilst some protist lineages seem ubiquitous in hydrothermal areas in multiple oceans, some lineages have only been detected in the Atlantic (Lopez-Garcia *et al.,* 2003). In other regions, folliculinid and foraminiferan protozoans were found in large numbers on settlement panels sited in Clam Acres on the East Pacific Rise (Van Dover *et al.*, 1988), which implies that microscopic foraminiferans are likely to occur in regions such as the northern MAR, and that some species may be common.

10.1.6.3 Hydrothermally inactive sulphide substrata

Incomplete information on the distribution of hydrothermally inactive sulphide habitat, and a lack of studies addressing the microbial communities at this habitat, means it is not possible to discuss the regional distribution of microorganisms at inactive sulphide habitat along the MAR. However, studies from other regions may provide insights on the broad distributional patterns and associations that could be expected to occur along the MAR.

Studies on microorganisms at hydrothermally inactive sulphide habitat in other regions (reviewed in Van Dover 2019) found different microbial communities occurring at active and inactive sulphide habitat, even when these habitats are only separated by a few meters (Suzuki *et al.,* 2004). Active and inactive sulphide habitat supports different bacterial communities, with the groups dominating active areas, such as ε-Proteobacteria and members of the Aquificae, not generally detected at inactive sulphides or present in very low abundance (Kato *et. al.,* 2010; Sylvan *et al.,* 2012; Zhang *et al.,* 2016; Christakis *et al.,* 2018). Some studies indicate that the abundance and activity of microbial communities on inactive sulphides may be comparable or even greater to that found at active sulphide habitat (Kato *et al.,* 2010; Li *et al.,* 2017). There is some support for the hypothesis that hydrothermally inactive sulphides may host microorganisms not found elsewhere or only detectable in very low numbers (Han *et al.,* 2018). However, other studies suggest that some microbial communities at inactive sulphides may be similar to groups common in other marine sediments (Meier *et al.,* 2019).

Some inactive sulphide habitat may be more favourable to microorganisms than others, with bacterial density at inactive sulphides along the Juan de Fuca Ridge decreasing according to the following mineral sequence: elemental sulphur, chimney sulphide, marcasite, pyrite, sphalerite, chalcopyrite (Edwards *et al.,* 2003). If the same pattern occurs along the MAR, then this will impact the regional distribution of bacterial communities, with the type of inactive sulphide mineral present determining the type and density of microorganism colonising it.

10.1.6.4 Soft sediment substrata

Few studies have been conducted on either pelagic or hydrothermal sediment microbial communities along the MAR, and insufficient information is available to describe the regional distribution of these communities for the northern MAR. One study at Menez Gwen along the MAR demonstrated that the microbial communities at hydrothermal sediment habitat are significantly different to those occurring at pelagic sediment some 6-km distant (Cerqueira *et al.,* 2015). Sediments close to Menez Gwen hydrothermal vents were dominated by specific thermophilic and hyperthermophilic Archaea and Bacteria, whereas off-axis the microbial community was more typical of deep-sea sediments (Cerqueira *et al.,* 2015).

Sediment samples from some locations along the southern MAR have been shown to be enriched in crude oil as sole carbon and energy sources, with eleven microbial oil-degrading entities being cultivated *in vitro* (Shao *et al.,* 2010; Gao *et al.,* 2015). Whether northern MAR sediments also host microbial communities capable of degrading oil remains to be seen. Bacteria with potential biotechnology applications have been isolated from deep equatorial MAR seafloor, such as *Bacillus stratosphericus* (Lima *et al.,* 2013). Further work on bacteria isolated from equatorial MAR sediments suggests that microorganisms associated with deep-sea sediments may have greater biotechnological application that those found in the water column, with the potential that additional studies in lesser studied parts of the MAR may uncover new microorganisms for the biotechnology industry (Odisi *et al.,* 2012).

10.1.7 Benthic invertebrates

Despite the North Atlantic being probably the best studied ocean basin for deep-water benthic invertebrates (Cairns, 2007; Mironov & Gebruk 2006a), data on the distribution of many organisms are still scarce. This lack of information may result from: 1) the absence of sampling in most deep-sea areas because of high costs and technological challenges; 2) difficulties with identification of the species sampled or in collections; or 3) they may simply be naturally rare across their distribution range.

The benthic invertebrates living on hydrothermally active substrata are the best studied, and of these, the most regional distribution information is available for the larger benthic invertebrates that can be identified from imagery (megafauna). Less is known about the regional distribution of macro- and meio-faunal benthic invertebrates at hydrothermally active substrata. There are considerable knowledge gaps in the regional distribution of the fauna on non-hydrothermal hard substrata, reflecting both the patchiness of this habitat along the MAR, and a lack of data. For the fauna at both non-hydrothermal substrata and soft sediment habitat, more regional information is available for the larger benthic invertebrate size classes. Very little is known about the benthic invertebrate fauna at inactive sulphide habitat. There is also a paucity of information regarding the benthic invertebrates in the lower water column (50 m above seabed) along the MAR.

Many of the non-hydrothermal benthic invertebrate megafauna along the MAR have wide geographic ranges, with the same morphotypes being found in other areas of the Atlantic or even extending into other oceans. Some species can be shared with continental slope or seamount habitats if the environmental conditions are suitable and if circulation allows connectivity. Other species may be specific to a particular area or be so rare/under-sampled that their regional distribution is not known. Even for the megafauna, the best-known size class of MAR benthic invertebrates, new megafaunal species are still being discovered. From a relatively low number of trawls during the MAR-ECO Project, fifteen new species were described, including new glass sponges, sea cucumbers, brittlestars, and one new sea star (Gebruk *et al.,* 2010).

From a geographical context, more detailed information exists for the Azores EEZ (Braga-Henriques *et al*., 2013; Tempera *et al*., 2012, Tempera *et al.,* 2013; Sampaio *et al.,* 2019a, Sampaio *et al.,* 2019b) and for non-ridge associated seamounts (Ramiro-Sanchez *et al*., 2019) than for the rest of the MAR. This is partly because the MAR around the Azores is shallower, and closer to shore, making it easier to sample and characterise the benthic fauna. These studies have identified the Azores as a hotspot for cold water corals in the North Atlantic (Braga-Henriques *et al.,* 2013; Sampaio *et al.,* 2019a) representing the highest known octocoral diversity within European waters (Costello *et al.,* 2001). Less information is available for rest of the MAR, however there is the potential that other hotspots for cold-water coral diversity could exist in additional locations along the MAR.

10.1.7.1 Hard non-hydrothermal substrata

10.1.7.1.1 Megafauna

The sessile megafauna associated with hard non-hydrothermal substrata along the MAR which have been the most studied are cold-water corals and sponges. These organisms are typically long-lived, slow-growing, and have low reproductive inputs, and as such many species are Vulnerable Marine Ecosystem (VME) indicator taxa (ICES 2016, 2019b).

10.1.7.1.1.1 Anthozoans (corals and anemones)

Many deep-sea Anthozoa species (including corals and anemones) are found on hard non-hydrothermal substrata along the northern MAR (Figure 10.7). During the ECO-MAR project, Anthozoa species from orders Actiniaria (anemones), Antipatharia (black corals), Scleractinia (hard corals), Alcyonacea (soft corals) and Pennatulacea (seapens) were collected from the MAR. The collected anthozoan specimens were found to have high affinities with the Atlantic European continental slope (62.5 %), the North-east American continental slope (59.4 %) and the North-west continental slope of Africa (50.0 %). There are also a high percentage of species shared with Iceland and Greenland (53.1 %) and the Azores (46.9 %) (Molodtsova *et al*., 2008). This means the MAR anthozoan fauna found North of the Azores EEZ appears to have a closer relationship to the anthozoan fauna of the continental slopes of Atlantic Europe, North-east America and North-west Africa, and Iceland and Greenland, than to the anthozoan fauna of the Azores. Thirteen of the anthozoan species collected along the MAR by the ECO-MAR project were also reported from outside of the Atlantic Ocean and would be considered cosmopolitan species.

Additional studies of the 'mushroom corals' from genera *Anthomastus, Heteroplypus* and *Pseudoanthomastus* collected for the MAR North of the Azores and the Reykjanes Ridge identified five species, three of which were described as new species: *Heteropolypus sol*, *Anthomastus gyratus,* and *Pseudoanthomastus mariejosea* (Molodtsova, 2013). Only one of the five species, *A. gyratus*, appeared to have a distribution limited to the MAR and Reykjanes Ridge, the other four species had wider distributions including a combination of the East Atlantic, West Atlantic, and the Azores regions (Molodtsova, 2013). One species of black coral, *Heteropathes opreski,* collected from within the Russian Exploration Area is so far only known to occur along the MAR between 34°46.7′ N and 13°19.43′ N at depths 1955–2738 m, and is considered to be potentially endemic to this region (Matos *et al.,* 2014; Molodtsova 2016). The Azores region of the MAR also supports species or species association that are not present elsewhere, such as the occurrence of the 'living fossil community' formed by a long-lived deep-sea oyster and a crinoid (Wisshak *et al.,* 2009) and coral reefs formed by the scleractinian coral *Eguchipsammia* cf. *cornucopia* (Tempera *et al.,* 2015). It is not known if other geographically restricted communities occur on the less-well studied sections of the MAR, for example South of the Azores.

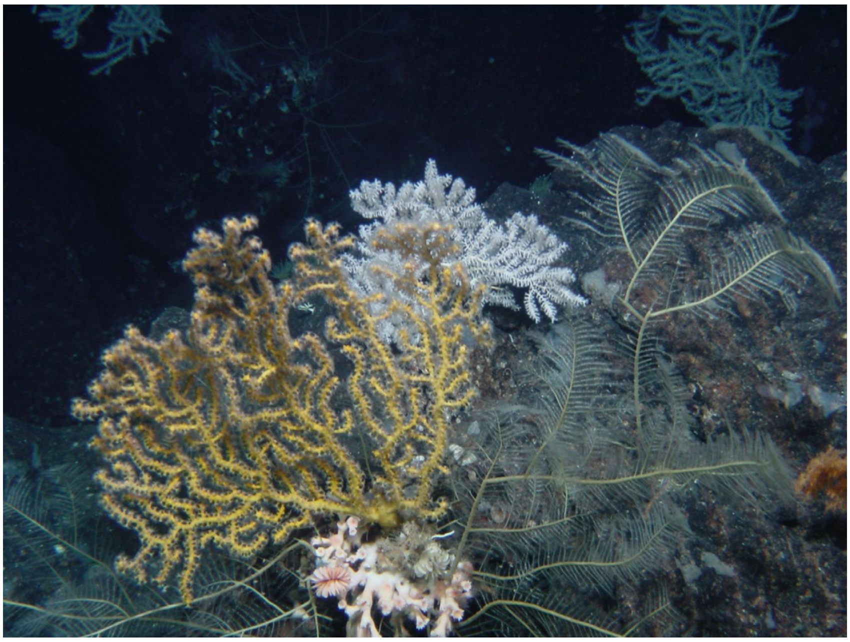

Figure 10.7. A coral garden on the northern Mid-Atlantic Ridge, near Menez Gwen hydrothermal vent field Marine Protected Area. Reproduced with permission: © SEAHMA - PDCTM/MAR/15281/1999.

Video-survey of Anthozoa along the MAR between the southern part of the Reykjanes Ridge and the Azores observed deep-water corals at all sites, across a depth range of 800 – 2400 m, although most corals were observed at 1400 m depth or shallower (Mortensen *et al,* 2008). A total of 40 taxa were observed from the eight survey sites, dominated by Octocorallia (27 taxa). The branching stony coral *Lophelia pertusa* (currently listed as *Desmophyllum pertusum* on the World Register of Marine Species[1], although this appears to be under dispute) was one of the most frequently observed species (Mortensen *et al,* 2008), occurring as small colonies (less than 0.5 m in diameter) on basaltic outcrops within the extensive sedimented areas. *L. pertusa* has a very broad regional distribution, including the East and West Atlantic, the Mediterranean, and parts of the Pacific.

Habitat suitability models for different deep-water coral species indicate that the MAR offers suitable habitat for a range of octocorals, such as Alcyoniina, Holaxonia, Calcaxonia, Scleraxonia, Sessiliflorae, Stolonifera and Subsessiliflorae (Yesson *et al.,* 2012; Figure 10.8). However, the predicted occurrence of suitable habitat does not guarantee that coral will colonise a given area. Also, if an area is predicted to have suitable habitat for a certain group of corals, different species from within this group may be present at different sites. The Azores has the greatest modelled habitat suitability for all these octocoral groups, with the MAR North of the Azores exhibiting the next greatest habitat suitability. Habitat suitability for octocorals decreases South of the Azores to the equator but suitable habitat is predicted to occur for each of the octocoral groups considered, to a greater or lesser extent according to group (Yesson *et al.,* 2012). These distribution models suggest that suitable habitat for octocorals occurs along the length of the MAR, on some seamounts, and on the continental slopes of Atlantic Europe, North-east America, and North-west Africa. These higher taxonomic level models provide some support that some octocoral species may be shared between the MAR, continental slopes and seamounts in the North Atlantic.

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[1] *Lophelia pertusa* (unaccepted) within the World Register of Marine Speices: http://www.marinespecies.org/aphia.php?p=taxdetails&id=135161

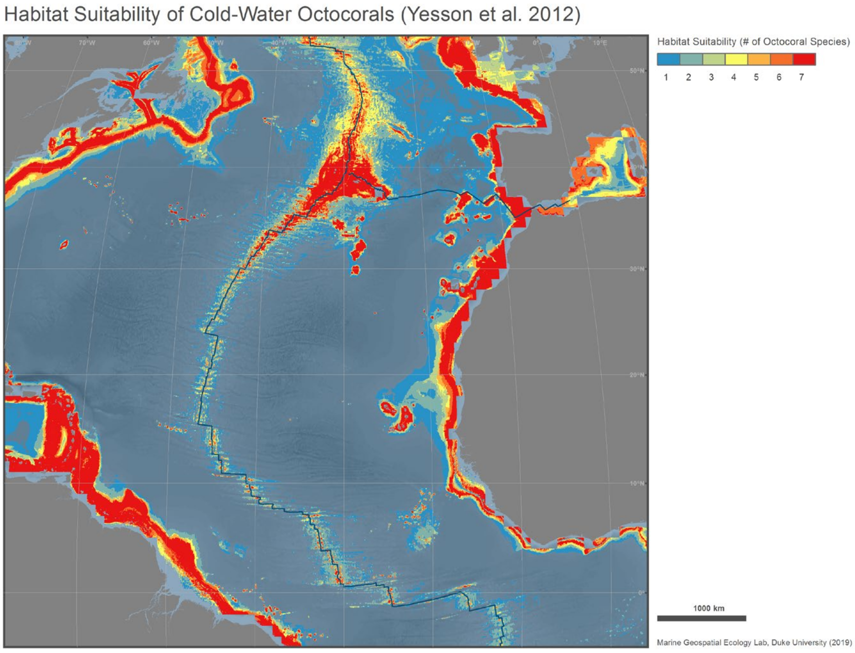

Figure 10.8. Modelled deep-sea octocoral habitat suitability. Map reproduced with permission from Cleary et al.*, 2019. Data taken from Yesson* et al.*, (2012). Map available:* [*https://ran-s3.s3.amazonaws.com/isa.org.jm/s3fs-public/files/documents/datareport-19nov-lowres.pdf*](https://ran-s3.s3.amazonaws.com/isa.org.jm/s3fs-public/files/documents/datareport-19nov-lowres.pdf).

Habitat suitability models also indicate that the MAR offers suitable habitat for a range of Scleractinia (stony corals), such as *L. pertusa*, *Madrepora oculata, Solenosmilia variabilis, Goniocorella dumosa* and *Enallopsammia rostrata* (Davies & Guinotte, 2011; Figure 10.9). As observed for octocoral groups, the Azores has the greatest modelled habitat suitability for all these five species, although the different species have different affinities for other sections of the MAR. *S. variabilis* has the greatest modelled availability of suitably habitat along the MAR, with suitable habitat predicted to occur from South of Iceland all the way to the equator, a similar distribution occurs for *E. rostrata.* Less suitable habitat is available for *L. pertusa, M. oculata* and *G. dumosa*; the only suitable habitat for these species (outside of the Azores) is predicted to occur to the North. As well as along sections of the MAR, suitable habitat is predicted to occur for all species on some seamounts, and on the continental slopes of Atlantic Europe, North-east America, and North-west Africa. These models provide support for the hypothesis that some Scleractinia species are shared between the MAR, continental slopes and seamounts in the North Atlantic.

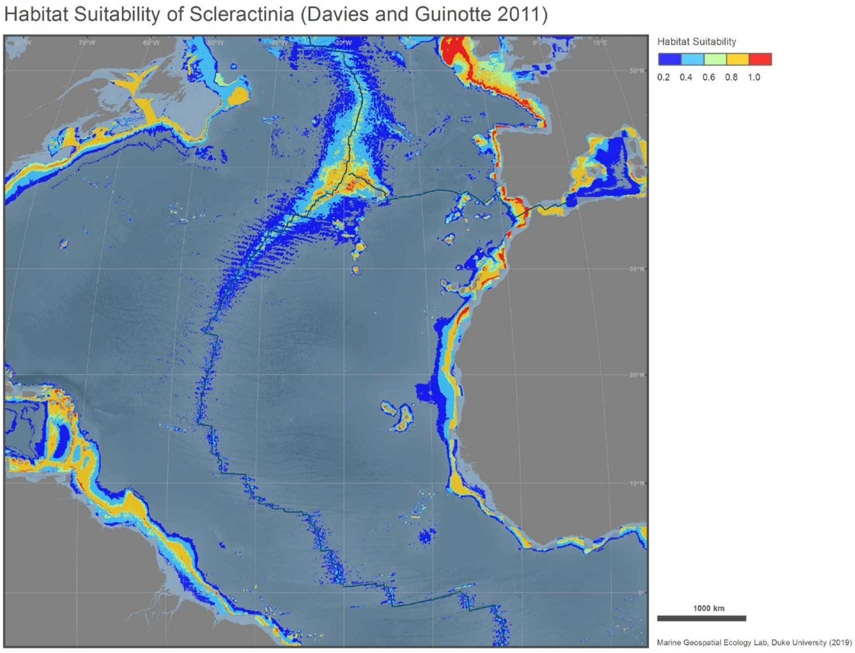

Figure 10.9. Modelled deep-sea Scleractinia habitat suitability. Map reproduced with permission from Cleary et al., *2019. Data taken from Davies & Guinotte, (2011). Map available: https://ran-s3.s3.amazonaws.com/isa.org.jm/s3fs-public/files/documents/datareport-19nov-lowres.pdf.*

10.1.7.1.1.2 Porifera (sponges)

The majority of deep-sea sponges recorded from the MAR belong to either Hexactinellida (glass sponges) or Demospongiae; one specimen of Calcarea sponge was collected during MAR-ECO but has not yet been described (Cardenas & Tore Rapp, 2015). There are few studies on the distribution of either hexactinellid or demosponge sponges along the MAR.

Cardenas & Torre Rapp (2015) found the Charlie-Gibbs Fracture Zone to be a major biogeographic barrier for deep-sea sponges, through acting as a latitudinal border for dispersal. Four of the sponge species collected during MAR-ECO are restricted to the boreal and/or Arctic waters and only occur North of the Charlie Gibbs Fracture Zone, whilst four species only occur South of the northern part of the Charlie Gibbs Fracture Zone. Eight of the demosponge species can be found both North and South of the Charlie Gibbs Fracture Zone.

The distribution of deep-sea sponges observed during the MAR-ECO project provides some support for the division of the North Atlantic lower bathyal habitat into two provinces by Watling *et al.,* (2013), with the Charlie Gibbs Fracture Zone acting as the barrier between the Northern Atlantic Boreal and North Atlantic provinces (Cardenas & Tore Rapp, 2015). There also appears to be a lower depth limit for bathyal demosponges of 3000 m for most species (Cardenas & Tore Rapp, 2015).

10.1.7.1.1.2.1 Hexactinellida (glass sponges)

From a study of Hexactinellida collected between the Azores and the Reykjanes Ridge (Tabachnick & Collins, 2008), it appears that the hexactinellid sponge fauna along the MAR shares similarities with the hexactinellid fauna in the East Atlantic and West Atlantic, and more surprisingly, with the hexactinellid fauna in the Indian Ocean and Indo-West Pacific. Some Farreidae hexactinellid sponges also demonstrate wide distribution, with *Farrea herdendorfi* collected from the Charlie Gibbs Fracture Zone on the MAR also known from the northwestern and southwestern Atlantic (Figure 10.10; Lopes & Tabachnick, 2013). Other hexactinellids sampled from the MAR are very rare, such as *Doconesthes sessilis*, previously known from a single specimen (Tabachnick & Collins, 2008); and some are new to science, such as *Sympagella cooki* and *Sympagella ecomari* (Tabachnick & Menshenina, 2013).

Figure 10.10. In-situ images of hexactinellids (glass sponges) from the northern Mid-Atlantic Ridge in the vicinity of the Charlie Gibbs Fracture Zone. Left: cf. Farrea herdendorfi. *Images taken by the ISIS ROV during the RRS James Cook ECOMAR cruise 048 in 2010. Courtesy of Monty Priede and Andrey Gebruk.*

The work conducted under MAR-ECO and ECOMAR brings the number of hexactinellid species known from the northern MAR to 24 (as of 2013 – Tabachnick & Menshenina, 2013). Whilst some of these species (such as *F. herdendorfi*) appear to be widespread, thirteen of these species are newly-described from the MAR during MAR-ECO, and it is not yet known how widely distributed they are. The European Union-funded project, 'Deep-sea sponge grounds ecosystems of the North Atlantic' (SponGES[1]), and the resulting portal for deep-sea sponge data (SponGIS) should lead to improved understanding of the regional distributions of sponges occurring along the MAR.

10.1.7.1.1.2.2 Demospongiae

For Demospongiae, twenty-two species were collected from the northern MAR between the Azores and Iceland during the MAR-ECO project at 753 – 3046 m depth (Cardenas & Tore Rapp, 2015). Fourteen of these demosponge species have an amphi-Atlantic distribution, being found on both the eastern and western sides of the Atlantic (Cardenas & Tore Rapp, 2015). Several of the demosponge species collected were rare and poorly known, such as *Craniella longipilis* (previously *Tetilla longipilis*), *Tetilla sandalina, Craniella azorica* and *Polymastia corticata,* whilst two were new to science, *Forcepia (Forcepia) toxafera* and *Iotroata paravaridens.* For new or rarely collected species, it is not clear whether these are truly restricted to the northern MAR, or if under-sampling means they have not yet been encountered elsewhere. One demosponge species of sponge, *Poecillastra compressa*, has numerous records and appears to be genuinely restricted to the North-East Atlantic and the MAR. According to distribution maps, 68 % of the MAR-ECO demosponge species (15 out of 22) are amphi-Atlantic. This agrees well with faunal distributions for the Reykjanes Ridge, where 61 % of 80 species collected (Scleractinia, Cirripedia, Echinoidea, Asteroidea and Brachiopoda) were amphi-Atlantic (Mironov & Gebruk, 2006b).

10.1.7.1.1.3 Coral- and sponge-associated fauna

Many deep-sea corals and sponges are framework species (Figure 10.11), with their complex three-dimensional structures creating a suite of micro-habitats available to benthic macrofauna and meiofauna. Some macrofauna and meiofauna species occurring at non-hydrothermal hard substrata may be reliant on the habitat complexity that corals and sponges provide, with coral and sponge patches typically supporting higher biomass and diversity than in locations where corals and sponges are absent. For example, a survey of the MAR between the southern part of the Reykjanes Ridge and the Azores found the abundance of non-coral megafauna (such as crinoids, certain sponges, the bivalve mollusc

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[1] Deep-sea sponge grounds ecosystems of the North Atlantic (SponGES): http://www.deepseasponges.org/

Acesta excavata and squat lobsters) to be 1.6 times higher where corals were present (Mortensen *et al.,* 2018).

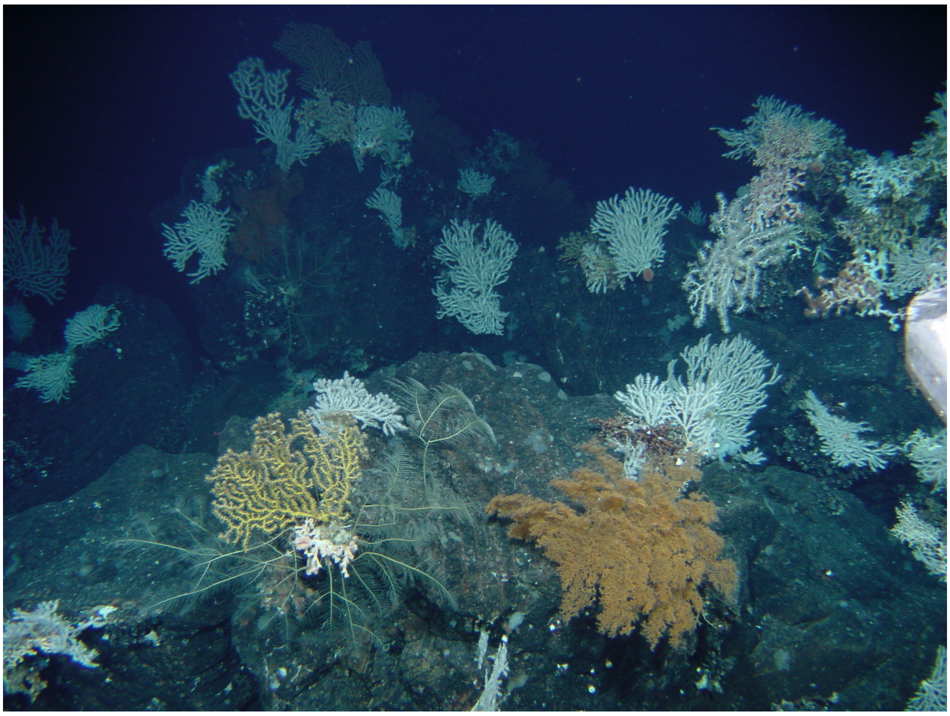

Figure 10.11. A mixed coral assemblage on non-hydrothermal hard substrata along the MAR. Reproduced with permission: © SEAHMA - PDCTM/MAR/15281/1999.

One important but often overlooked group of cold-water coral-associated sessile fauna is the Zoantharia, a group of cnidarians (including some sea anemones) that use corals as substrata and feeding areas, often with a long evolutionary relationship to the coral host. Studies on zoantharians associated with Stylasteridae hydroids and Antipatharia, and Octocorallia corals at depths 110 – 800 m in the Azores revealed five species new to science (Carreriro-Silva *et al.,* 2011; Carreriro-Silva *et al.,* 2017). These findings highlight the limited knowledge on cold-water coral-associated fauna more generally, with the potential for new species to be discovered along other less studied sections of the MAR, such as the MAR between south of the Azores and the equator.

10.1.7.1.2 Macrofauna and Meiofauna

Very little information is available on the macrofauna and meiofauna found in association with sponge and coral patches or inhabiting hard non-hydrothermal substratum along the MAR more generally. There is currently insufficient information available to describe the regional distributions of these fauna.

A recent study on the Bryozoa (often found in association with coral and sponge habitat) near the Hayes Fracture Zone (1067 – 1477 m depth), South of the Azores, hints at a diverse and relatively unknown Bryozoa fauna (Souto & Albuquerque, 2019). Some of the bryozoans collected were identified from other localities, however seven of the 15 bryozoans were described as new species. The work of Souto & Albuquerque (2019) is the first report of cheilostome bryozoans form the MAR, and the regional patterns of this group are not known.

10.1.7.2 Hydrothermally active hard substrata

The distribution of benthic invertebrates endemic to hydrothermally active hard substrata is closely tied to the patchy occurrence of hydrothermal activity along the MAR, and not all locations may support thriving benthic invertebrate communities. Whilst species records exist for some hydrothermally active sites along the MAR, these are rarely updated and may only address a few taxonomic groups. There is also a paucity of quantitative data, which would be needed to determine locations where hydrothermal vent communities are particularly diverse or productive in terms of abundance or biomass.

Reliable species identifications are key to describing regional diversity patterns, with genetic data being an increasingly important component of modern species identification. Whilst genetic techniques are increasingly used, these techniques were not necessarily employed to support species identifications in older datasets. As a result, there is the possibility that some species records contain cryptic species, which may only be identified with genetic data, and could alter current understanding of distribution patterns. Given the temporal variability in the environmental characteristics of hydrothermal habitat, it is also possible that species distributions captured in historic records may have changed, particularly where fluid flow has altered and a site is no longer 'active' or has lower levels of activity. Historic records are particularly important for understanding temporal variability, however repeat surveys to the same location are needed to confirm the continued presence of hydrothermal vent species at a site.

10.1.7.2.1 Biogeography and biodiversity

The most comprehensive species list for hydrothermal vent fauna recorded along the MAR was last updated in 2006 (Desbruyeres *et al.,* 2006). Further survey and research efforts along the MAR have led to the discovery of new species, and species lists may have been updated for some taxonomic groups. However, the Desbruyeres *et al.,* (2006) taxa listing currently provides the most comprehensive overview of hydrothermal vent fauna along the MAR.

The MAR hydrothermal vent benthic invertebrates are phyletically diverse, with taxa representative of nine marine phyla recorded by Desbruyeres *et al.,* (2006) (Table 10.2). Organisms within these phyla include carnivorous sponges, a foram, hydroids, an anemone, limpets, marine snails, a sea slug, mussels, an octopus, a nematode, various worms, a mite, sea spiders, copepods, a cumacean, tanaids, isopods, amphipods, shrimp, squat lobsters, a lobster, crabs, a sea star, a sea urchin, brittlestars, and an arrow worm (Table 10.2). Together, these total 100 taxa, which at the time the records were published, represented nearly 20 % of the global hydrothermal vent fauna diversity (primarily megafauna and macrofauna) known at that time. Not all of the benthic invertebrate taxa recorded from MAR hydrothermal vents are endemic to this habitat (see Table 10.2) and it is possible that some of these taxa may have been recorded from hydrothermal vent habitat beyond the northern MAR or from other chemosynthetic habitats or general deep-sea habitats in subsequent years. Based on the 2006 listing, 71 species recorded from the MAR were only known from active hydrothermal vents, 4 species were also recorded from other chemosynthetic habitats (such as cold seeps and whale falls) in the North Atlantic, and 25 species were also recorded from other deep-sea habitats in the North Atlantic and other oceans.

Table 10.2. Invertebrate species from hydrothermal vents along the Mid-Atlantic Ridge. Species records and distributions were taken from Desbruyeres et al.*, (2006). Taxonomic status was updated using the World Register of Marine Species. Abbreviations: * vent species;* ^{Ch} *species found at other chemosynthetic habitats;* ^{G} *general deep-sea species. These assignations were made based on the text and species listing of Desbruyeres* et al.*, (2006).*

Phylum	Common name	Species name
Foraminifera	Foram	*Luffammina atlantica**
Porifera	Sponge	*Asbestopluma (Asbestopluma) pennatula*^{G}, *Cladorhiza abyssicola*^{G}, *Euchelipluma pristina*^{G}
Cnidaria	Hydroid	*Candelabrum phrygium*^{G}, *C. serpentarii**, *Ectopleura larynx*^{G}, *Eudendrium rameum*^{G}, *Grammaria abietina*^{G}, *Halisiphonia arctica**, *Hydrallmania falcata*^{G}, *Lafoea dumosa*^{G}, *Polyplumaria flabellata*^{G}, *Sertularella tenella*^{G}, *Stegolaria geniculata*^{G}, *Symplectoscyphus bathyalis*^{G}, *Zygophylax echinata**, *Z. leloupi**
	Anemone	*Maractis rimicarivora**
Mollusca	Limpet	*Divia briandi**, *Lepetodrilus atlanticus**, *Paralepetopsis ferrugivora**, *Pseudorimula midatlantica**, *Sutilizona pterodon**

	Sea snail	*Alvania stenolopha*, Laeviphitus desbruyeresi*, Lirapex costellatus*, Lurifax vitreus*, Neusas marshalli*^{G}*, Peltospira smaragdina*, Phymorhynchus carinatus*, Ph. moskalevi*, Ph. ovatus*, Protolira thorvaldssoni*^{Ch}*, Pr. valvatoides*, Xylodiscula analoga**
	Sea slug	*Dendronotus comteti**
	Mussel	*Bathymodiolus azoricus*, B. puteoserpentis**
	Octopus	*Cirrothauma magna*^{G}
Nematoda	Nematode	*Moravecnema segonzaci**
Annelida	Scale worm	*Branchipolynoe seepensis*^{Ch}*, Lepidonotopodium jouinae*, Levensteiniella iris**
	Bristle worm	*Amphisamytha lutzi*, Glycera tesselata*^{G}*, Laonice asaccata*, Prionospio unilamellata**
	Tube worm	*Spiochaetopterus* sp.*
Arthropoda	Mite	*Halacarellus auzendei**
	Sea spider	*Sericosura heteroscela*, Sericosura mitrata*^{G}
	Benthic copepod	*Ambilimbus arcuscelestis*, Aphotopontius atlanteus*, Bathylaophonte azorica*, Heptnerina confusa*, Rimipontius mediospinifer*, Smacigastes micheli*, Stygiopontius cladarus*, St. latulus*, St. mirus*, St. pectinatus*, St. regius*, St. rimivagus*, St. serratus*, St. teres**
	Cumacean	*Bathycuma brevirostre*^{G}
	Tanaid	*Armaturatanais atlanticus*, Leptognathiella fragilis*, Mesotanais styxis*, Obesutanais sigridae*, Pseudotanais vulsella*^{G}*, Typhlotanais incognitus**
	Isopod	*Heteromesus calcar*, H. ctenobasius**
	Amphipod	*Gitanopsis alvina*, Autonoe longicornis*, Bouvierella curtirama*, Kyphometopa saldanhae*^{G}*, Luckia strike*, Bonnierella compar*, Steleuthera ecoprophycea*, Stenothoe menezgweni**
	Shrimp	*Alvinocaris markensis*, A. williamsi*, Mirorcaris fortunate*, Rimicaris chacei*, R. exoculata*, Thysanoessa parva*^{G}
	Squat lobster/Lobster	*Munidopsis acutispina*^{Ch,G}*, Munidopsis exuta*, Thymopides laurentae**
	Crab	*Bathynectes maravigna*^{G}*, Chaceon affinis*^{G}*, Segonzacia mesatlantica**
Echinodermata	Brisingid	*Brisinga endecacnemos*^{G}
	Sea urchin	*Gracilechinus alexandri*^{G}
	Brittlestar	*Ophiactis tyleri*, Ophioctenella acies*^{Ch}
Chaetognatha	Arrow worm	*Calispadella alata**

Global occurrence records for hydrothermal vent taxa have been used to conduct biogeographic analyses, to understand the relationship between vent fauna in different regions. Biogeographic studies depend on the number of vent fields explored, and the methods and underlying hypotheses used to delineate them. Different analyses have characterised the northern MAR as either a single biogeographic province (Bachraty *et al.*, 2009; Moalic *et al.*, 2012; Figure 10.12) or split it into two (Van Dover *et al.*, 2002). Whilst the most recent of these analyses consider the northern MAR to be one province, they do not include faunal records from the Moytirra vent field discovered North of the Azores (Moytirra *et al.,* 2013). Future biogeographic analyses using these and other new records may alter the current view of hydrothermal vent biogeographic provinces.

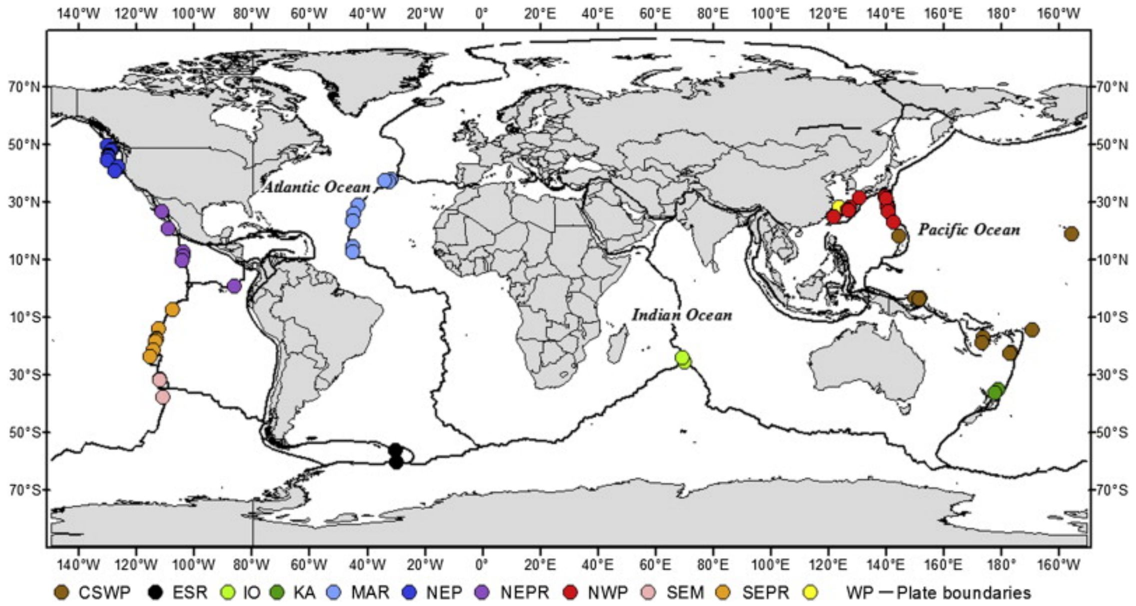

Figure 10.12. Map of the global biogeography of hydrothermal vents communities, after Rogers et al. *(2012). Abbreviations are CSWP: Central South West Pacific, ESR: East Scotia Ridge, IO: Indian Ocean, KA: Kermadec Arc, MAR: Mid-Atlantic Ridge, NEP: Northeast Pacific, NEPR: North East Pacific Rise, NWP: North West Pacific, SEM: South of the Easter Microplate, SEPR: South East Pacific Rise, WP: Western Pacific. Reproduced from Boschen* et al.*, (2013).*

At the regional scale, apart from the earlier work of Desbruyeres *et al.,* (2000), there have been few studies on the differences between vent fauna at different localities along the MAR. As for all the benthic habitats along the MAR, the megafauna is the best studied group at hydrothermally active hard substrata. This is in part because they can be studied more readily through imagery, whereas macrofauna are often too small to be reliably identified using imagery alone. Whilst some macrofauna, such as certain polychaetes and gastropods may be identifiable from imagery, abundances of these taxa generated from imagery are often considerably lower than abundances generated from physical samples (Cuvelier *et al.,* 2012). Some macrofaunal taxa which were identifiable from physical samples at the Eiffel Tower in the Lucky Strike vent field were not recorded from imagery, including smaller polychaetes and gastropods, pycnogonids, ostracods, actinids, halacarids, nematodes, copepods, tanaids and amphipods (Cuvelier *et al.,* 2012). Considering that many biogeographical analyses are based on the megafauna and larger macrofauna visible from imagery, some of these analyses may not capture the regional differences in distribution of the smaller size-class fauna.

10.1.7.2.2 Megafauna

Whilst some species are shared between one or more vent sites, different vent sites are often characterised by different groupings of hydrothermal vent fauna, with the dominant species changing between sites. The different habitats within vent fields are also dominated by different species, and there are patterns in species dominance related to latitude and depth (for example fauna, see Figure 10.13). These patterns are generally characterised using observations of megafauna distribution, as these can be more readily surveyed using imagery. At Moytirra (45° 28'N: 2095 m) the dominant species in high temperature fluid areas were *Peltospira* sp. limpets and *Mirocaris* sp. shrimp, whilst bathymodiolid mussels were absent from the vent field (Wheeler *et al.,* 2013). Moving South, as summarised by Rybakova & Galkin (2015), Menez Gwen (37° 51'N: 840 – 865 m) and Lucky Strike (37° 17'N: 1620 – 1730 m) were dominated by the vent shrimp *Mirocaris fortunata* in high temperature (20 – 40°C) habitats, and the vent mussel *Bathymodiolus azoricus* in lower temperature (2 – 20°C) habitats. Continuing South, high temperature habitats are dominated by the shrimp *Rimicaris exoculata* at Rainbow (36° 13'N: 2260 – 2350 m), Broken Spur (29° 10'N: 3000 m), Snake Pit (23° 23'N: 3480 m) and Logatchev (14° 45'N: 2930 – 3020 m). Low temperature habitats remained dominated by *Bathymodiolus azoricus* at Rainbow, but switched to dominance by *Bathymodiolus puteoserpentis* at

Broken Spur, through Snake Pit and Logatchev. Broken Spur represented a hybridization zone between *B. azoricus* and *B. puteoserpentis*, with both species present and apparently able to interbreed (O'Mullan *et al.,* 2001; Breusing *et al.,* 2015). The hard substrata of the most southern vent field on the northern MAR, Ashadze-1 (12° 58'N: 4080 m) was dominated in terms of biomass by the sea anemone *Maractis rimicarivora*, whilst Bathymodiolid mussels were absent (Fabri *et al.,* 2011). Of the vent shrimp present at Ashadze-1, *M. fortunata* occurred in the highest abundance (Fabri *et al*., 2011). These differences between more northern shallow vent sites and deeper southern sites along the northern MAR led to the shallow North and deeper South being interpreted as separate vent fauna biogeographic provinces by Van Dover *et al*., (2002).\

Figure 10.13. Bathymodiolus *mussels,* Rimicaris *shrimp and vent crabs on the northern Mid-Atlantic Ridge. Reproduced with permission: © SEAHMA - PDCTM/MAR/15281/1999.*

10.1.7.2.3 Macrofauna

There are some quantitative studies of the macrofauna at hydrothermally active hard substrata along the MAR, however these studies are few in number and collectively span a relatively small number of hydrothermally active sites. Studies on the vent mussel bed fauna of areas along the northern MAR indicate that different mussel bed sites support different macrofaunal assemblages, with the structure of these assemblages thought to be related to depth and spatial separation (Van Dover & Doerries, 2005). Quantitative samples of the bathymodiolid vent mussels and associated macrofauna were compared from Logatchev (Van Dover & Doerries 2005), Snake Pit (Turnipseed *et al.,* 2004) and Lucky Strike (Van Dover & Trask 2000). The benthic macrofauna at Logatchev mussel bed was dominated by the ophiuroid *Ophioctenella acies*, whilst Lucky Strike was dominated by the amphipod *Bouvierella curtirama* (Van Dover & Doerries 2005). Logatchev and Snake Pit mussel beds shared 55% of associated macrofaunal benthic invertebrate species, whereas Logatchev and Snake Pit only shared 20 – 25% of species with Lucky Strike. Statistical analyses demonstrated that Logatchev, Snake Pit, and Lucky Strike mussel bed macrofauna had different species-abundance characteristics (Van Dover & Doerries, 2005). More recent work by Rybakova and Galkin (2015) identified Menez Gwen mussel beds as being different from all other MAR mussel beds, through dominance of the vent limpet *Lepetodrilus atlanticus.*

10.1.7.2.4 Meiofauna

There are some quantitative studies of the meiofauna at hydrothermally active hard substrata along the MAR, however these studies are few in number and collectively span a relatively small number of hydrothermally active sites. From these studies, it appears that meiofaunal diversity may be low, with only 15 meiofauna species found associated with *B. puteoserpentis* mussel beds at Snake Pit (Zekely et al., 2006a). These metazoan meiofauna consisted of seven nematode species, six copepod species, one ostracod species and one mite species. Of these, nematodes were the most numerous, representing 63 % of the sampled meiofauna individuals, and all seven species were new to science.

Copepods were the second most numerous, representing 35 % of the meiofauna, with two species new to science (Zekely et al., 2006a). A similar low diversity of meiofauna was observed at Lucky Strike *B. azoricus* mussel beds, where 25 meiofaunal taxa were identified following a 2-year colonisation experiment (Cuvelier *et al.,* 2014). The same broad meiofaunal taxa were recorded from Lucky Strike as from Snake Pit, including nematodes, copepods and a mite species.

10.1.7.2.4.1 Nematoda

Both Zekely *et al.,* (2006a) and Cuvelier *et al.,* (2014) found nematodes to be typically the most numerous meiofauna at the MAR. Until recently, only one nematode species was described from the MAR, *Halomonhystera vandoverae*, which was sampled from *B. puteoserpentis* mussel beds at Snake Pit (Zekely *et al.,* 2006b). Tchesunov (2015) identified a total of 26 nematode morpho-species from MAR hydrothermal vent sites, although only seven of these could be described and identified to species level. Four of these nematodes were new species, and all were associated with *B. azoricus* mussels: *Paracanthonchus olgae* from Rainbow; and *Prochromadora helenae, Prochaetosoma ventriverruca*, and *Leptolaimus hydrothermalis* from Lucky Strike. *Oncholaimus scanicus* was formerly known only from the type locality in the Norway Sea, but was recorded by Tchesunov (2015) in high abundances at Menez Gwen (98.5% of nematodes collected), and at Lucky Strike and Lost City sites in lower abundances. *Oncholaimus scanicus* from Menez Gwen and Lucky strike were sampled from *B. azoricus* mussel beds, however bathymodiolid mussels do not occur at Lost City, and the *O. scanicus* individuals sampled from this site occurred in bacterial mat on rocks. Tchesunov (2015) noted that *O. scanicus* from Lost City were morphologically distinct from individuals at Menez Gwen and Lucky Strike, and that genetic studies were needed to determine if the Lost City individuals were a different species.

A recent study by Zeppilli *et al.,* (2019) suggests that *O. scanicus* collected from the MAR may be a new species, *O. dyvae*, although this has yet to be accepted by the World Register of Marine Species. *Desmodora marci* was formerly known from hydrothermal sites in the Pacific but was recorded from Lucky Strike by Tchesunov (2015). Lucky strike was the site with the most abundant (700 individuals) and diverse (16 species morpho-species) nematodes, whilst Lost City had the lowest abundance (172 individuals) but similar diversity (14 morpho-species). The northern-most site Menez Gwen, and southern-most site Snake Pit, were both characterised by low diversity with high dominance of one species; *O. scanicus* for Menez Gwen (99 % of specimens: Tchesunov, 2015) and *H. vandoverae* for Snake Pit (75 – 91 % of specimens: Zekely *et al.,* 2006b; Tchesunov, 2015).

10.1.7.2.4.2 Copepoda

Copepods were consistently the second most abundant meiofauna at hydrothermal sites along the MAR (Zekely *et al.,* 2006a; Cuvelier *et al.,* 2014). The most common of these were dirivultid copepods, a family of copepods which occur almost exclusively at hydrothermal vents (Gollner *et al.,* 2010a). Twelve dirivultid copepods from three genera have been recorded from MAR vents. One genus, *Rimipontius*, is endemic to the MAR, the other two genera *Stygiopontius* and *Aphotopontius* have been recorded from multiple regions in the Pacific Ocean. The majority of MAR dirivultids only occur along the MAR, however four species *Stygiopontius mirus, Stygiopontius rimivagus, Stygiopontius pectinatus* and *Aphotopontius forcipatus,* have been recorded from at least one Pacific Ocean region (Gollner *et al.,* 2010a). Harpacticoid copepod species have also been recorded from the MAR, with *Smacigastes micheli* being reported several times from *B. azoricus* mussel beds at Lucky Strike (Ivanenko & Defaye, 2004; Ivanenko *et al.,* 2012; Cuvelier *et al.,* 2014), *Bathylaophonte azorica* reported from Snake Pit and Lucky Strike (Zekely *et al.,* 2006a; Cuvelier *et al.*, 2014), and *Xylora bathyalis* found both at Lucky Strike and at East Pacific Rise vents (Cuvelier *et al.,* 2014, Gollner *et al.*, 2010b).

10.1.7.3 Hydrothermally inactive sulphide substrata

The benthic invertebrates of inactive sulphide habitat are poorly characterised in all regions, with practically nothing known about this fauna along the MAR. Whilst there is the potential for benthic invertebrate species to occur that are endemic to the weathered sulphide environment (Van Dover 2011), there is currently no evidence for this along the MAR. Invertebrate-symbiont associations, similar to those seen at hydrothermally active habitat, are as yet unknown from inactive sulphides (Van Dover 2019).

To date, there are no publically available, dedicated studies of benthic fauna occurring at MAR inactive sulphides and the regional distribution of this fauna is unknown. The majority of inactive sulphide occurrences reported along the MAR do not describe biological communities in association with inactive sulphide habitat (Rona *et al.*, 1993; Krasnov *et al.,* 1995; Lalou *et al.,* 1998; Gablina *et al.,* 2012; Bel'tenev *et al.,* 2017). However, this apparent absence of biological communities may reflect the geological focus of these studies and not a true absence of fauna at inactive sulphides. Small patches of inactive sulphide substratum on the Eiffel Tower edifice, Lucky Strike, were colonised by scavenging bythorgraeid crabs and hydroids, as identified from imagery survey (Cuvelier *et al.,* 2009). A similar occurrence of mobile scavengers, including bythograeid crabs, was reported from the inactive sulphide edifice Mag Mell in the Moytirra vent field (Wheeler *et al.,* 2013).

Preliminary data on inactive sulphide fauna collected along the MAR between 12°58'N and 13°31'N using geological sampling gear suggested that fauna is scarce on inactive sulphide habitat (Molodtsova *et al.,* 2014). The fauna collected was mostly represented by sessile suspension feeders, such as Porifera (sponges), Alcyonacea (soft corals), Antipatharia (black corals), Hydrozoa (hydroids), Cirripedia (barnacles) and Bryozoa (bryozoans) (Molodtsova *et al.,* 2014). Some of the species collected from hydrothermally inactive sulphide habitat, such as the black coral *Alternatipathes alternata*, golden coral *Metallogorgia melanotrichos* and its associated basket star *Ophiocreas oedipus* are widely-distributed, lower bathyal-species (Molodtsova *et al.,* 2014). There did not appear to be any benthic megafaunal species endemic to inactive sulphide habitat collected during this survey.

Studies in other regions suggest that not all inactive sulphide habitat is colonised by benthic invertebrates. Some inactive sulphide chimneys along the Kermadec Arc in the southwest Pacific appeared to be devoid of benthic invertebrate megafauna, whereas other chimneys supported elevated abundances of fauna (Boschen *et al.,* 2016). Studies in the southwest Pacific suggest that where benthic invertebrate assemblages occur at inactive sulphides, they tend to be dominated by suspension feeding hard corals, soft corals, anemones, hydroids, sponges, crinoids, brittlestars, brisingids and urchins (Galkin 1997; Collins *et al*., 2012; Boschen *et al.,* 2016; Sen *et al.,* 2014). Some of these organisms can be sessile and slow-growing, such as hard corals observed on inactive sulphide chimneys along the Kermadec Arc, which were estimated to be at least 160 years old (Boschen *et al.,* 2016). The vast majority of benthic invertebrates observed at inactive sulphide habitat to date have also been recorded from non-hydrothermal hard substrata in the region, suggesting a broad regional distribution of taxa occurring at inactive sulphides. However, some of these taxa can occur in greater numbers at inactive sulphides, with the grouping and abundance of these taxa being 'unique' to inactive sulphide habitat (Boschen *et al.,* 2016).

Occasionally, benthic invertebrates more typical of hydrothermally active hard substrata may be observed at inactive habitat, however these are not considered true 'inactive' sulphide fauna. Van Dover (2019) provides three explanations for the occurrence of vent endemic fauna at inactive sulphide habitat: 1) hydrothermal activity has recently ceased at the site but has not yet resulted in the mortality of all vent-endemic fauna; 2) fluid flows have waned below detectable levels, so the habitat appears 'inactive' when low-level activity continues; 3) some vent species, such as bathymodiolid mussels, may be able to feed independently of chemosynthetic symbionts for short periods post vent fluid cessation.

10.1.7.4 Soft sediment substrata

10.1.7.4.1 Biogeography and biodiversity

Given that sedimented gentle slopes and discontinuous flat plains make up > 95 % of the MAR (Niedzielski *et al.,* 2013) many of the benthic invertebrates inhabiting soft sediments may have broad regional distributions. Species records of benthic megafauna in the deeper parts of Reykjanes Ridge (> 1000 m) determined that approximately 60 % of the benthic invertebrate species on the Reykjanes Ridge section of the MAR at bathyal depths occurred at similar depths on the continental margins on both sides of the Atlantic (Mironov & Gebruk 2006b; Alt *et al.,* 2013; Alt *et al.,* 2019). The soft-sediment fauna of the Reykjanes Ridge section of the MAR appears to have greater linkages with the bathyal eastern Atlantic than the bathyal western Atlantic, with 3.7 times more species shared with the eastern Atlantic (Mironov & Gebruk, 2006b). Some faunal groups of the MAR even share species with other oceans, such as stony coral and asteroid species, which according to Mironov & Gebruk (2006b) shared 38% of species sampled with the Pacific Ocean fauna. Only 1% of the invertebrate species sampled on the Reykjanes Ridge section of the MAR were endemic to the MAR (Mironov & Gebruk, 2006b).

There are differences between the benthic invertebrate fauna of the Reykjanes Ridge section of the MAR and the MAR between north of the Azores and the CGFZ, which is thought to represent a biogeographic boundary occurring near the CGFZ (Dilman, 2008, Mironov & Gebruk 2006b; Gebruk *et al.,* 2010). This major faunal boundary appeared to correlate with the position of the overlying Sub-Polar Front in surface waters, which influences primary productivity and particle flux to the seabed north and south of the front (Gebruk *et al.,* 2010).

More recent work by Alt *et al.,* (2019) suggests that the MAR may act as a stronger barrier between the eastern and western Atlantic basins to the North of the CGFZ than it does to the South of the CGFZ. Soft-sediment benthic megafauna communities either side of the MAR were similar South of the CGFZ, whereas communities either side of the MAR North of the CGFZ were distinct (Alt *et al.,* 2019). However, this biogeographic boundary did not apply to all of the soft-sediment benthic invertebrate faunal groups sampled. For example, the large foraminiferan *Discospirina italica* (approximately 1 cm diameter) occurred either side of the MAR and North and South of the CGFZ, and has also been recorded from the Indian Ocean (Gooday *et al.*, 2013). Very little is known about the potential for other fracture zones along the MAR, such as Vema or the Romanche fracture zones, to act as barriers to benthic fauna North and South of these fractures zones. However, given the apparent role of the CGFZ and overlying Sub-Polar Front in structuring benthic communities, it is possible that Vema and the Romanche fracture zones could have similar influences on regional distribution.

The benthic invertebrate fauna of soft sediments along the MAR can be very diverse, with sampling within the Russian Exploration Area collecting at least 136 species, based on both live and dead material (Molodtsova *et al.,* 2017). The most common species in all hauls was the hermit crab *Parapagurus* cf. *nudus*, whilst the brittlestars *Ophiotypa simplex* and *Ophiomusium* cf. *lymani* were recorded from several stations and appeared to be widespread (Molodtsova *et al.,* 2017). Several species of abyssal bryozoans and the sea anemone *Monactis vestita* also occurred in a number of soft sediment samples, with the brachiopod *Nanacalathis atlantica* being unexpectedly abundant in two samples (Molodtsova *et al.,* 2017). This brachiopod species was previously described on the basis of one empty shell, with the new material enabling a full re-description of this poorly known species (Bitner & Molodtsova, 2017). *Nanacalathis atlantica* is now known to occur in the Central Western Atlantic (off the Bahamas), at Great Meteor Seamount and in the northern tropical Mid-Atlantic Ridge. Some *N. atlantica* specimens were attached to pteropod shells, which have also been found in high concentrations on the seafloor in some locations along the MAR, such as South of the Charlie Gibbs Fracture Zone (CGFZ) (Alt *et al.,* 2019). Sea stars were only recorded from shallower stations, not deeper than 2700 m within the Russian Exploration Area, whilst sea cucumbers were only occasionally observed (Molodtsova *et al.,* 2017).

Two ascidians (sea squirts) were only recorded from deeper samples, *Bathystyeloides enderbyanus* and *Proagnesia depressa*, as was the pen coral *Umbellula* sp. Taxonomic studies of the benthic invertebrates collected from soft sediment habitat within the Russian Exploration Area are ongoing, with the aim for results for different taxa to be published separately (Molodtsova *et al.,* 2017).

10.1.7.4.2 Megafauna

The most regional distribution information is available for the larger (megafauna) benthic invertebrates inhabiting soft sediment along the MAR, as records for megafaunal species can be obtained from physical sampling via trawl or Remotely Operated Vehicle (ROV), and also from video survey, as they are large enough to be identified from imagery. Differences in benthic megafauna at soft sediment locations along the MAR can also be visually determined by marks in the sediment surface (lebensspuren) created through the bioturbation of large epibenthic and infaunal organisms (Bell *et al.,* 2013). Lebensspuren for the CGFZ of the MAR provided an alternative impression of the abundance, activity and distributions of organisms that live on and in sediments, and suggested that different lebensspuren-forming megafaunal assemblages occurred both East and West of the MAR, and North and South of the CGFZ (Bell *et al.,* 2013). Information on lebensspuren distribution on sediments at 4200 – 4500 m water depth along the MAR was also obtained through manned submersible dives during the MAR-ECO project (Felley *et al.,* 2008).

Physical samples of the MAR benthic megafauna from North of the Azores to South of the Reykjanes Ridge from predominantly sedimented areas during MAR-ECO were dominated by the phylum Echinodermata, which comprised 49.5 % of the total species sampled (Gebruk *et al.,* 2010). More comprehensive distribution information is available for the benthic soft sediment fauna in this area, than from South of the Azores to the Equator. Information collected from this northern area is used to discuss the regional distributions of echinoderm classes (Holothuroidea, Ophiuroidea, Asteroidea and Echinoidea) and Enteropneusta recorded from soft sediments along the MAR in more detail below.

10.1.7.4.2.1 Holothuroidea (sea cucumbers)

Holothurians (sea cucumbers) were a conspicuous element of the sediment fauna on the MAR, as observed by Remotely Operated Vehicle (ROV) survey (Gebruk & Krylova 2013; Figure 10.14). During the MAR-ECO expedition, holothurians were collected from the MAR between the Azores and the southern tip of Reykjanes Ridge, and were the most diverse megafaunal group in the total trawl catch (Gebruk, 2008). In total, 36 species were collected, including four news species: *Benthodytes gosarsi*, *Penilpidia midatlantica*, *Peniagone marecoi* and *Peniagone longipapillata* (Gebruk, 2008). Thirty-two species of holothurians were also collected from the Charlie-Gibbs Fracture Zone region by ECOMAR, including a further three new species, *Laetmogone billetti*, *Ellipinion alani*, *Peniagone coccinea* (Rogacheva *et al.,* 2013). Whilst there was some overlap in holothurian species collected by MAR-ECO and ECOMAR, sampling occurred at different depths and across different sections of the MAR meaning that some additional species were collected by each expedition (Rogacheva *et al.,* 2013).

The holothurians collected from the MAR during ECOMAR belong to the following ecological categories (Rogacheva *et al.,* 2012): infaunal (5 species), epibenthic (6 species) and benthopelagic (21 species). Most epibenthic deep-sea holothurians are deposit feeders with the majority of MAR holothurians typically found on flat areas of soft sediments (Rogacheva *et al.,* 2012). *In situ* observations discovered that 17 of the species identified during ECOMAR could swim, with swimming ability thought to enable holothurians to reach otherwise inaccessible feeding locations, such as cliffs and steep slopes (Rogacheva *et al.,* 2012).

Some holothurians observed from the MAR can occur in large numbers, with aggregations (23 – 76 individuals per m^2) of small (10 – 15 mm length) *Kolga nana* holothurians discovered in the CGFZ region (Gebruk & Krylova 2013). Aggregations of *K. nana* have also been observed at the Porcupine Abyssal Plain (aggregations with a mean density of 50 individuals per m^2), where *K. nana* were thought to aggregate in response to periodical fluxes of organic matter to the seafloor (Billett & Hansen, 1982).

Figure 10.14. In-situ images of holothurians (sea cucumbers) from the northern Mid-Atlantic Ridge in the vicinity of the Charlie Gibbs Fracture Zone. Left: Ellipinion alani*; centre:* Laetmogone billetti*; right:* Peniagone longipapillata*. Images taken by the ISIS ROV during the RRS James Cook ECOMAR cruise 048 in 2010. Courtesy of Monty Priede and Andrey Gebruk.*

10.1.7.4.2.2 Ophiuroidea (brittlestars)

Ophiuroids (brittlestars) were also observed on the soft sediments of the MAR (Gebruk & Krylova, 2013), although they can also occur on non-hydrothermal hard substrata, and two species have been recorded from hydrothermally active areas of the MAR. Martynov & Litvinova (2008) provide the most comprehensive account of recent MAR ophiuroid collections, although it is not always clear whether species were collected from soft sediment or non-hydrothermal hard substrata. A total of 31 ophiuroid species were identified from the section of the MAR between the Reykjanes Ridge and the Azores. The majority of these species had broad distributions, with 74 % of species shared between the Reykjanes Ridge and the MAR between the CGFZ and the Azores. 52 % of species occurred along the MAR and on both the East and West sides of the North Atlantic, with 35 % of species occurring along the MAR and in either the East or the West. Only 13 % (four species) had a species distribution limited to the MAR, and of these three were new species. *Ophiura nitida* was previously described from Reykjanes Ridge, and was sampled form the CGFZ during MAR-ECO. *Ophioplinthus pseudotessellata* was described from the MAR North of the Azores, *Ophiocamax patersoni* was described from the MAR North of the Azores and the CGFZ, and *Ophiophyllum nesisi* was described from the Reykjanes Ridge (Martynov & Litvinova, 2008).

10.1.7.4.2.3 Asteroidea (sea stars)

Asteroids (sea stars) were found at all of the MAR-ECO stations, typically on sediment, at depths ranging from 966 to 3509 m (Dilman, 2008). Despite the geographical proximity, the asteroid fauna collected from the Azores to the southern tip of Reykjanes Ridge (Dilman, 2008) and the Reykjanes Ridge (Dilman, 2006) were different. Whilst a similar number of species were identified from both regions (32 from Reykjanes Ridge, and 34 from the MAR-ECO samples), only 11 species were shared between these regions at the same depth, with 25 species occurring northward of 57° N and 30 species occurring southward of 53° N (Dilman, 2008; Dilman, 2013). This provides additional support for the occurrence of a biogeographic boundary around 53° N to 57° N, coinciding with the Charlie-Gibbs Fracture Zone and the Sub-Polar Front (Dilman, 2008). The subsequent ECOMAR expedition also identified a similar number of asteroids (30 species) from the CGFZ, providing the first records on the MAR north of the Azores for 11 species.

Alongside extension of the vertical and geographic ranges for many species, MAR-ECO and ECOMAR also provided descriptions of three new species, *Hymenasterides mironovi* (Dilman, 2008), *Hymenaster ecomari* and *Hymenaster rotundus* (Dilman, 2013). Apart for the new species, all of the asteroids identified from the Azores to Reykjanes Ridge during MAR-ECO and ECOMAR had broad distributions, occurring either in other parts of the Atlantic (in the North-East, North-West, or South) or in other oceans. The link with asteroid fauna from other oceans varied by species, with many species occurring in at least one other ocean (Indian, Pacific or Southern Oceans), whilst some species distributions extended into either the Arctic or Antarctic polar regions (Dilman, 2008; Dilman, 2013). Given the generally broad distributions of asteroid species identified from the MAR, additional sampling efforts may discover a wider distribution for the new species described during MAR-ECO and ECOMAR. Summarizing records from the Reykjanes Ridge and MAR-ECO and ECOMAR expeditions, 69 asteroid species are now known to occur between south of Iceland and 42° N off the Azores (Dilman, 2013).

10.1.7.4.2.4 Echinoidea (sea urchins)

Echinoids (sea urchins) were collected from fourteen out of the sixteen MAR-ECO sampling locations between the Azores and Reykjanes Ridge (Gebruk *et al.,* 2010), with certain groups, such as pourtalesiid echinoids, often observed on soft sediment (Gebruk & Krylova, 2013; Figure 10.15). Thirteen species of echinoids were collected during the MAR-ECO expedition (Gebruk *et al.,* 2010), including at least one new species, *Solenocystis imitans* (Mironov 2008). Comparison with records of 29 echinoid species collected from seamounts and continental slopes of the northeast Atlantic (Mironov 2006) indicate that some echinoids appear to be restricted, whilst other echinoid species are more widely distributed. Eight of the species collected by MAR-ECO appear to have only been recorded from the MAR; the other five echinoid species have wide regional distributions, with one species occurring on the CGFZ of the MAR and the European continental slope, and four species occurring at the CGFZ of the MAR and continental slopes and seamounts in the northeast Atlantic (Mironov 2006; Mironov 2008).

Figure 10.15. In-situ *images of echinoids (sea urchins) from the northern Mid-Atlantic Ridge in the vicinity of the Charlie Gibbs Fracture Zone. Left:* Echinus *sp.; right:* Pourtalesia *sp. Images taken by the* ISIS *ROV during the* RRS James Cook *ECOMAR cruise 048 in 2010. Courtesy of Monty Priede and Andrey Gebruk.*

10.1.7.4.2.5 Enteropneusta (acorn worms)

Enteropneusta (acorn worms) were also conspicuous, albeit infrequent, members of the soft sediment megafauna at the CGFZ of the MAR (Figure 10.16). Three new species were identified during ECOMAR, *Yoda purpurata*, *Tergivelum cinnabarinum,* and *Allapasus isidis* (Priede *et al.,* 2012). Enteropneusts are thought to be able to float in the water column to passively move from one benthic foraging site to the next, in a similar fashion to benthopelagic holothurians, and produce distinctive feeding patterns on the seafloor (Priede *et al.,* 2012). Very little is known about enteropneusts in general, and there is insufficient information available to describe their regional distribution along the MAR. On a local scale, enteropneust lebensspuren exhibited a clumped distribution, suggesting a relationship with the quality of the substrata for feeding (Felley *et al.,* 2008).

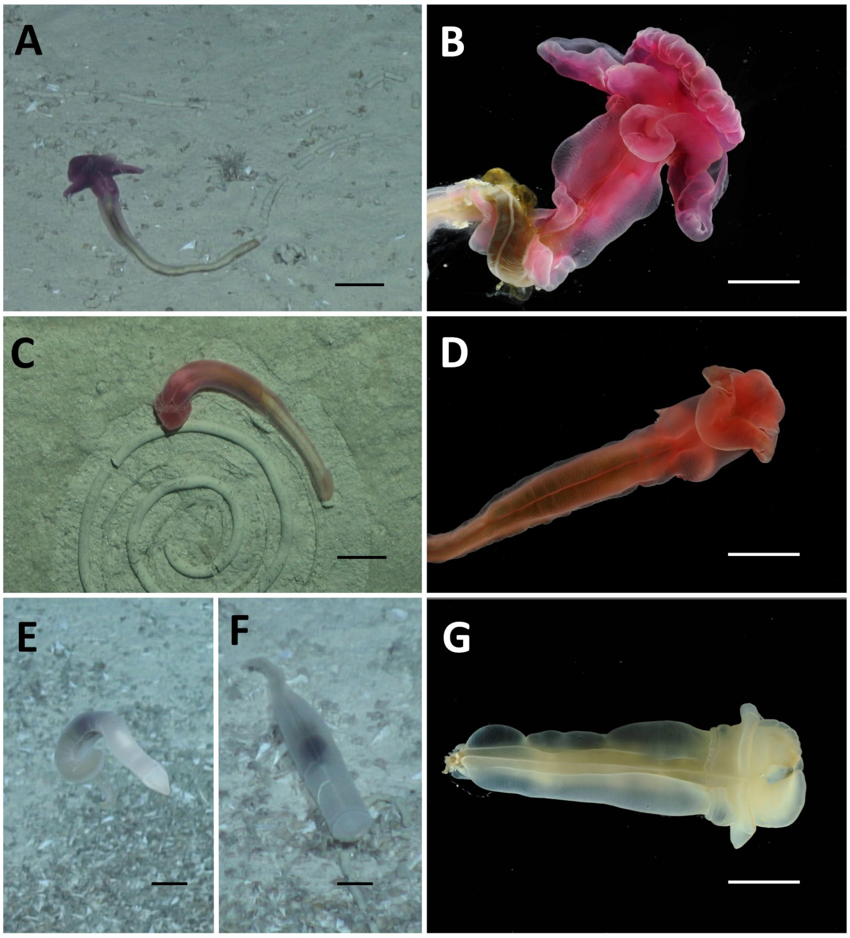

Figure 10.16. Three new species of enteropneustes (free-living acorn worms) discovered on the Mid-Atlantic Ridge (Priede et al. *2012).* Yoda purpurata *A: On the sea floor before capture. B: Fresh, in chilled aquarium on board ship.* Tergivelum cinnabarinum *C: On the sea floor before capture, note the spiral trace it produces. D: In aquarium.* Allapasus isidis *E: curled body floating 0.5 m above the sea floor, F: Settled on the sea floor, G: In aquarium. Scale bars 2 cm long except E, F and G where it is 1 cm long. All specimens were found at around 2500 m depth. Courtesy of Monty Preide and David Shale.*

10.1.7.4.3 Macrofauna

Less is known about the regional distribution of smaller (macrofauna) benthic invertebrates at soft sediments along the MAR, in part because these may not be too small to sample by trawl, and because they are too small to identify from video or may live below the sediment surface. Almost nothing is known about the regional distribution of the smallest metazoan benthic invertebrates (meiofauna) found at soft sediments along the MAR. Four macrofaunal groups were collected from different sites along the MAR during MAR-ECO and ECOMAR, and are considered below: Polychaeta, Echiura (a subclass of Polychaeta), Sipunculida, and Isopoda.

10.1.7.4.3.1 Polychaeta (bristle worms)

Polychaete worms were the most abundant and diverse (133 identified species) members of the macrofaunal soft sediment community sampled from the CGFZ of the MAR during ECOMAR (Shields & Blanco-Perez, 2013). The majority of polychaete species occurred in the upper 2 cm of sediment at all sites, with the dominant polychaete families in terms of abundance being Spionidae, Cirratulidae, Syllidae and Glyceridae. Rarefaction curves of individuals versus species for each site did not reach an asymptote, suggesting that despite the high number of species identified, this did not represent the full range of species occurring at the CGFZ (Shields & Blanco-Perez, 2013). Comparisons between samples collected from the North East, North West, South East and South West of the CGFZ found no significant difference in polychaete abundance, biomass or diversity between either side of the MAR, or North and South of the CGFZ. This suggested that that neither the CGFZ nor the MAR presented a physical barrier to the distribution of bathyal polychaetes (Shields & Blanco-Perez, 2013).

10.1.7.4.3.2 Echiura (spoon worms) and Sipuncula (peanut worms)

Very little is known about the Echiura (spoon worms) and Sipuncula (peanut worms) of the soft sediment along the MAR. Echiurans were considered separately form polychaetes during MAR-ECO, although they were subsequently made a subclass within Polychaeta. In the North Atlantic more broadly, at least 24 species of bathyal and abyssal echiurans have been recorded, whilst at least 23 species of deep-sea sipunculans are known from this region (Murina, 2008). Echiurans were collected from five of the MAR-ECO sites, including the known species *Jakobia birsteini* and new species *Jakobia edmonsi*. So far, the new echiuran species is only known from the MAR between the Azores and Reykjanes Ridge, whereas *J. birsteini* has been recorded from the CGFZ along the MAR, the Romanche Trench and also from the Pacific. Sipunculans were collected from eight of the sixteen sites, and comprised of three known species or sub-species: *Golfingia (Golfingia) anderssoni*, *Phascolosoma (Phascolosoma) agassizii agassizii,* and *Sipunculus (Sipunculus) norvegicus* (Murina 2008; Gebruk *et al.,* 2010). All three of these sipunculans are widespread, occurring in multiple oceans.

10.1.7.4.3.3 Isopoda

Even less is known about the regional distribution of Isopoda occurring in the soft sediment along the MAR. Seven isopods were identified from the MAR-ECO material, but only two could be confidently identified to species level; *Aegiochus sarsae* was a new species, whilst *Syscenus atlanticus* had been previously recorded from other locations in the North Atlantic, including off north-east America and West Greenland (Brandt & Andres, 2008). A subsequent expedition along the Vema Fracture Zone (occurring at approximately 11° N) suggested that certain macrostylid isopods have ranges extending more than 2000 km, in some cases across ocean ridges and trench-abyss transitions, although there was some evidence of population structure either side of the MAR (Reihl *et al.,* 2018). At least one isopod was collected from the Russian Exploration Area, *Munneurycope* sp., which only occurred in the deepest sample (Molodtsova *et al.,* 2017).

10.1.7.5 Hydrothermal sediment benthic invertebrates

Whilst there is some information available on the benthic invertebrates living on or within soft sediments of pelagic origin along the MAR, very little is known about the benthic invertebrate community of soft sediments of hydrothermal origin. There is almost nothing known for benthic invertebrates occurring in hydrothermally inactive sediments, other than the apparent association of *Paleodictyon nodosum* traces (Figure 10.17) with sediments surrounding inactive sulphide mounds at the TAG hydrothermal mound (Van Dover, 2019). No one knows what organism forms *Paleodictyon* traces, although these traces can occur in high densities (more than 40 m^{-2}) on the margins of the Mir relict hydrothermal zone (Rona *et al.,* 2009). *Paleodictyon* traces have also been reported from other abyssal locations, such as the Clarion Clipperton Zone in the central Pacific (Durden *et al.,* 2017). Very little is known about the benthic invertebrate fauna inhabiting hydrothermally active sediments along the MAR, other than the reported dominance of the new species of chaetopterid polychaete *Phyllochaetopterus polus* at hydrothermally active sediments around TAG (Figure 10.17; Morineaux *et al.,* 2010; Fabri *et al.,* 2011). This polychaete was reported in dense mats on sediments at the base of hydrothermally active chimneys.

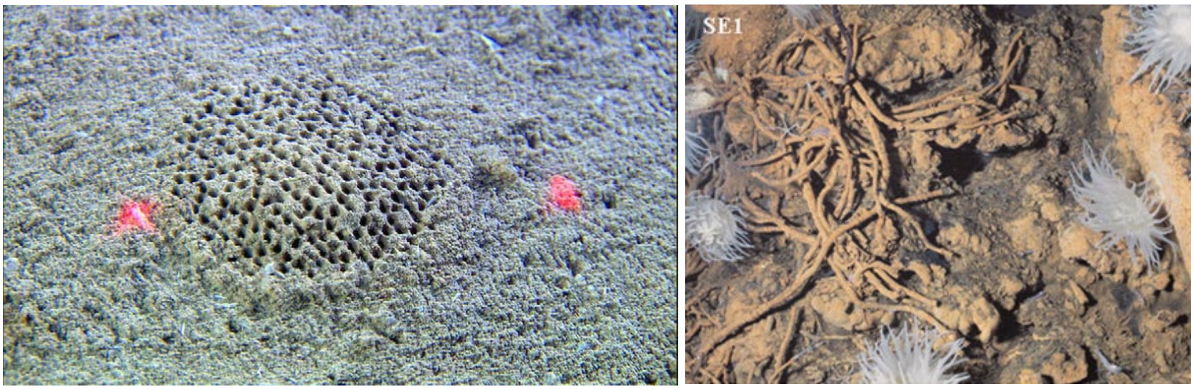

Figure 10.17. Left: High-definition image of Paleodictyon nodosum *trace at the Mid-Atlantic Ridge, with laser beams for scale (10 cm apart), reproduced with permission from the Stephen Low Company. Right:* Phyllochaetopterus polus *at the base of an active chimney in Ashadze-1 vent field. Reproduced with permission from Fabri* et al.*, (2011).*

10.1.8 Benthic and demersal zooplankton

The benthic and demersal zooplankton, whilst not being able to actively swim, can be passively transported in the water column, and may occur within more than one benthic habitat type along the MAR. These drifting organisms can be found not just on the seafloor but in the water column immediately above (the benthopelagic). As a result, this section is not sub-divided into seafloor habitat types. Where benthopelagic zooplankton are predominantly found either on or immediately above a particular seafloor habitat type, this is emphasised in the text below. ‘Swimming’ holothurians are not considered here, as they have already been discussed within the previous section: ‘Regional distribution: Benthic invertebrates’. Overall, whilst there is some information available on the benthopelagic environment in other locations, very little is known about the benthopelagic zooplankton along the MAR.

Zooplankton biomass decreases exponentially with increasing depth in the ocean (Wishner, 1980a; Angel & Baker, 1982; Roe, 1988). At a depth of 5000m the biomass is 0.1% of that of zooplankton in surface waters (Wishner, 1980a). Zooplankton biomass may rise slightly close to the seabed within the Benthic Boundary Layer (BBL - water lying within 100m of the seabed) (Wishner, 1980a; Angel & Baker, 1982). This may vary depending on location, depth, surface water primary productivity and the method used to sample zooplankton within the BBL (Roe, 1988; Vinogradov *et al*., 1996; Christiansen *et al*., 2010; Christiansen, 2016).

Certain taxa will be found preferentially, and perhaps only, in the BBL zone, such as copepods, medusa, cirrate octopods, swimming holothurians and appendicularians (Barnes *et al.* 1976; Billett *et al.,* 1985; Wishner, 1980b; Pawson & Foel, 1986; Miller & Pawson 1990; Larson *et al.,* 1992; Christiansen *et al.,* 1999; Bühring & Christiansen, 2001; Vinogradov, 2005; Collins & Villaneuva, 2006). During submersible dives in the vicinity of the CGFZ on the MAR Vinogradov (2005) observed directly high densities of gelatinous appendicularian houses close to the seabed. The appendicularians were the most abundant group in the BBL. There is growing evidence that other gelatinous organisms may also be patchy, but at times very abundant near the bottom, at certain locations and at certain times (Larson *et al.,* 1992).

In a detailed study of the abyssal BBL in the NE Atlantic Christiansen *et al.,* (2010) sampled at 1, 15, 50 and 100m above the seabed. They found that while zooplankton communities (excluding gelatinous forms) in the upper three layers were similar and were dominated by copepods (c. 75%) the community close to the seabed (1m above bottom) showed distinct differences; here, copepods still dominated the zooplankton, but polychaetes, malacostraceans and chaetognaths also became important groups. A shift from pelagic feeders to benthic feeders was evident in the sample closest to the seabed. A similar taxonomic shift was found by Grice (1972) at bathyal depths on the continental margin using plankton nets attached to a submersible. Within the copepods, a geographically extensive study of benthopelagic calanoid copepods study in the South Atlantic and Southern Ocean found that the dominant benthopelagic family was composed mainly of detritivores (Renz & Markhaseva, 2015).

Not all of the zooplankton within the BBL are permanent members of this community. The BBL is also a key environment for benthic organisms that have pelagic larval stages, also known as the meroplankton. There have not been any dedicated studies of the meroplankton within the BBL overlying the MAR. However, studies in other regions suggest that this environment can be particularly important for the dispersal of the larval stages of hydrothermal vent invertebrate fauna (Metaxas 2011).

10.1.9 Benthic and demersal nekton

The benthic and demersal nekton, being mobile, often occur within more than one benthic habitat type along the MAR. As these organisms have the ability to actively swim, they can be found not just on the seafloor but in the water column immediately above (the benthopelagic). As a result, this section is not sub-divided into seafloor habitat types. Where benthic and demersal nekton are predominantly found either on or immediately above a particular seafloor habitat type, this is emphasised in the text below.

Typically, benthic and demersal nekton of the MAR consists of different fishes, cephalopods, and some crustaceans, such as shrimp and amphipods. Some of these species (generally the best swimmers) are particularly widespread, others may have a relatively localised distribution. ‘Swimming’ holothurians (discussed earlier) are not considered here, as they are unable to swim against the prevailing currents, and would not strictly be considered as nekton (Rogacheva *et al.,* 2012).

10.1.9.1 Amphipoda

Necrophagous scavenging amphipods occur in the benthopelagic overlying multiple MAR seafloor types and are present in both hard substrata and soft sediment communities along the MAR (Duffy *et al.*, 2013; Horton *et al.,* 2013; Horton & Thurston, 2013). A total of 39 different scavenging amphipod taxa were collected by baited traps at the CGFZ, with more than half of the amphipods collected being new to science (Horton *et al.,* 2013). The regional distributions of these new species are not known. However, more than 25 % of the species recorded occurred North and South of the CGFZ and East and West of the MAR, suggesting that necrophagous amphipods in general have wide distributions (Horton *et al.,* 2013).

Despite many species being shared North and South of the CGFZ, there were significant differences in community composition and species richness either side of the CGFZ (Horton *et al.,* 2013). The dominant species collected (> 90 % of the specimens in some samples) was *Abyssorchomene abyssorum*, which is found throughout the world’s oceans (Duffy *et al.,* 2013), and was previously recorded from the MAR south of the Azores (Chevreux, 1903). *Abyssorchomene abyssorum* and its congeners are also found on the continental margins, although they occur at shallower depth and in greater abundance on the MAR (Horton *et al.,* 2013).

10.1.9.2 Shrimp

Comparing shrimp species collected North and South of the equatorial Romanche Fracture Zone along the MAR suggests that more shrimp species occur to the North than to the South, with greater species richness of pelagic shrimp compared to benthic demersal shrimp (Cardoso *et al.,* 2014). However, these trends may also reflect sampling effort to some degree, with the number of sampled species in the North approaching the true number of species for the region, and the smaller number of species in the South potentially resulting from under-sampling (Cardoso *et al.,* 2014).

10.1.9.3 Fishes

Video observations of deep-demersal nekton from within the Charlie-Gibbs Fracture Zone of the MAR suggested that fish distribution patterns were related to depth (Felley *et al.,* 2008). The fishes found during shallower dives were characteristic of Haedrich & Merrett’s (1988) ‘rise’ fauna, found along continental slopes at depths < 4500 m, whilst the few forms seen on deeper dives were those more typically associated with the abyssal plain (depths > 4500 m: Felley *et al.,* 2008). Deeper dives passed over abyssal plains dominated by soft sediments, with far fewer countable organisms than observed on shallower dives that traversed mixed seafloor types (Felley *et al.,* 2008).

Bottom trawling of soft sediment areas around 2500 m in the CGFZ region collected a total of 22 fish species, none of which were restricted to the MAR in terms of regional distribution, being also found at similar depths on the Porcupine Sea Bight (Cousins *et al.,* 2013b). Baited cameras on the seafloor at similar sites in the CGFZ region observed 19 different fish taxa (Cousins *et al.,* 2013a), with 65 % of trawled species also observed at baited camera landers, indicating a high proportion of scavenging fish species at the MAR (Cousins *et al.,* 2013a). Comparisons between the diversity and distribution of demersal fish species in the North Atlantic on continental margins, slopes of oceanic islands and seamounts, and the MAR determined that species diversity was greatest in the western North Atlantic, and significantly lower on the MAR and eastern North Atlantic. MAR demersal fish assemblages were most similar to those on eastern North Atlantic slopes and rises, and were different from assemblages in the western Atlantic, Greenland, northwest Africa, and Azorean seamounts and islands (Bergstad *et al.,* 2012). In trawls conducted on the MAR between the Azores and South of Iceland, demersal fish species diversity decreased with increasing latitude, and was lower at greater depth (Bergstad *et al.,* 2008). Differences in pelagic productivity and species composition of zooplankton and pelagic nekton between areas north and south of the Sub-Polar Front, which aligns with the CGFZ, were thought to underlie these latitudinal changes in species composition (Bergstad *et al.,* 2008).

The MAR fish fauna appeared to differ North and South of the CGFZ, as evidenced by bottom trawl collections (Cousins *et al.,* 2013b) and baited camera observations (Cousins *et al.,* 2013a). Both bottom trawl sites and baited camera sites North and South of the CGFZ showed significant differences in fish species composition (Cousins *et al.,* 2013b; Cousins *et al.,* 2013a). No differences could be discerned between bottom trawl or baited camera sites at the same latitude either side of the MAR (Cousins *et al.,* 2013b; Cousins *et al.,* 2013a).

Some fish species are found in consistently high numbers both North and South of the CGFZ, with no significant difference in biomass or abundance of *Antimora rostrata* between CGFZ trawl sites or CGFZ video transect sites (Cousins *et al.,* 2013b; Linley *et al.,* 2013). For some species, different sampling methods give different perspectives on abundance, with bottom trawl collections finding no significant difference in biomass or abundance of *Coryphaenoides armatus* and *Coryphaenoides brevibarbis* (Cousins *et al.,* 2013b), whilst video transects and baited cameras recorded higher abundances of both species North of the CGFZ compared to the South (Cousins *et al.,* 2013a; Linley *et al.,* 2013). Many of the MAR scavenging fish species (see Figure 10.18 for examples) appear to be widespread across the CGFZ, with ten of the 19 species observed at all baited camera locations (Cousins *et al.,* 2013a).

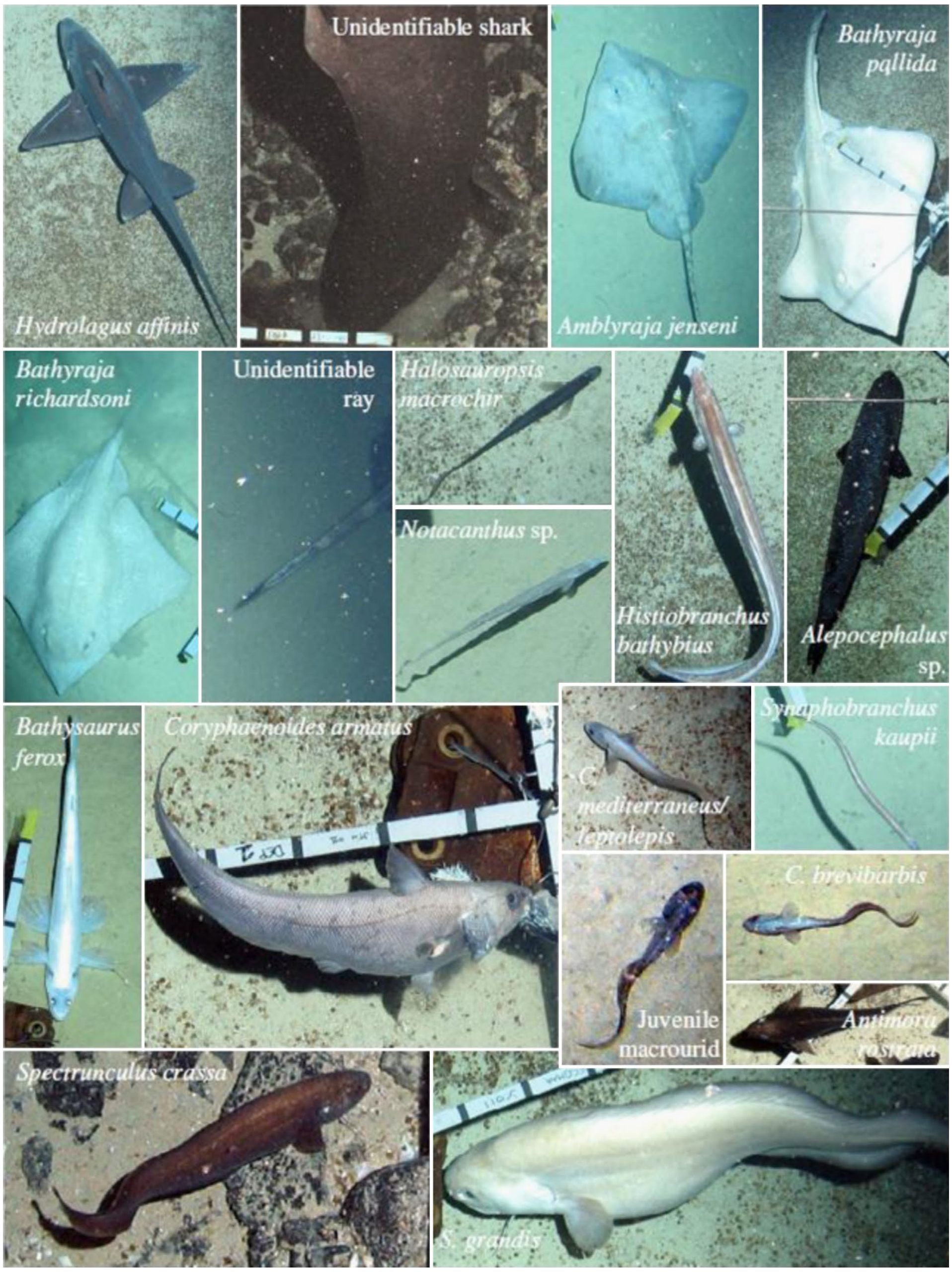

Figure 10.18. Images of scavenging fishes observed attracted to bait deployed at around 2500 m depth on the Mid-Atlantic Ridge. Reproduced from Cousins et al., *(2013a).*

Different MAR fishes exhibit different behaviours within the benthopelagic (Felley *et al.,* 2008), which may influence their distribution. According to Felley *et al.,* (2008), macrourid fish, including *Coryphaenoides rupestris,* were the most commonly observed fish on CGFZ dives, and usually seen hovering over the bottom, and sometimes in contact with the bottom. *Coryphaenoides rupestris* is one of the most common benthopelagic fishes on the northern MAR (Bergstad *et al.,* 2010) and was also collected during multiple trawls as part of the MAR-ECO project, occurring both North and South of the Charlie-Gibbs Zone, and at Faraday Seamount (Bergstad *et al.,* 2010). The distribution of *C. rupestris* is broader than the MAR region, with the species also recorded from the East and West Atlantic. Closely related *C. armatus* was the most abundant fish observed at CGFZ baited camera sites (Cousins *et al.,* 2013a), whilst *C. brevibarbis* was the most abundant species during video survey (Linley *et al.,* 2013).

Other fishes observed by Felley *et al.,* (2008) during dives in the CGFZ region included *Halosauropsis macrochir,* which was usually seen on the bottom with its belly on the substratum and its tail extended perpendicular to the bottom. *Aldrovandia* sp. was also observed, with its lower jaw touching or close to the bottom and its body straight and extended to up at an angle to the seafloor. The fish *Bathysaurus mollis* was observed motionless on the bottom, whilst *Antimora rostrata* was seen swimming either close to or several meters above the seafloor. Two ophidiid fish individuals and one synaphobranchid eel were also observed swimming 1 – 2 metres above the seafloor.

10.1.9.4 Cephalopoda (squid and octopus)

Cephalopods (squid and octopus) were sampled along the MAR from north of the Azores to south of Iceland during the MAR-ECO Project, using a range of trawl types (Vecchione *et al.,* 2010a). Cephalopods collected using bottom trawls may be considered part of the benthopelagic and demersal nekton; other trawl types predominantly sampled the mid-water and surface environments. Bottom trawls along the MAR collected 239 cephalopod individuals, belonging to 34 species (Vecchione *et al.,* 2010a). Nineteen species of cephalopod were collected using both the bottom and pelagic trawls, with many of these species thought to be pelagic species accidentally collected during deployment or recovery of the trawl (Vecchione *et al.,* 2010a). The most abundant species within the bottom trawls were those that were also collected in pelagic trawls. *Mastigoteuthis agassizii* squid were the most abundant, making up 31% of individuals collected by benthic trawls (74 individuals), followed by the squid *Gonatus steenstrupi* (47 individuals), and octopod *Stauroteuthis syrtensis* (25 individuals). The other 13 species collected in both benthic and pelagic trawls occurred in very low abundance (< 10 individuals), with nine of these species only being sampled once across all benthic trawls.

The squid *G. steenstrupi* appeared to have a depth-related size distribution, although there is the potential for confounding effects from using multiple sampling gears with different collection mesh sizes (Vecchione *et al.,* 2010a). Larger-sized individuals were more common in benthic trawls than smaller individuals, whilst smaller individuals occurred almost exclusively within pelagic trawls. In discreet pelagic trawls by depth band, smaller *G. steenstrupi* were most abundant in the surface samples, and particularly so in the CGFZ area. Only large *G. steenstrupi* were observed at the seafloor from ROV imagery. This may suggest that smaller individuals develop and feed in the surface and mid-water environments, whilst some of the larger adults may venture to the benthopelagic to feed. Very few individuals of *G. steenstrupi* of all size ranges were collected South of the Sub-Polar Front (approximately 50° N), with the vast majority of individuals being sampled around the CGFZ or North of this region. Vecchione *et al.,* (2010a) suggested that the Sub-Polar Frontal Region may be the effective southern limit for *G. steenstrupi*, although the boundary was not absolute. *G. steenstrupi* has a relatively broad distribution, being also recorded from the East Atlantic.

The squid *M. agassizii* was broadly distributed along the MAR north of the Azores to south of Iceland and is also known from the West Atlantic (Vecchione *et al.,* 2010a). This squid was considered to be bottom-associated, with benthic trawls in the CGFZ regions capturing nearly three times as many *M. agassizii* as the pelagic trawls, indicating a concertation of this species near the bottom (Vecchione *et al.,* 2010a). High abundances of *M. agassizii* in bottom trawls is supported by submersible observations of mastigoteuthid squids commonly drifting just above the seafloor (Roper & Vecchione 1997; Young *et al.,* 1998; Vecchione *et al.,* 2002).

The octopod *S. syrtensis* is generally considered a pelagic species, although it was the third most abundant species in the benthic trawls and was also observed during ROV dives near the seafloor (Vecchione *et al.,* 2010a). It is thought that this species may aggregate near the seafloor with a distribution that extends vertically up into the deep water-column (Vecchione *et al.,* 2010a). Benthic trawl catches of *S. syrtensis* were greatest on the flanks of the Mid-Atlantic Ridge; however, it has a broad distribution, having been also recorded from both the West and East Atlantic (Vecchione *et al.,* 2010a).

Fifteen species of cephalopod were only collected using the benthic trawl and are more likely to be restricted to the benthopelagic than those collected with both benthic and pelagic trawls. Of these putative benthopelagic species, the octopod *Opisthoteuthis grimaldii* was the most abundant (14 individuals), followed by the octopod *Grimpoteuthis discoveryi* (8 individuals) and octopod

Cirrothauma murrayi (6 individuals). The other 12 cephalopod species from benthic trawls occurred in very low abundance, with 5 or less individuals sampled across all benthic trawls.

The octopod *O. grimaldii* was only confidently identified in benthic trawls from the CGFZ area, although the type specimen occurred northwest of the Azores (Vecchione *et al.,* 2010a). Reliable records of *O. grimaldi* also occur in the East Atlantic. *Grimpoteuthis discoveryi* is a common octopod in the northeast Atlantic, although in the MAR-ECO survey it was only identified from the CGFZ area. All of the *Grimpoteuthis* (4 species) and *Opisthoteuthis* (2 species) octopods sampled during MAR-ECO were only collected by bottom trawl (Vecchione *et al.,* 2010a), which is supported by submersible observations that these octopod genera often sit on the seafloor or swim and drift just above it (Vecchione & Roper 1991; Vecchione & Young 1997; Felley *et al.,* 2008).

The octopod *C. murrayi* was only collected in benthic trawls from North of the Azores and in the southern part of the CGFZ, although the species is broadly distributed in the deep waters of the Atlantic, Pacific, and Indian Oceans. All of the cirroteuthid octopods collected during MAR-ECO (genera *Cirroteuthis*: 2 species, and *Cirrothauma*: 1 species) were only collected from bottom trawls. Whilst cirroteuthid octopods are thought to be wholly pelagic (Roper & Brundage, 1972; Vecchione & Young 1997), they have a benthopelagic distribution (Villanueva *et al.,* 1997; Collins & Henriques 2000), which would support their abundance in MAR-ECO bottom trawl collections.

10.1.9.5 Hydrothermal vent benthic and demersal nekton

There is little information available on the benthic and demersal nekton found at hydrothermal vents along the MAR. The most comprehensive species list for hydrothermal vent fauna recorded along the MAR was last updated in 2006 (Desbruyeres *et al.,* 2006). Further survey and research efforts along the MAR have led to the discovery of new species, and species lists may have been updated for some taxonomic groups. However, the Desbruyeres *et al.,* (2006) taxa listing currently provides the most comprehensive overview of hydrothermal vent fauna along the MAR. Within this list, 10 species of fish were recorded from hydrothermal active habitat, with four of these species thought to be specific to vents (Table 10.3). The remaining six species are known from other habitats in the North Atlantic, and in some cases, from other oceans.

Table 10.3. Fish species recorded from hydrothermal vents along the Mid-Atlantic Ridge. Species records were taken from Desbruyeres et al., *(2006). Taxonomic status was updated using the World Register of Marine Species. Abbreviations: * vent species; ^{G} general deep-sea species.*

Family	Species name	Common name
Bythitidae	*Cataetyx laticeps*^{G}	Bythitid fish
Chimaeridae	*Hydrolagus affinis*^{G}	Small-eyed rabbit fish
	Hydrolagus pallidus^G	Pallid ghost shark
Lotidae	*Gaidropsarus* sp.*	Gadoid fish
Macrouridae	*Coryphaenoides armatus*^{G}	Armed grenadier
Moridae	*Lepidion schmidti*^{G}	Schmidt's cod
Sebastidae	*Trachyscorpia echinata*^{G}	Spiny scorpion fish
Synaphobranchidae	*Ilyophis saldanhai**	Arrow-tooth eel
Zoarcidae	*Pachycara saldanhai**	Eel pout
	*Pachycara thermophilum**	Eel pout

The biological communities of inactive sulphide substrata have been very poorly studied along the MAR, and there is very little known about the benthic and demersal nekton that are found here. *Pachycara* sp. zoarcid fish were the only fauna observed at the inactive chimneys of Mag Mell, an edifice in the Moytirra vent field, although these mobile predators also occur elsewhere within the vent field (Wheeler *et al.,* 2013).

10.2 Temporal variability

The benthic biota not only exhibit distribution patterns in space but also over time. Temporal variability in benthic communities can be related to food availability, breeding and reproductive cycles, ontogenetic shifts, and changes in environmental parameters. These factors can lead to variability over multiple time scales, including diurnal, monthly, seasonal, inter-annual or even decadal time scales. Temporal variation can be particularly complex for hydrothermally vent communities, with multiple scales of both temporal and spatial scale potentially interacting to influence overall productivity of this community (see Figure 10.19). Episodic events can also result in temporal variability in the benthic biota, although the periodicity of these events may be less predictable.

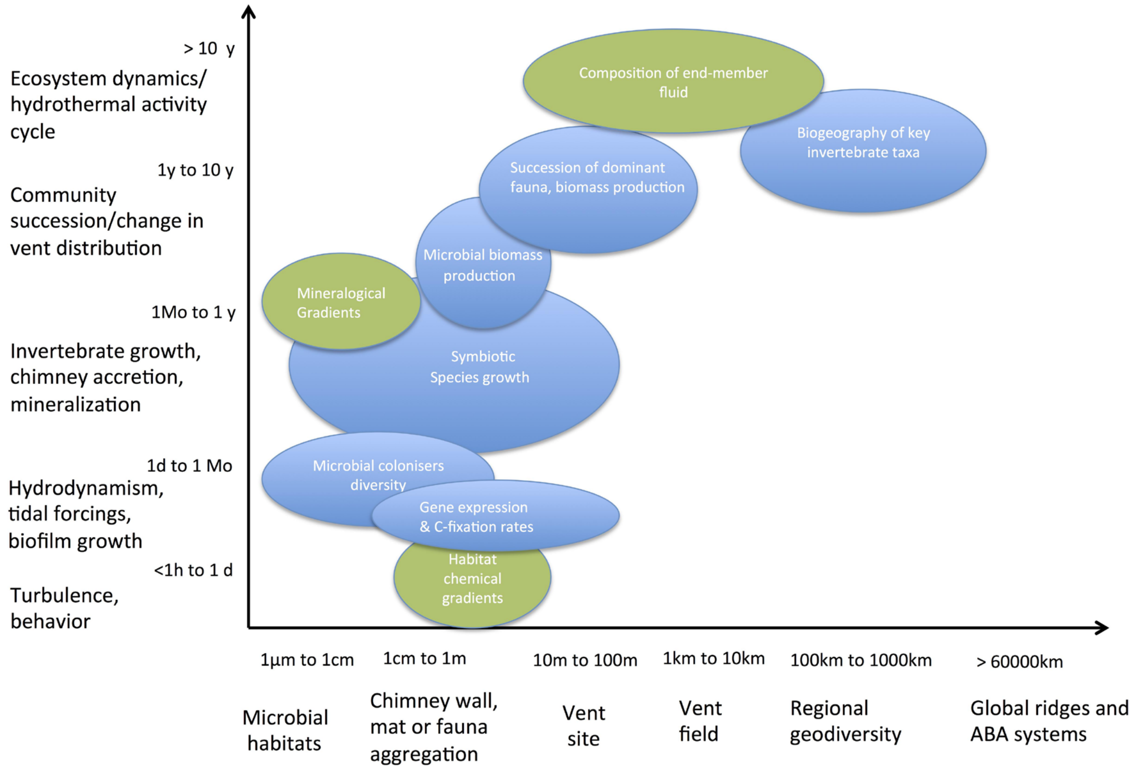

Figure 10.19. Temporal and spatial scales of key processes driving the chemoautotrophic productivity in deep-sea hydrothermal vent systems. Reproduced from Le Bris et al.*, (2019).*

Different MAR benthic habitats experience variability on different time scales, and biota within the same habitat may not exhibit the same temporal variability. In general, very little is known about the temporal variability of benthic biota along the MAR. This is largely because to appreciate the different scales of temporal variability, there need to be repeat observations at multiple spatial resolutions spanning the time period that correlates with the factor with the longest period of temporal variability. Spatial and temporal drivers of benthic biota variability can often interact, and to separate temporal and spatial factors, repeat observations need to be made from the same location. Multiple long-term sites would be needed to appreciate temporal variability along the length of the MAR.

The following sections review the available information available on the temporal variability of benthic biota along the MAR. The least information is available for microbial communities, with very little information available on the benthic and demersal nekton. More information is available on temporal variation in the benthic invertebrate fauna, whilst hydrothermally active communities are the best studied to date.

10.2.1 Microorganisms

Despite ongoing research efforts, little is known about the microorganisms along the MAR in any benthic habitat, and almost nothing is known about the temporal variability of microbial communities. As such, temporal variability of microorganisms is not addressed under separate headings for each benthic habitat type. Where information is available for a specific benthic habitat, this is highlighted below.

There do not appear to be any studies of the temporal variability of microbial communities at hard non-hydrothermal substrata along the MAR. Information on the temporal variability of the microbes within surficial soft sediment is equally absent. There is also no published information available on temporal variation of the microbial communities within the benthopelagic habitat of the MAR. Whilst there are no published studies on the temporal variability of microbial communities at inactive sulphide habitat along the MAR. However, if microbial communities at active vents experience shifts in composition relating to changes in the geochemical environment, then it is possible shifts could also occur within microbial communities colonising inactive sulphides, in response to the changing chemical environment of weathering sulphides.

The most information available on the temporal variability of microbial communities along the MAR is for hydrothermal vent microbial communities. Although the studies conducted to date have been informative, there are few studies addressing this generally understudied aspect of vent ecology (Le Bris *et al.,* 2019). One study conducted at mussel beds in the Clueless vent field (5°S on the MAR) suggested that microbial communities in low-temperature hydrothermal fluids (circa 8°C) exhibit greater short-term variability (minutes to hours) that those at high-temperature habitat (Perner *et al.,* 2009). This was attributed to short-term hydrothermal fluid variability resulting from dynamic sub-seafloor fluid mixing and highlights the difficulty in obtaining a ‘representative’ microbial sample of a given location from vent fluids (Perner *et al.,* 2009).

On a considerably longer timescale, studies at Lost City hydrothermal vents discovered shifts in archaea and bacteria communities over 1000-year time scales (Brazelton *et al.,* 2009). Correlations between carbonate chimney ages and RNA sequences from the associated archaeal and bacterial communities suggested that ‘rare’ members of the microbial community can become dominant when environmental conditions change, on 1000-year timescales (Brazelton *et al.,* 2009). It was concluded that the long history of chimney growth cycles at Lost City has resulted in numerous closely related microbial ‘species’, each preadapted to a particular set of reoccurring environmental conditions (Brazelton *et al.,* 2009).

Lost City presents a different environment for microbial communities, with its carbonate chimneys forming through highly alkaline vent fluid, in contrast to the acidic vent fluids occurring at all other known vent fields along the MAR. Microbial communities from vent fields with acidic vent fluid, also demonstrate shifts in community composition over time, although these shifts have generally been assessed over much shorter time scales. Deployment of an *in-situ* growth chamber (vent cap) in the Snake Pit vent field resulted in the formation of a white microbial mat following just 5 days of deployment, demonstrating the microbial community’s potential for rapid colonisation of ‘new’ suitable substrata (Reysenbach *et al.,* 2000). The microbial community contained a mix of hyperthermophiles, moderate thermophiles, and mesophiles, which was thought to reflect the gradual reduction in temperature within the chamber (70 – 20°C) during the five days of deployment (Reysenbach *et al.,* 2000). These results provide support for the existence of highly diverse microbial communities at acidic MAR vents, with the ability to rapidly colonise new substrata and to respond (at a community level) to rapid changes in environmental parameters.

A study conducted at the EMSO-Azores non-cabled seafloor observatory (37° N) along the MAR demonstrated that the composition of prokaryote communities can also change in response to natural de-gassing events, as observed under the Lucky Strike vent field between 2009 and 2010 (Rommevaux *et al.,* 2019). The microbial community of the Eiffel Tower site, Lucky Strike, was characterised each year from 2008 to 2011, providing insights into the interannual changes in microbial community at Lucky Strike. The magmatic event seemed to impact microbial communities colonizing the Eiffel Tower high temperature chimney, alongside the basalts in the more diffuse and mixed zone, ultimately promoting the development of thermophilic/anaerobic Archaea and Bacteria (Archaeoglobales, Nautiliales, Nitratiruptoraceae) (Rommevaux *et al.,* 2019). The periodicity of natural de-gassing events at Lucky Strike is not known, meaning that the frequency of this disturbance and related shift in microbial community is also unknown.

The horizontally-dispersing neutral phase of vent plumes is also expected to have dynamic microbial communities exhibiting complex patterns of spatio-temporal succession over a course of weeks and across tens of kilometres (Reed *et al.,* 2015), although this has not been investigated for the MAR. Studies in other ocean regions suggest that the microbial communities at hydrothermal vents can stabilize on intermediate time scales (over multiple years) (Fortunato *et al.,* 2018), although this has yet to be tested along the MAR.

10.2.2 Benthic invertebrates

Whilst some informative studies have been conducted on the temporal variability of benthic invertebrates along the MAR, collectively these studies span a small number of locations and may not have been conducted over the range of timescales that would be needed to fully appreciate temporal variation. The limited number of locations where time series studies have been conducted makes it challenging to assess the temporal variability of benthic invertebrates in a regional context. In general, little is known about the temporal variability of benthic invertebrates along the MAR within any habitat. Where information is available for a specific benthic habitat, this is highlighted below.

10.2.2.1 Hard non-hydrothermal substrata

The temporal variability of the benthic invertebrates at hard non-hydrothermal substrata along the MAR is poorly known. For sessile framework-forming species, such as corals and sponges, changes in spatial distribution either relate to localised changes in colony size, or colonisation of new areas through larvae. Temporal variation can still occur for these sessile organisms, for example in terms of their feeding and reproductive activity.

The vast majority of sponges along the MAR are filter feeders, straining food particles from the water column. These food particles consist of surface derived material, and so may exhibit seasonality in quality and abundance, reflecting any seasonal patterns in surface productivity along the MAR. Deep-sea corals are suspension feeders, with species such as *L. pertusa* snatching both food particles and live zooplankton from the water column (Henrich & Freiwald, 1997; Dodds *et al.,* 2009). Again, these food particles could exhibit seasonal patterns in quality and abundance, whilst the availability of zooplankton prey may be linked to cycles of daily vertical (diurnal) migration or seasonal blooms.

Some coral species found along the MAR are also known to have seasonal spawning, such as *L. pertusa*, which has a 6 – 8 week spawning period starting in late-January for North-East Atlantic populations (Waller & Tyler 2005), whilst western Atlantic populations have an earlier spawning period estimated to start in September (Demopoulos *et al.,* 2017). The periodicity of spawning of *L. pertusa* in the North-East Atlantic was thought to be in response to seasonal phytoplankton blooms, which lead to an increased input of organic matter to the seafloor around July, acting as the cue for *L. pertusa* to initiate gametogenesis (Waller & Tyler, 2005). The MAR falls in the centre of the North Atlantic *L. pertusa* distribution, and the timing of its reproduction is not known.

There may also be temporal variability in the fitness of the benthic invertebrate community, as a result of climate fluctuations, such as the North Atlantic Oscillation (NAO). The NAO is a large-scale alternation of atmospheric mass between subtropical high surface pressure, centred on the Azores, and subpolar low surface pressures, centred on Iceland. The NAO determines the speed and direction of the westerly winds across the North Atlantic, as well as winter sea surface temperature. Strong links have been drawn between the state of the NAO and the relative abundance of zooplankton species in the North Atlantic (Piontkovski *et al.,* 2006). As many benthic invertebrates are dependent on surface derived material, the state of the NAO could impact the quality, quantity and timing of food supply to benthic invertebrates along the MAR.

In the longer term, there may be temporal changes in the distribution of benthic invertebrates, including *L. pertusa*, in response to climate change impacts including ocean acidification, deoxygenation and warming (Lunden *et al.,* 2014). The potential impacts of climate change are considered in more detail within the Cumulative Impacts chapter.

10.2.2.2 Hydrothermally active hard substrata

To fully appreciate the temporal variation in benthic invertebrates at hydrothermally active hard substrata, there is a need for long-term monitoring stations, such as the EMSO-Azores non-cabled seafloor multidisciplinary observatory at 37° N (Lucky Strike vent field), which was established in 2010[1]. Annual cruises to the EMSO-Azores observatory coordinated by Ifremer through the international MOMAR: Monitoring the Mid-Atlantic Ridge project[2] allow for physical samples to be collected and for data from monitoring equipment to be downloaded. MOMAR cruises have been conducted annually since 2010. Many of the studies conducted at Lucky Strike vent field utilise data or samples collected during the time series at the EMSO-Azores observatory.

Temporal variability of benthic invertebrates at hydrothermally active hard substrata can span multiple time scales. These may include changes in feeding behaviour corresponding to semi-diurnal tidal cycles, as has been observed on the MAR and elsewhere (Cuvelier *et al.,* 2017; Lelievre *et al.,* 2016), seasonality in reproduction for some MAR species (Dixon *et al.,* 2006), and successional changes in response to changes in hydrothermal flow (Sen *et al.,* 2014). Not all hydrothermal vent species along the MAR exhibit the same periodicity of temporal variation. For example, *Bathymodiolus azoricus* mussels from Menez Gwen demonstrates seasonal patterns in reproduction linked to the timing of the winter-spring phytoplankton bloom (Dixon *et al.,* 2006), whereas there was no evidence for seasonal reproduction in *Rimicaris exoculata* shrimp from TAG (Copley *et al.,* 2007).

Day-to-day variations in *B. azoricus* mussel assemblages were assessed through 48 days of video footage obtained from the TEMPO module deployed at Lucky Strike on the MAR in 2006 (Sarrazin *et al.,* 2014). These daily observations showed that vent mussel assemblages were quite stable over the 48-day period, which reflected the relative stability of environmental conditions during this period. At the same site, intermediate-term changes in *B. azoricus* coverage and density were also observed, with increases of 11% and 140 individuals m^{-2} respectively between 2006 and 2008 (Sarrazin *et al.,* 2014). A later study using the TEMPO module in the same location over a period of nine months also observed stable spatial distribution patterns for the more mobile vent shrimp *Mirocaris fortunata* and crab *Segonzacia mesatlantica* (Matabos *et al.,* 2015). Whilst there was no evidence of periodicity related to tides for the distribution of MAR vent mussels, shrimp, crabs or bucciniform gastropods, polynoid worms exhibited significant multi-day periodicities, suggesting that the harmonics of tidal cycles may be influencing their distribution (Cuvelier *et al.,* 2017).

Benthic invertebrate communities at MAR hydrothermally active hard substrata can also exhibit high levels of stability over multiple years, even decadal periods (Copley *et al.,* 2007; Cuvelier *et al.,* 2011). The MAR has a slow spreading rate and does not experience the same frequency of episodic destructive events (such as earthquakes and volcanic eruptions) as fast-spreading locations, such as the East Pacific Rise and Juan de Fuca Ridge. As a result, the slow-spreading MAR axis should have distantly spaced vent fields (clusters of vents) that are relatively stable (Vrijenhoeck, 2010).

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[1] EMSO-Azores non-cabled seafloor observatory: http://www.emso-fr.org/EMSO-Azores

[2] MOMARSAT: Monitoring the Mid-Atlantic Ridge: https://campagnes.flotteoceanographique.fr/series/130/

Vent shrimp populations at Broken Spur were stable over a 15-month time period (Copley *et al.,* 1997), whilst studies of mature vent communities at TAG (Copley *et al.,* 2007) and Lucky Strike (Cuvelier *et al.,* 2011) demonstrated decadal stability in the abundance of dominant species at the edifice scale. At smaller spatial scales, such as within the Eiffel Tower edifice, significant differences occurred in individual assemblage coverage and distribution over a 14-year time period, in part related to changes in hydrothermal activity (Cuvelier *et al.,* 2011).

Significant changes in the population density of predatory gastropods *Phymorchynchus* spp. and the disappearance of a live vesicomyid clam population within the Logatchev area over a 10-year period were also linked to fluctuations in hydrothermal activity (Gebruk *et al.,* 2010).

The studies to date assessing temporal variation in hydrothermal vent benthic invertebrates have focussed on the larger fauna visible from imagery survey (megafauna). Less is known about the temporal variability of macrofaunal or meiofaunal communities. Relatively diverse assemblages of meiofauna and macrofauna taxa may be able to colonise new substrata within a short (2 year) time period, as observed at Lucky Strike, where 45 taxa (20 macrofaunal and 25 meiofaunal) colonised artificial substrata placed on the Eiffel Tower edifice (Cuvelier *et al.,* 2014). However, temporal variation of the macrofauna and meiofauna at hydrothermally active substrata along the MAR spanning greater or lesser time periods is unknown.

10.2.2.3 Hydrothermally inactive sulphide substrata

There is very little information on the benthic invertebrates at hydrothermally inactive sulphide habitat along the MAR in general, and there have been no dedicated studies addressing temporal variation for this fauna. Sulphide edifices can contain a mosaic of hydrothermally active and inactive habitat, with the potential to change from active to inactive (and vice versa) over short periods of time. Along the MAR, the Eiffel Tower edifice within Lucky Strike saw changes in the coverage of inactive sulphide patches (‘Substratum 1a’: Cuvelier *et al.,* 2009) over a 14-year time period, with increased colonisation of these patches by *Bathymodiolus azoricus* mussels consistent with alterations in hydrothermal fluid flux (Cuvelier *et al.,* 2011). It would be expected that as hydrothermally active areas along the MAR become inactive, there would be a decrease in hydrothermal vent endemic species, and over time there may be an increase in benthic invertebrates who can either tolerate or exploit the inactive sulphide habitat. Whilst this style of succession has been suggested for other ocean regions (Sen *et al.,* 2014), it has yet to be observed for the MAR. In the case of relict or extinct sulphide structures, in other ocean regions these substrata may provide stable habitat for colonisation by benthic invertebrates (Boschen *et al.,* 2016), although this has yet to be assessed on the MAR.

10.2.2.4 Soft sediment substrata

Whilst soft sediment habitats experience fewer temporal fluctuations in environmental conditions compared to hydrothermally active hard substrata, temporal variation does occur, largely in relation to food supply from surface waters. Soft sediment benthic invertebrates along the MAR are dependent on the surface-derived organic material that sinks to the seafloor, such as phytodetritus, and also larger food falls, such as Sargassum weed and cetacean carcasses.

Large variations occur in the seasonality, chemical composition, magnitude and source of sinking particulate material between different areas on the MAR (Abell *et al.,* 2013), which may result in temporal fluctuations of the structure of MAR soft sediment benthic invertebrate assemblages. Sites North of the CGFZ experience greater mean primary production and particle mass flux than South of the CGFZ, although inter-annual variation within sites was larger than the differences between sites (Abell *et al.,* 2013). However, comparisons of the benthic communities North and South of the CGFZ on both the East and West sides of the MAR found no apparent correlation between surface productivity, particle flux and benthic community structure (Alt *et al.,* 2013). This indicates that there is a complex set of drivers influencing benthic invertebrates along the MAR (Alt *et al.,* 2013), and that to understand temporal variability of the benthic community, repeat sampling would be needed over appropriate time scales.

Seasonal fluxes in organic matter to the seafloor, such as pulses of phytodetritus following the spring bloom, have been observed to influence the structure of soft sediment benthic invertebrate assemblages along the MAR. Video transects in the CGFZ of the MAR observed large patches of phytodetritus derived from surface water primary production concentrated in seafloor depressions, which supported increased numbers of giant Syringamminidae forams, polychaete tubes, and anemones (Gebruk & Krylova, 2013). These organisms all have limited mobility, suggesting a longer-term enrichment of the seafloor, perhaps associated with the retention of phytodetrital material in seafloor hollows. Seasonal phytodetritus enrichment of the seafloor can also lead to high abundances of opportunistic mobile benthic invertebrates, such as the aggregations (23 – 76 individuals per m^2) of small (10 – 15 mm length) *Kolga nana* swimming holothurians discovered in the CGFZ region (Gebruk & Krylova 2013). Similar aggregations of *K. nana* observed at the Porcupine Abyssal Plain were thought to occur in response to periodical fluxes of organic matter to the seafloor (Billett & Hansen, 1982).

Alongside seasonal variation in particle flux to the soft sediment community, episodic events that provide highly localised, short-lived increases in food supply to the seafloor could temporarily support larger populations of soft sediment fauna or may even support specialist communities that are adapted to these food-falls. Episodic food-falls, such as *Sargassum* weed and cetacean carcasses may occur in some areas of the northern MAR, and so have a temporal influence on the structure of benthic invertebrate assemblages. *Sargassum* weed has been observed on abyssal sediments in the vicinity of the MAR near the VEMA Fracture Zone, approximately 10 degrees North of the equator (Baker *et al.,* 2018), and within the Russian Exploration Area between 17°14′N and 16°40′N (Molodtsova *et al.,* 2017) and may influence the structure of soft sediment benthic assemblages.

Whale carcasses which fall to the seabed can stimulate the formation of specially-adapted benthic communities for a period of time, as has been observed for a natural whale fall in the deep South Atlantic (Sumida *et al.,* 2016), and also from a shallow-water whale fall experiment in the North Atlantic (Dahlgren *et al.,* 2006). Many baleen whale species, including *Balaenoptera musculus* (Blue whale), *Balaenoptera physalus* (Fin whale), *Megaptera novaeangliae* (Humpback whale) and *Balaenoptera borealis* (Sei whale) have been observed feeding around the Azores, with peak whale observations coinciding with large zooplankton concentrations following the spring bloom (Visser *et al.,* 2011). Whilst the exact paths of migration routes in the North Atlantic are unknown, whales may follow large topographic features such as the MAR, and many of baleen whale species appear to feed at mid-latitude locations, such as the Azores and off Northwest Africa, during their northward migration to summer feeding grounds near the Arctic (Visser *et al.,* 2011; Silva *et al.,* 2019). If there are whales that perish during migration, their carcasses could sink to the seafloor of the MAR and stimulate changes in the structure of soft sediment fauna communities.

10.2.3 Benthic and demersal zooplankton

The benthic and demersal zooplankton, whilst not being able to actively swim, can be passively transported in the water column, and may occur within more than one benthic habitat type along the MAR, as a result, this section is not sub-divided into seafloor habitat types.

Very little is known about the temporal variability of benthic and demersal zooplankton along the MAR. Observations from other regions suggest that some large gelatinous zooplankton may be abundant within the benthopelagic, but with unknown temporal periodicity (Larson *et al.,* 1992). High densities of gelatinous appendicularian have been observed close to the seabed in the vicinity of the CGFZ on the MAR (Vinogradov, 2005), however it is not clear if appendicularian abundances exhibit periodicity related to temporal variation in environmental conditions. Vertical migration of zooplankton within the water column overlying the MAR may also bring some of these zooplankton into the benthopelagic on diurnal timescales.

10.2.4 Benthic and demersal nekton

The benthic and demersal nekton, being mobile, often occur within more than one benthic habitat type along the MAR, as a result, this section is not sub-divided into seafloor habitat types.

Very little is known about the temporal variability of benthic and demersal nekton along the MAR. Some of the benthopelagic micronekton have the capacity, through migrations, to link the seabed environment with higher levels within the water column (Billett *et al*., 1985; Angel, 1990; Roe *et al*., 1990), some of these migrations may occur on a diurnal basis in response to diurnal zooplankton migrations.

As for the soft-sediment benthic invertebrates, some of the benthic and demersal nekton may exhibit temporal variation in their spatial distribution in response to periodic food-falls, either on a seasonal or episodic basis. Whale carcasses which fall to the seabed along the MAR could lead to a localised increase in the populations of benthopelagic scavengers, such as the necrophagous scavenging amphipods (Duffy *et al*., 2013; Horton *et al.,* 2013; Horton & Thurston, 2013) collected with baited traps in the vicinity of the CGFZ on the northern MAR. Scavenging fish, also collected with baited traps near the CGFZ (Cousins *et al.,* 2013a), could also exhibit localise increases in population in response to whale falls. The periodicity of whale falls to the MAR seafloor is unknown, but any influence on the local populations of benthic and demersal scavengers is likely to be short-lived, on the scale of months to a year, depending on the size of the carcass.

Some benthic and demersal nekton may have periodicity or even seasonality in their reproductive cycles, which could influence their spatial distribution over time, for example if different habitats are required for feeding and breeding. However, whether this type of periodicity occurs for the MAR benthic and demersal nekton appears to be unknown.

10.3 Trophic relationships

The trophic benthic assemblages of the MAR North and South of the Charlie-Gibbs Fracture Zone (CGFZ) were studied by Reid *et al.,* (2012), who demonstrated that the MAR is similar to other deep-sea habitats, being generally dependent on photosynthetic primary production being transported from the surface waters to the seafloor. Reid *et al.,* (2012) described two major trophic pathways: 1) mobile predators and scavenging fishes and crustaceans linked to aggregations of mesopelagic and bathypelagic biomass associated with the MAR (Sutton *et al.,* 2008); and 2) benthic invertebrates dependent on the downward flux of phytodetritus. Reid *et al.,* (2012) also demonstrated that these trophic pathways will be interconnected at various stages of organic matter recycling within the water column and benthos as organic matter is ingested, processed and excreted, becoming available to different trophic guilds. According to Reid *et al.,* (2012) for non-chemosynthetic benthic environments along the MAR, the predator – scavenger and phytodetrital trophic pathways are the two most dominant, but not mutually exclusive, trophic pathways for highly mobile benthopelagic fishes and crustaceans, and benthic invertebrates, respectively.

Similar to the findings of Reid *et al.,* (2013), a study by Colaço *et al.,* (2013) conducted on the ridge-associated Condor Seamount found the food chain to be composed of five trophic levels, with mesopelagic organisms forming the link between the pelagic environment and the benthic and benthopelagic organisms effectively bridging the gap between primary consumers and the 4th an 5th trophic chain levels.

In a different study Morato *et al.,* (2016) presented an ecosystem model for the MAR and associated seamounts within the Azores EEZ. Approximately 45 functional groups were modelled, including a detritus group, two primary producer groups, eight invertebrate groups, 29 fish groups, three marine mammal groups, one turtle group, and one seabird group.

Trophic levels for the different functional groups were similar to those published for individual species using stable isotopes and stomach contents. According to Morato *et al.,* (2016) omnivory indices were in general low, indicating prey specialisation for the majority of groups. Cephalopods, pelagic sharks and toothed whales were identified as groups with key ecological roles in the ecosystem, with trophic relationships that extend into the benthic environment.

In general, there are few dedicated studies addressing the trophic relationships of the MAR benthic environment, with very little information available for the MAR between South of the Azores and the

Equator. Preliminary studies from within the Russian Exploration Area along the MAR (Galkin *et al.,* 2019) have revealed the importance of small-sized surface deposit-feeders where food conditions are limited, alongside smaller filter feeders. The main feeding zones were identified as being in the upper sediment layers and within the near-bottom water layer. Seafloor depressions and seafloor massive sulphide outcrops were characterized by low densities of megafauna, whereas non-hydrothermal rocky habitats were colonised by assemblages of larger filter feeders, especially at elevated locations.

Of all the biological components, the least information is available for the microorganisms, followed by the benthic and demersal zooplankton and nekton. Slightly more information is available for the benthic invertebrates, although for some benthic habitats there is still very little information available. Given the linkages between biological components in the benthic environment, the trophic relationships section is structured by benthic habitat instead of being divided by biological component. As was the case for the Regional Distribution Section, the benthic and demersal zooplankton and nekton are discussed as whole, as these are able to move freely and often occupy the benthopelagic environment overlying multiple habitat types.

10.3.1 Hard non-hydrothermal substrata

Very little information is available regarding the role of microorganisms in trophic relationships within hard non-hydrothermal substrata habitat along the northern MAR, although it may be expected that they would play an important role in the recycling of nutrients on the seafloor. There is also little information available on the role of the benthic invertebrates occurring on hard non-hydrothermal substrata, although food chains in this habitat can be short with a simple structure (Colaço *et al*., 2013; Samadi *et al.,* 2007), reflecting the dominance of suspension and filter feeding corals and sponges that consume organic particles which are transported vertically by currents, or laterally when on slopes.

10.3.2 Hydrothermally active substrata

The most information on trophic relationships in the benthic environment of the MAR is available for hydrothermally active substrata habitat. At the microbial level, vent fields with different geochemistry along the MAR are known to host functionally different microbial communities, for example, the absence of methanogens at certain sites (Flores *et al.,* 2011).

At the food web level, there are complex relationships between different hydrothermal vent taxa and microbial communities, which have been investigated using a range of techniques across multiple northern MAR vent fields. Colaço *et al*., (2002) investigated the isotopic composition of hydrothermal vent biota from seven hydrothermal vent fields along the northern MAR: Menez Gwen, Lucky Strike, Rainbow, Broken Spur, TAG, Snake Pit and Logatchev.

The δ^{13}C and δ^{15}N values of 24 taxa, bacterial mat and filamentous bacteria were determined. According to Colaço *et al*., (2002), individual vent fields displayed similar general patterns and across vent fields, isotopic signatures were independent of depth. Colaço *et al*., (2002) used stable isotope information and stomach contents to describe the general structure of MAR vent field food webs. According to Colaço *et al*., (2002) chemolithotrophic bacteria (both symbiotic and free-living) form the basis of the food web, and these support primary consumers including bathymodiolid mussels, which host symbiotic bacteria, and *Rimicaris exoculata* shrimps, which feed on free-living bacteria in the warmer vent habitat.

Small invertebrates living amongst the byssus threads of the bathymodiolid mussel colonies either feed on bacteria or detritus trapped within the byssus net. The crab *Segonzacia mesatlantica* predates shrimps and small invertebrates and the gastropod snail *Phymorhynchus* sp. feeds almost exclusively on the bathymodiolid mussels. Both *Chorocaris chacei* and *Mirocaris fortunata* shrimp are mixotrophic, feeding on bacteria, shrimps and other small invertebrates (Colaço *et al*., 2002). The shrimp *Alvinocaris markensis* is considered predatory, consuming other shrimps. The top predators consist of common bathyal species, such as the crab *Chaceon affinis* and some fishes, which make incursions into the vent fields to feed, particularly at shallower sites where the phase separation of fluids and depletion in metals makes these environments less hospitable to non-vent predators (Colaço *et al*., 2002).

A later study utilised a different methodology, polar lipid fatty acid (PLFA) profiles, to determine the degree to which hydrothermal vent fauna depend on specific types of bacteria (Colaço *et al*., 2007). The trophic patterns demonstrated by Colaço *et al*., (2007) using PLFA profiles support the findings of Colaço *et al*., (2002). PLFA profiles were determined for 11 species from seven northern MAR vent fields: Menez Gwen, Luck Strike, Rainbow, Broken Spur, TAG, Snake Pit and Logatchev. Colaço *et al*., (2007) identified two associations representing different feeding groups: 1) mussels, commensal polychaetes and gastropods; 2) and shrimps and crabs. The first group was dependent more on sulphur-oxidizing bacteria, whilst the second group had more anaerobic sulphate-reducing bacteria biomarkers. Other species fell between these two groups and presented a more mixed feeding strategy, feeding on bacteria in additional to other types of food. The most diversified bacterial diet was presented by the ampharetid polychaete *Amathys lutzi*, which had fatty acid biomarkers from both S-oxidizing and S-reducing bacteria.

Stable isotope ratios have also been measured for four species of hydrothermal vent fauna at Ashadze-1 vent field: the gastropod snail *Phymorhynchus moskalevi*, sea anemone *Maractis rimicarivora*, shrimp *Mirocaris fortunata,* and chaetopterid polychaete worm *Phyllochaetopterus polus* (Fabri *et al.,* 2011). All four species were discovered to be heterotrophic, and there were too few species assessed to construct the food web structure for Ashadze-1. However, comparisons between the of $\delta^{13}C$ values for these species from Ashadez-1 and other vent fields along the northern MAR suggested that they have the same food source at all vent sites (Fabri *et al.,* 2011). The generally high $\delta^{15}N$ values for these four species at Ashadze-1 suggests that their nitrogen source does not stem directly from local origin but from recycled organic matter, supporting the concept that these species all play the same secondary consumer role in the Ashadze-1 ecosystem (Fabri *et al.,* 2011). The mean $\delta^{34}S$ values for these species at Ashadze-1 fell within the range of values found for vent species, indicating a food web based on locally produced organic matter, such as vent sulphides, pore-water sulphides and thiosulphate (Fabri *et al.,* 2011). The high trophic level of the four species investigated, which were also visually the most dominant species, alongside the sulphur isotopic values, were considered evidence for the existence of a chemosynthetic ecosystem at Ashadze-1, despite the visual absence of species known to exhibit chemosynthetic symbiosis during the survey (Fabri *et al.,* 2011).

A recent study by Portail *et al.,* (2017) investigated the trophic relationships of 13 hydrothermal vent assemblages at three hydrothermal vent fields within the Azores: Menez Gwen (five assemblages), Lucky Strike (three assemblages) and Rainbow (five assemblages). Portail *et al.,* (2017) provide a detailed assessment of the trophic relationships within these vent fields, providing stable isotope values for 29 taxa and two bacterial mat types, and assigning the majority of taxa to one of five feeding guilds: symbiont bearing, bacteriovore/archivore, detrivore/scavenger, predator, and commensal/parasite. Sampling multiple assemblages from within the three vent fields enabled the pursuit of a regional approach to food web construction.

Portail *et al.,* (2017) demonstrated that whilst the potential dominant basal organic matter sources of the different vent field food webs are similar, there are intra- and inter-field variations in their relative contributions. The dominant organic matter sources for food webs were related to methanotrophy and chemoautotrophy (using both the Calvin-Benson-Bassham cycle and the reductive tricarboxylic acid cycle), with the contribution of these sources varying according to the availability of reduced compounds. The contribution of photosynthetic-derived organic matter was negligible in all vent fields, irrespective of vent field depth. Portail *et al.,* (2017) also utilised a subset of species to assess intra-field variability (nine species) and inter-field variability (six species) in $\delta^{13}C$ and $\delta^{15}N$ signatures. All of those species shared amongst sites appeared to exhibit high trophic flexibility, suggesting that differences in the metabolic diversity of basal organic matter sources amongst sites may not be a structuring factor. Food-web structure analysis at the community level by Portail *et al.,* (2017) demonstrated that metrics of functional structure were similar across assemblages, despite variation in environmental conditions and community structure. This functional similarity was thought to reflect the ability of vent fauna to adapt to several geological contexts, and the trophic flexibility of vent heterotrophs.

Smaller scale variation in trophic relationships may also occur within a single hydrothermally active edifice, as demonstrated the study of de Busserolles *et al.,* (2009) on the Eiffel Tower edifice within Lucky Strike vent field. Trophic relationships of *Bathymodiolus azoricus* mussel bed communities were determined based on samples from 12 different locations on the Eiffel Tower edifice. Three faunal species exhibited significant spatial variability in isotopic signatures at the scale of the edifice (*B. azoricus*, *Branchipolynoe seepensis* and *Amathys lutzi*), with environmental conditions explaining variation in isotopic signatures for one-third of the species. de Busserolles *et al.,* (2009) suggest that vent fluid characteristics, by influencing microbial production, are key factors in the variation of local carbon sources at vents. In support of previous work (Colaço *et al*., 2002; Colaço *et al*., 2007), de Busserolles *et al.,* (2009) also found two apparently independent trophic groups, the symbiont-bearing fauna (*B. azoricus* and associated polychaete *B. seepensis*), and the heterotrophic fauna (bacterivores, detritivores, scavengers, and predators). Thiotrophy was identified as the dominant nutritional pathway at Eiffel Tower, with methanotrophy and filter feeding emerging as secondary strategies, although larger *B. azoricus* mussels appeared to rely more heavily on their methanotrophic endosymbionts.

Less information is available on the trophic relationships of the benthic invertebrate meiofauna at hydrothermally active substrata. Zekely *et al.,* (2006a) determined the feeding guild of meiofauna collected from Snake Pit vent field on the MAR, and discovered that primary consumers, mostly deposit feeders, comprised more than 95 % of the total meiobenthos at the site, followed by parasitic copepods and mites. All the nematodes and the majority of copepod individuals (80% of Dirivultidae) were primary consumers, with parasites only making up 20% of the copepod community. Predators were absent in all samples. Portail *et al.,* (2017) also included three meiofaunal taxa in their analyses, determining that suspension-feeding ostracods and deposit-feeding *Aphotopontius* sp. copepods were detrivore/scavengers or bacteriovore/archivores, depending on the assemblage they occurred within. The deposit-feeding *Oncholaimus dyvae* nematodes were either detrivore/scavengers or predators.

Many benthic invertebrates at hydrothermally active substrata along the MAR have complex symbiotic relationships with chemosynthetic bacteria. For example, the vent shrimp *Rimicaris exoculata* harbours two different bacterial epibionts on specialized appendages and on the inner surface of its gill chamber (Petersen *et al.,* (2010). The vent mussel *Bathymodiolus puteoserpentis* harbours both sulphur-oxidizing and methane-oxidizing bacteria in specialised organs, bacteriocytes, within its gill tissue (Duperron *et al.,* 2016). Most recently, is has been suggested that a new species of nematode described from Lucky Strike, *Oncholaimus dyvae*, may harbour symbiotic sulphur-oxidising bacteria (Bellec *et al.,* 2018; Zeppilli *et al.,* 2019).

Hydrothermal activity also has a trophic influence beyond the vent-endemic microbial communities and metazoan fauna. The non-vent benthic and benthopelagic fauna of the MAR can exhibit distinct isotopic compositions in proximity to hydrothermal venting, with the benthopelagic fauna of the Broken Spur vent field exhibiting isotopic signatures closer to the vent chemosynthetic fauna than might be expected (Vereschaka *et al.,* 2000). This may indicate some degree of coupling between benthopelagic shrimp and fish and the chemosynthetic communities more typical of hydrothermally active substrata habitat.

10.3.3 Hydrothermally inactive sulphide substrata

The trophic structure of the fauna inhabiting inactive sulphide substrata along the MAR is unknown, largely because the fauna of this habitat has not yet been well characterised. In other regions, there is some evidence that non-vent suspension feeders colonising inactive sulphide habitat may benefit from secondary production at active vents (Erickson *et al.,* 2009), but this has not yet been demonstrated for the MAR. Whether the microbial community colonising inactive sulphide habitat along the MAR provides an important nutritional source for any colonising benthic invertebrates is not known (Van Dover, 2019).

10.3.4 Soft sediment substrata

The food web structure of the soft sediment habitat along the MAR was constructed as part of the study by Reid *et al.,* (2012), which addressed the MAR non-hydrothermal benthic environment as a whole. The soft sediment fauna of the MAR is entirely dependent on surface-derived material for their nutrition, either as particulate organic matter or the occasional food-fall, such as *Sargassum* weed, which has been observed on abyssal sediments in the vicinity of the MAR near the VEMA Fracture Zone (Baker *et al.,* 2018), and within the Russian Exploration Area (Molodtsova *et al.,* 2017).

Additional trophic information for soft sediment fauna has been obtained from visual observations using ROV and submersible imagery. Gebruk (2008) discovered feeding aggregations of small of small (10 – 15 mm length) *Kolga* sp. holothurians (later identified as *Kolga nana*: Rogacheva, 2012) on soft sediment habitat at approximately 4500 m depth within the CGFZ. This swimming holothurian is an opportunistic species, which forms aggregations in response to periodical fluxes of organic matter to the seafloor (Billett & Hansen 1982). Also, within the deep central part of the CGFZ, Gebruk & Krylova (2013) describe large patches of phytodetritus derived from surface water primary production (Billett et al. 1983), which were notable for the apparent increase in abundance of the giant protozoan *Syringammina*, polychaete tubes and anemones. A recent study by Alt *et al.,* (2019) using video transects conducted North and South of the CGFZ determined that unsurprisingly the flat, sedimentary habitats were dominated by megafaunal deposit feeders, regardless of whether they were to the east or the west of the MAR.

Physical sampling of the MAR polychaete community near the CGFZ by Shields & Blanco-Perez (2013) determined that surface deposit feeders represented more than 70 % of polychaete abundance at each soft sediment site visited. Carnivore or scavenging species accounted for much less, being approximately 15 % of the relative abundance at the majority of sites.

10.3.5 Benthic and demersal zooplankton and nekton

Very little is known about the trophic structure of the MAR benthopelagic environment, which is the habitat for the benthic and demersal zooplankton and nekton. In a detailed study of the abyssal Benthic Boundary Layer (BBL) in the Northeast Atlantic, Christiansen *et al*., (2010) sampled at 1, 15, 50 and 100 m above the seabed and found a shift from pelagic feeders to benthic feeders in the sample closest to the seabed. As is the case for the fauna colonising soft sediment and non-hydrothermal hard substrata, the benthopelagic fauna are generally considered to be dependent on food supply from the surface. Pond *et al.,* (2000) demonstrated that the lipid and stable isotope data from three species of bathypelagic shrimp (*Ephyrina bidentata, Parapasiphaea sulcatifrons* and *Sergia japonicus*) collected from 2000 m water depth along the MAR were consistent with unmodified photosynthetic food source, showing dependence on nutrition from the photic zone for these species.

There are also some species-specific papers addressing the diet of MAR benthic and demersal nekton. For example, Bergstad *et al.,* (2010) investigated the diet of *Coryphaenoides rupestris* (roundnose grenadier), one of the most common benthopelagic fishes on the northern Mid Atlantic Ridge. Bergstad *et al.,* (2010) determined that the diet of *Coryphaenoides rupestris* mainly comprised of cephalopods, pelagic shrimps and fish; pelagic and benthopelagic copepods were the most numerous prey items but did not provide a substantial contribution by weight. Cephalopods were by far the most important prey of the smaller individuals, with shrimps and fish becoming increasingly significant with increasing size.

10.4 Ecosystem function

According to de Groot *et al*., (2002), ecosystem function is the capacity of natural processes and components to provide goods and services that satisfy human needs, either directly or indirectly (de Groot *et al.,* 2002). de Groot *et al*., (2002) consider there to be four primary groups of ecosystem functions:

- Regulatory functions: the capacity of natural ecosystems to regulate essential ecological processes and life support systems.
- Habitat functions: in which natural ecosystems provide refuge and reproductive habitat to wild organisms.

- Production functions: photosynthesis, chemosynthesis and nutrient uptake by autotrophs converts energy, carbon dioxide, water and nutrients into a wide variety of carbohydrate structures which are then used by secondary producers.
- Information functions: natural ecosystems provide an essential 'reference function' and provide important contributions to cultural appreciation of the natural environment

The first two function-groups (regulation and habitat) are essential to the maintenance of natural processes and components and are considered conditional to the maintenance of the availability of the other two function-groups.

According to Thurber *et al.,* (2014), the deep-sea environment provides a multitude of services. Some of these could be classified as regulatory services, such as carbon sequestration, biological regulation, nutrient regeneration, bioremediation, biological habitat formation. Others could be classified as supporting services, such as nutrient cycling, circulation, chemosynthetic and secondary production, biodiversity. Yet other functions could be considered provisioning services such as carbon dioxide storage, fisheries, oil and gas, and rare minerals.

Many of the functions provided by the deep sea, even though they occur on small spatial and temporal scales, have direct implications for global services owing to the large size of the deep-sea environment. These functions and services are habitat/ecosystem dependent, with a generally positive relationship between diversity and ecosystem functioning and efficiency, although the strength of this diversity–function relationship may differ amongst habitats (Danovaro *et al.,* 2012).

In the following section, the ecosystem functions provided by the microorganisms, benthic invertebrates and benthic and demersal nekton of the MAR are considered. These biological components are not subdivided by habitat, as there is very little information available for each biological component.

10.4.1 Microorganisms

Ascertaining the functional roles of microorganisms in the deep sea is challenging, particularly as these microbes have adapted to the high pressure, low light and potentially niche temperature or chemical environments. As a result, it can be very difficult to retrieve and maintain microbial samples in the same conditions as their natural environment, which would be required to assess gene expression and other parameters that would indicate their functional role within the ecosystem. *In situ* experiments are also challenging, due to the requirements for specialised (and expensive) methods and equipment.

The information on microorganisms at non-hydrothermal hard substrata along mid-ocean ridges is scarce. Studies on the East Pacific Rise showed that show that the abundance of prokaryotic communities, dominated by the bacterial domain, positively correlates with the extent of rock alteration – the oldest, most altered basalt harbours the greatest microbial biomass, with phylogenetic analyses suggesting that the basalt biome may contribute to the geochemical cycling of iron, sulphur, manganese, carbon and nitrogen in the deep sea (Santelli *et al.,* 2009).

Incubations with isotopes at several seafloor exposed basalts showed the presence of genes from bacteria in the orders Acidimicrobiales, Acidithiobacillales, Chromatiales, and Mariprofundales which are all active carbon-fixing bacteria in seafloor-exposed basalts (Orcutt *et al.,* 2015). Subsurface basalt-associated microbial communities have also been found on the western flank of the MAR, which may utilise iron oxidation for metabolic activity, (Zhang X *et al.,* 2016).

Deep-sea hydrothermal vent environments represent highly productive ecosystems, entirely fuelled solely by the reduced inorganic substances (for example, reduced sulphur compounds, hydrogen or methane) contained within hydrothermal fluids. Chemolithoautotrophic microorganisms use the energy released through the oxidation of such compounds for the fixation of inorganic carbon. Thereby, these microorganisms mediate the transfer of energy from the geothermal source to higher trophic levels and thus form the basis of the unique food webs existing in these environments (Hügler *et al.,* 2010). Vent microorganisms can perform several functions, for example, sulphur oxidation and sulphate reduction; ammonia and nitrite oxidation; nitrate reduction; hydrogen and methane oxidation; manganese oxidation; and iron II oxidation and reduction (Ding *et al.,* 2017). Over recent years, microbial functional diversity has been central to understanding the functional role of key genes involved in biochemical pathways.

Few studies on the ecosystem function of microorganisms have been conducted at hydrothermal vent habitat along the MAR. Hügler *et al.,* (2010) at the Logatchev vent field determined that two important groups of primary producers, *Epsilonproteobacteria* and *Gammaproteobacteria,* both at the Irina II site, may use different pathways for sulphur oxidation and carbon fixation. The *Epsilonproteobacteria* can oxidize reduced sulphur compounds via the Sox pathway and fix carbon dioxide via the reductive tricarboxylic acid cycle, whilst the *Gammaproteobacteria* can oxidize sulphur mainly via the adenosine 5′-phosphosulfate pathway and fix carbon dioxide via the Calvin-Benson-Bassham cycle. Hügler *et al.,* (2010) also suggest that a variety of *Gammaproteobacteria* at the Irina II site can utilise sulphite as a free intermediate during the oxidation of sulphur via the adenosine 5′-phosphosulfate pathway (Hügler *et al.,* 2010). A range of sulphate-reducing prokaryotes were identified from the Irina II site, including *Deltaproteobacteria*, the thermophilic *Thermodesulfobacteria* and hyperthermophilic *Archaeoglobales.* The latter two prokaryotes are anticipated to inhabit the seafloor subsurface, where higher temperatures are reached, and are carried to the seafloor within the vent fluids (Hügler *et al.,* 2010).

Chemolithoautotrophic iron-oxidizing bacteria play an essential role in the global iron cycle, and have also been recorded from the MAR. The marine iron-oxidizing bacteria (Zetaproteobacteria) has been identified from Rainbow, Trans-Atlantic Geotraverse (TAG), and Snake Pit vent fields (Scott *et al.,* 2015). This study demonstrated that Zetaproteobacteria are rare if an iron source is not readily available and suggested that this organism is likely locally restricted to iron-rich marine environments but may exhibit wide-scale geographic distribution, further underscoring the importance of Zetaproteobacteria in global iron cycling. These microorganisms have also been reported in association with the gill chamber of the shrimp, *Rimicaris exoculata*, from the Rainbow hydrothermal system (Jan *et al.,* 2014; Zbinden *et al.,* 2004).

There have been no studies on the ecosystem function of microbial communities colonising inactive sulphides along the MAR. However, work in other regions suggests that microorganisms colonising inactive sulphides can perform a range of functions, as reviewed by Van Dover (2019). There is growing evidence for chemoautolithotrophic carbon fixation by microorganisms utilising inactive sulphide substrata as an energy source (Kato *et al.,* 2010). Bacteria and Archaea in this habitat are through to have the metabolic potential for nitrogen (nitrogen fixation, ammonia oxidation, denitrification) and methane cycling, in addition to iron and sulphide oxidation (Li *et al*., 2017; Zhang *et al*., 2016). Magnetotactic bacteria allied to *Magnetobacterium bavaricum* (Nitrospirae) have been recorded at inactive sulphide habitat, with suggestions that these bacteria may use iron or sulphur metabolic pathways (Edwards *et al*., 2005; Suzuki *et al*., 2004,) and so be important in the biogeochemical cycles of iron and sulphur (Lin *et al*., 2014). Macroscopic filamentous bacteria at inactive sulphides may also play a role in the sulphur cycle, either as sulphur oxidisers or sulphate reducers; these ‘cable bacteria’ are thought to harvest and transport electron donors and electron receptors across centimetres, using electrical currents (Meysman, 2018).

The microbial ecosystems of cold, dark, sub-seafloor sulphides may be different from the microbial communities colonising surface sulphide habitat, including the potential for carbon dioxide and nitrogen fixation as well as oxidation of hydrogen, sulphide, and intermediate sulphur species (Kato *et al*., 2015; Kato *et al*., 2018). It has also been suggested that microbes associated with inactive sulphides have the potential to enhance bioleaching of potentially toxic metals (iron, copper, zinc) from sulphides and to accelerate galvanic interactions that increase metal dissolution rates (Fallon *et al*., 2017).

10.4.2 Benthic invertebrates

There are few studies on the functions and services that MAR benthic invertebrates perform. However, the patterns of functions and services can be described as they are often group dependent, with functional traits often being shared between closely related taxonomic groups. One of these functions is the provision of three-dimensional habitat structure by bioengineering species such as corals and sponges.

Cold-water coral reefs, coral gardens, sponge grounds, and massive sponges support and enhance highly diverse benthic invertebrate communities, leading to faunal biomass that is orders of magnitude above that of the surrounding seafloor (Beazley *et al*., 2013; Henry & Roberts, 2007; Roberts *et al*., 2008). The composition of benthic invertebrate megafauna is also significantly different between sponge ground and non-sponge ground habitat, and between different sponge morphologies (Beazley *et al*., 2013).

Corals and sponges can serve as important spawning, nursery, breeding and feeding areas for a multitude of fishes and invertebrates (Ashford *et al*., 2019; Gomes-Pereira *et al*., 2017; Pham *et al*., 2015; Porteiro *et al*., 2013). The ability to construct calcium carbonate frameworks means that deep-sea corals provide an important biogeochemical function in both the carbonate system (Doney *et al*., 2009) and in calcium balance (Moberg & Folke, 1999).

Sponges, with their filter-feeding capacity, can filter more than 90 % of bacteria and organic matter from seawater, so acting as carbon sinks, impacting both the benthic-pelagic coupling of carbon and the microbial loop (Leys *et al*., 2017; Maldonado *et al*., 2012; Yahel *et al*., 2007). Sponges also have an important role within inorganic nutrients cycles, including nutrients such as silicate, nitrate, nitrite, ammonium and phosphate (Maldonado *et al*., 2012).

Hydrothermally active habitat is biologically more productive and supports greater biomass relative to the surrounding non-hydrothermal deep-sea habitat. On a global scale, hydrothermal vents are involved in the biogeochemical cycling and elemental transformation of carbon, sulphur, and nitrogen (Lilley *et al*., 1995; Petersen *et al*., 2011; Sievert & Vetrini, 2012). These ecosystems support enhanced trophic and structural complexity relative to the surrounding deep sea and provide the setting for complex trophic interactions (Colaço *et al*., 2007; Portail *et al*., 2017). A recent study by Chapman *et al.,* (2019) has produced the first global hydrothermal vent fauna functional traits database, which will enable more detailed studies of the functions of vent fauna, including species recorded from the MAR. Very little is known about the benthic invertebrates colonising inactive sulphides, both along the MAR and globally, meaning the ecosystem function of this fauna is unknown.

10.4.3 Benthic and demersal nekton

Very little is known about the ecosystem function of benthic and demersal nekton along the MAR. Ridges can harbour an important fraction of the large reproductive individuals in some populations, at least for fishes (Sutton *et al.,* 2008). Highly motile scavenging amphipods observed on the MAR (Duffy *et al.,* 2013; Horton *et al.,* 2013) also play a role in recycling and dispersing carrion organic matter inputs to deep-sea habitats.

10.5 Connectivity

This MAR is effectively an underwater mountain chain, which separates the east and west basins of the North Atlantic and can act as either a barrier or a pathway for connectivity, depending on the biota considered. Oceanographic fronts associated with some of the larger fracture zones, such as the Charlie Gibbs Fracture Zone (CGFZ), can also act as barriers between North and South sections of the MAR, whilst connecting the east and west North Atlantic basins.

Connectivity is a very important concept within environmental management, and there are multiple molecular tools which can be utilised to help determine the connectivity of potential set-aside sites, or preservation reference zones, in the context of deep-sea mining. Boschen *et al.,* (2016) provided an overview of the use of genetic tools in selecting and testing the suitability of set-aside sites protected from deep-sea polymetallic sulphide mining, the principles of which could be applied to the MAR.

Connectivity can be considered multiple ways, and it is beyond the scope of this version of the document to consider all the different forms of connectivity for the MAR benthic biota. In general, there are few population connectivity studies on benthic biota of the MAR, making it challenging to assess the connectivity of benthic biological components. Future versions of this document may address the connectivity of MAR benthic biota in more detail.

10.5.1 Microorganisms

Surface and deep-sea prokaryotic communities are strongly connected, constituting a vast oceanic metacommunity where local assemblages are linked through the transport of sinking particles. This vertical dispersal, mediated mainly by the largest sinking particles, emerges as a fundamental process shaping the assembly and biogeography of deep ocean prokaryotic communities (Mestre *et al.,* 2018).

The dominant habitat-creating species of the MAR hydrothermal vent fields are the vent mussels *Bathymodiolus azoricus* and *B. puteoserpentis.* Duperron *et al.,* (2006) demonstrated that individual mussels from both species collected from vent sites along the MAR share highly similar to identical 16S rRNA phylotypes of the two dominant thiotroph- and methanotroph-related symbionts. However, populations genetic studies of MAR symbionts have not yet been performed. A study from East Pacific Rise, Galápagos Rift, and Pacific-Antarctic Ridge demonstrated that despite mussel species hybridizing along the Easter Microplate, the northern and southern symbionts appear to be completely isolated (Ho *et al.,* 2017). It is not yet known if a similar pattern occurs in Bathymodiolid symbionts at hybridization zones along the MAR, such as Broken Spur.

Whilst microbial communities colonising inactive sulphide habitat are increasingly the focus of research attention, very little is known about these communities along the MAR, and their connectivity has not yet been investigated.

10.5.2 Benthic invertebrates

More is known about the connectivity of the MAR benthic invertebrates, although there are still considerable knowledge gaps, which may complicate environmental management. In general, very little is known about patterns of connectivity in the deep sea, although recent studies have suggested that the stepping stone model may be appropriate for many deep-sea populations (Morrison *et al*., 2017), particularly those arranged linearly along mid-oceanic ridge axes (Coykendall *et al*., 2011; Vrijenhoek 2010) or linear arrays of seamounts (Samadi *et al*., 2006). Mullineaux *et al*., (2013) studied the various trajectories that larvae may take from the adult site based on buoyancy, active upward and downward swimming, and advection in currents and thermal plumes. Observations were made that indicated that (on the East Pacific Rise) downward movements constrained the larvae within the axial valley and reduced the loss of larvae to cross-ridge currents. In contrast, modelling of currents on the MAR in close proximity to the seabed highlighted the role of sub-mesoscale and tidal currents in creating greater turbulence and therefore ensuring the wider dispersion of larvae (Vic *et al*., 2018). A greater understanding of larval behaviours on the MAR is needed as well detailed spatial and time series mapping of near-seabed currents, especially in and around the mid axial valley. These data are missing at present but in the future, could be collected using autonomous underwater profiling vehicles (Billings *et al*., 2017).

Many of the cold-water corals along the MAR are thought to have lecithotrophic larvae, although the larvae nutritive modes for the majority of coral species are still unknown. In general, larval dispersal distances for cold-water corals tends to be short, although this will in part depend on local currents. Some deep-sea cold-water coral species have been studied from the North Atlantic, although not from ridge habitats. Mitochondrial DNA and microsatellites markers demonstrated that some species are highly connected (Thoma *et al*., 2009); some are connected at the regional scale, with moderate connectivity (Morrison *et al*., 2011); and others present regional structure (Herrera *et al*., 2012).

Most sponge species are hermaphrodites or, more rarely, egg and sperm cells are produced by separate individuals (dioecious). Patterns of sexual reproduction vary from one group to another, but in general sponge reproduction is poorly known (Hogg *et al*., 2010). Sponge larvae generally settle a few days after leaving the parent (Fell 1974; Ruppert *et al*., 2004), attaches to the substratum, and develops into a juvenile sponge.

There is very little information on the connectivity of sponges generally, with next to nothing known about the connectivity of deep-sea sponges. Connectivity studies of some mesophotic sponge species demonstrate high levels of population structure, with some horizontal and vertical connectivity between neighbouring populations, but high dependence on self-recruitment (Bernard *et al.,* 2019). Shallow-water species also show high levels of inbreeding, which in combination with the low dispersal abilities of sponge larvae, results in strong population divergence (Riesgo *et al.,* 2016; Riesgo *et al.,* 2019; DeBiasse *et al*., 2010). If these connectivity patterns also occur in deep-sea sponges along the MAR, then this low level of connectivity may influence their resilience to disturbance on a metapopulation level.

The connectivity of benthic invertebrates colonising hydrothermally active habitat is better known than those inhabiting hard non-hydrothermal substrata, although there are still many unknowns, and population connectivity studies in general are scarce. Active hydrothermal vents are localized, fragmented habitats, harbouring endemic species reliant on chemosynthetic primary production. Several vent species exhibit evidence for stepping-stone dispersal along relatively linear, oceanic ridge axes. Other species exhibit very high rates of gene flow, although natural barriers associated with variation in depth, deep-ocean currents, and lateral offsets of ridge axes often subdivide populations (Vrijenhoek, 2010).

The MAR vent shrimp *Rimicaris exoculata* produces very large lecithotrophic eggs and planktotrophic larvae that feed in the photic zone before settling as juveniles (Dixon & Dixon 1996). As a result, this species exhibits extraordinarily high rates of gene flow along the MAR (Teixeira *et al*., 2010). Population genetic studies of MAR vent mussels led to the first report of a mid-ocean hybrid zone. *Bathymodiolus azoricus* occurs at the shallower (850–2251 m) northern localities, and *B. puteoserpentis* occurs at the deeper (3080–3650 m) southern localities (Maas *et al.,* 1999). Examination of DNA sequences from seven nuclear loci and a mitochondrial locus suggest that these closely related species may have split <1 million years ago (Faure *et al*., 2009), with both species occurring and hybridizing at an intermediate latitude (O'Mullan *et al*., 2001). Genetic population studies demonstrated that at intermediate latitudes, there was a genetically mixed population which showed no evidence for hybrid incompatibilities (Breusing *et al*., 2017). However, studies using biophysical and genetic models showed that the Mid-Atlantic vent mussel populations are contemporarily isolated, and that population connectivity can only be maintained in a stepwise manner (Breusing *et al*., 2016)

The clam *Abyssogena southwardae* has been recorded from hydrothermal vents on the MAR North and South of the Romanche Fracture Zone, and from cold seep sites on the West Florida Escarpment, the Barbados Accretionary Prism and the Lobes of the Congo (Krylova *et al.,* 2010; LaBella *et al.,* 2017). An assessment of genetic variation amongst these populations determined that there were two lineages of *A. southwardae.* The MAR population was included within lineage 1, which also encompassed the West Florida Escarpment, Barbados Accretionary Prism and Lobes of the Congo populations. Lineage 2 was restricted to the Lobes of Congo population (LaBella *et al.,* 2017). Bidirectional gene flow was detected between the Mid-Atlantic Ridge and the Barbados Accretionary Prism populations, and also between the West Florida Escarpment and Lobes of the Congo populations (LaBella *et al.,* 2017). The only haplotype of *A. southwardae* shared between two or more populations was shared between the Barbados Accretionary Prism and MAR populations, occurring at both Logatchev (northern MAR) and Clueless vent (southern MAR). This haplotypic evidence suggests that there is no major hydrographic barrier for *A. southwardae* populations North and South of the Romanche Fracture Zone (van der Heijden *et al.,* 2012; LaBella *et al.,* 2017). Genetic variation, gene flow and haplotypic evidence all support connectivity between the MAR and Barbados Accretionary Prisms populations of *A. southwardae* (LaBella *et al.,* 2017). These connectivity results provide support for the concept of wider connectivity for those MAR hydrothermal vent species which are able to utilise multiple chemosynthetic habitat types, such as cold seeps.

The red-blooded limpet *Shinkailepas briandi*, which is common on several hydrothermal vent fields from the MAR, exhibited a panmictic population through its geographic and bathymetric zones (38°N, 814–831 m depth at Menez Gwen to Ashadze field at 13°N, 4090 m depth). Retention of eye pigmentation in newly settled juveniles, along with the genetic panmixia, suggests that the hatched larva of *S. briandi* migrates vertically to the surface waters, presumably to take advantage of richer food supplies and stronger currents for dispersal (Yahagi *et al.,* 2019).

A first molecular study on dirivultids showed that this taxon might have high dispersal potential (Gollner *et al.,* 2011), whilst further molecular studies by Gollner *et al*., (2016) confirm high diversity, expansive population growth and high genetic connectivity of vent copepods along MAR. Connectivity between active vent sites for these copepods may be also accomplished through the use of intermediate habitats as stepping stones (Gollner *et al*., 2016), as also proposed for vent mussels.

The benthic invertebrate fauna at hydrothermally inactive sulphide habitat along the MAR is poorly known, and its connectivity has not yet been investigated. In other regions, the vast majority of species observed at inactive sulphides have been recorded from other habitats, but the genetic connectivity of inactive sulphide habitat with broader populations in the region is not known. The potential for inactive sulphides to support source populations important for regional population connectivity is also unknown.

Very little is known about the connectivity of soft-sediment benthic invertebrates along the MAR. Benthic sediment-dwelling crustacean species that were able to swim show gene flow across the MAR (between the eastern and western basins either side of the MAR), with several species found on both sides of the MAR (Bober *et al.,* 2018). However, for non-swimming and weakly-swimming species, the MAR may restrict their distributions between the western and eastern basins. Whilst genetic studies support the potential for differences in connectivity related to life history characteristics, sample sizes were small, and the number of locations studied was low (Brix *et al*., 2018; Riehl *et al*., 2018).

10.5.3 Benthic and demersal nekton

Very little is known about the connectivity of the benthic and demersal nekton, other than the trophic connections between the benthic and pelagic environment previously discussed. Scavenging and necrophagous amphipods are highly mobile and are found across multiple benthic habitats, but there seem to be significant differences in community composition and species richness north and south of the Charlie Gibbs Fracture Zone. It is possible that this is related to larger fish and cetaceans being associated with this region, resulting in elevated carrion food supplies for deep-living amphipods and so influencing their distribution (Horton *et al*., 2013).

10.6 Resilience and recovery

Very little is known about the resilience of the benthic biota of the MAR to potential future polymetallic sulphide mining impacts. Some inferences can be drawn from the benthic fauna’s response to other anthropogenic disturbances, such as deep-sea fishing, or the colonisation rates observed in nature when new habitat becomes available.

It is beyond the scope of this version of the document to provide a detailed account of the resilience of the MAR benthic biota, although future versions of this document may consider this in greater detail. However, some general observations can be made on traits that may influence resilience. For example, motile fauna such as the benthic and demersal nekton may be able to swim/crawl away from some mining disturbances, although they may still be impacted by the turbidity or toxicity of mining plumes.

Sessile suspension or filter feeding organisms, such as corals and sponges, cannot physically escape disturbances and are likely to suffer loss of fitness or even death if feeding or respiratory appendages are clogged from suspended sediment, or they are buried under plume fallout.

If fauna, such as hydrothermal vent species, are endemic to a habitat which is impacted by mining activities, then their recovery will depend on the existence of suitable habitat for colonisation and the connectivity of that habitat to the larger metapopulation of individuals for the supply of either larvae or motile adults. Recovery of some MAR hydrothermal vent species may be rapid, as was the case for copepods and nematodes during colonisation experiments (Plum *et al.,* 2017; Zepilli *et al.,* 2015). However, the potential to recover from large-scale habitat removal, as may be anticipated with deep-sea mining, is not known and is particularly important, as the global extent of active hydrothermal vent ecosystems is estimated to cover only 50 km^2, less than 0.00001% of the surface area of the planet (Van Dover *et al.,* 2018). Very little is known about the benthic biota potentially colonizing inactive sulphide habitat along the MAR. If endemic biota does exist, then mining activities may lead to loss of habitat, which given the cessation of hydrothermal activity at these sites, is unlikely to regenerate, making biotic recovery uncertain.

The time it takes for ecosystems to recover, if suitable habitat still exists, will depend on many factors, including individual growth rate, the time it takes to reach sexual maturity, the fecundity of the species, and connectivity to neighbouring habitats. Some of the organisms which are expected to take the longest time to recover from potential mining impacts are cold-water corals and sponges. These organisms are typically long-lived, slow-growing and have low reproductive outputs, which makes them extremely vulnerable to fisheries or other human impacts, with recovery times of individual coral colonies and communities requiring decades to centuries. For example, the black coral *Leiopathes* spp. can live for centuries (Carreiro-Silva *et al*., 2013) and is expected to be slow to recover from disturbance.

10.7 References

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