

ISA TECHNICAL STUDY NO. 28

Regional
environmental
assessment of the
northern
Mid-Atlantic Ridge



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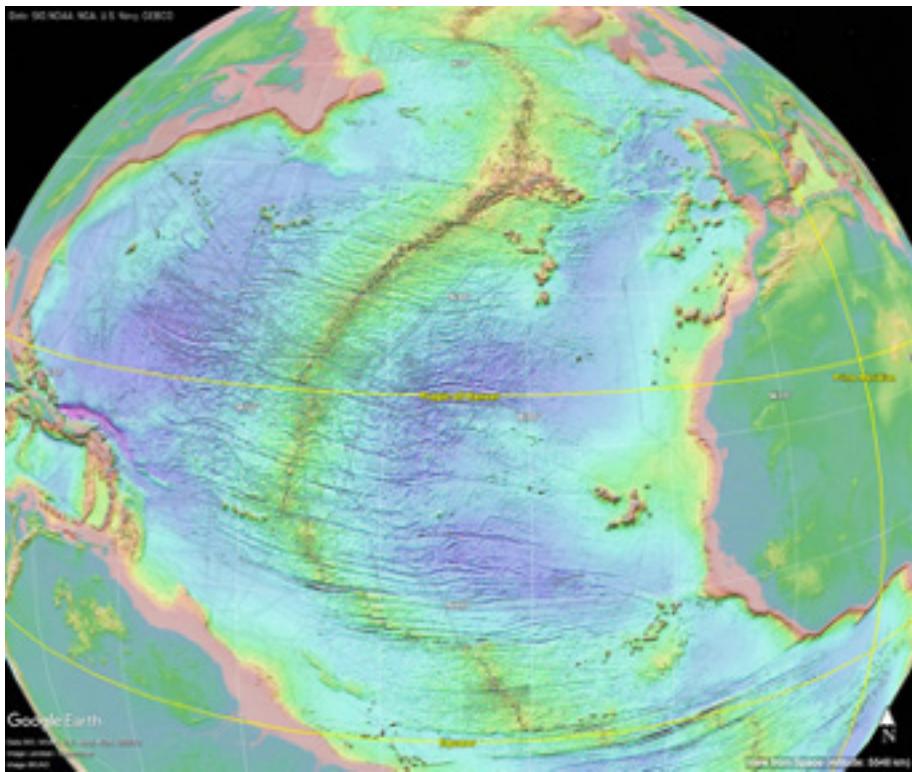
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ABBREVIATIONS

AABW	Antarctic Bottom Water
AMOC	Atlantic Meridional Overturning Circulation
AMV	Atlantic Multidecadal Variability
AUV	autonomous underwater vehicle
BBL	benthic boundary layer
CGFZ	Charlie-Gibbs Fracture Zone
COML	Census of 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
GOODS	Global Open Oceans and Deep Seabed
ICCAT	International Commission for the Conservation of Atlantic Tunas
ISA	International Seabed Authority
ISOW	Iceland-Scotland Overflow Water
IUCN	International Union for Conservation of Nature
LTC	Legal and Technical Commission
MAR	Mid-Atlantic Ridge
MAR-ECO	Patterns and Processes of the Ecosystems of the Northern Mid-Atlantic
METI	Ministry of Economy, Trade and Industry, Government of Japan
MiCO	Migratory Connectivity in the Ocean
MoMAR	Monitoring the Mid-Atlantic Ridge
Mt	million tonnes
NAC	North Atlantic Current
NADW	North Atlantic Deep Water
NAO	North Atlantic Oscillation
nMAR	northern Mid-Atlantic Ridge
PMS	polymetallic sulphides
REMP	regional environmental management plan
ROV	remotely operated vehicle
SponGES	Deep-sea Sponge Grounds Ecosystems of the North Atlantic
TAG	Trans-Atlantic Geotraverse
UNCLOS	United Nations Convention on the Law of the Sea
VTS	vertical transport system
WOCE	World Ocean Circulation Experiment

FOREWORD BY THE ISA SECRETARY-GENERAL

I am pleased to present Technical Study No. 28 on Regional environmental assessment of the northern Mid-Atlantic Ridge. This study was prepared by the Atlantic Regional Environmental Management Plan (REMP) project funded by the European Commission. It was conducted in collaboration with the Secretariat of the International Seabed Authority (ISA) in support of the development of a REMP for the international seabed areas (the Area) of the northern Mid-Atlantic Ridge (MAR).

Development and implementation of REMPs are at the core of the efforts of ISA to fulfill its mandate to ensure the effective protection of the marine environment under Article 145 of the United Nations Convention on the Law of the Sea. Building on the experience in developing and implementing the environmental management plan for the Clarion-Clipperton Zone, ISA is currently developing REMPs for key parts of the Area where exploration activities under contracts are carried out. The Area of the MAR has been identified by the Council of ISA as one of such key areas for the development of REMPs. Since 2018, in collaboration with various partner organizations, three expert workshops have been convened by ISA to support the Legal and Technical Commission of ISA to develop the draft REMP for the Area of the northern MAR with a focus on polymetallic sulphides deposits.

This technical study presents a synthesis of existing scientific and technical information relating to the northern MAR that informed the deliberations on area-based management tools and assessment of cumulative impacts as part of the REMP expert workshops. Information compiled in this study covers diverse topics, including the geomorphology, geology, physical oceanography and biological

communities of the northern MAR. It also includes information relating to the exploration and future exploitation of polymetallic sulphides in this mineral province. As such, it enables an improved scientific understanding of environmental characteristics, biodiversity and ecosystems in the northern MAR and helps guide future survey and research efforts. It is envisaged that this regional environmental assessment will be reviewed and updated as new scientific information becomes available.

I am grateful to the European Commission for supporting the Atlantic REMP project. I particularly wish to acknowledge the contributions of Pr. Philip Weaver, Dr. Rachel Boschen-Rose and other experts who helped write various chapters. This collaborative work sets a good example for future collaborative efforts between the ISA Secretariat, ISA members and scientific and other institutions in support of the REMP development in other mineral provinces. I greatly look forward to continuing this excellent collaboration with relevant stakeholders and experts.



Mr. Michael W. Lodge
Secretary-General
International Seabed Authority

PREFACE BY THE DIRECTOR GENERAL FOR MARITIME AFFAIRS AND FISHERIES OF THE EUROPEAN COMMISSION

As Director General for Maritime Affairs and Fisheries in the European Commission, I would like to congratulate the International Seabed Authority (ISA) for publishing this regional environmental assessment of the northern Mid-Atlantic Ridge.

In 2019, the European Commission launched the European Green Deal, our new growth strategy for making the EU's economy sustainable. To support its objectives and become the first climate neutral continent, the European Union has the ambition to lead globally on the conservation and protection of our environment, including seas and oceans, through developing a circular economy and clean technologies.

The European Commission is thus following very closely the ongoing process of the International Seabed Authority to develop the regulations for exploitation of the mineral resources in the Area (the Mining Code), including through enhancing the knowledge base of deep-sea ecosystems and related organisms.

In recent years, the EU has invested more than EUR40 million in research projects related to deep-sea mineral exploration. These projects assessed our current understanding of ecosystem functioning, recoverability, connectivity and associated ecological processes in the deep sea, and highlighted how further scientific advancement can be achieved to adequately address the environmental effects that may arise from future exploitation activities, including through long-term environmental baseline studies.

In light of the above, the European Commission, in partnership with the ISA Secretariat, launched a project in 2018 to support the development of a regional environmental management plan (REMP) for the Area of the northern Mid-Atlantic Ridge. This project was key in successfully delivering this Regional Environmental Assessment report, which offers a robust scientific basis for this REMP development.

On behalf of the European Commission, I wish to congratulate ISA for the impressive work achieved throughout this process. I am convinced that, ultimately, the regional environmental management plan for the Area of the northern Mid-Atlantic Ridge will be a concrete example that can be replicated elsewhere in the international seabed area.



Ms. Charlina Vitcheva, Director General
for Maritime Affairs and Fisheries,
European Commission

1. EXECUTIVE SUMMARY

Technical study No. 28 on Regional environmental assessment of the northern Mid-Atlantic Ridge was prepared to support the development of a regional environmental management plan (REMP) for the international seabed area (the Area) in the northern Mid-Atlantic Ridge (MAR) with a focus on polymetallic sulphide (PMS) deposits. This study provides aggregation and synthesis of existing scientific and technical information relating to the northern MAR, including geomorphology, physical characteristics, geology and biological communities, and a description of the current exploration activities and future mining processes.

The MAR is a slow-spreading ridge system, forming an elevated area of seafloor that runs roughly north-south through the middle of the Atlantic Ocean. The ridge axis is broken into numerous segments by fracture zones formed by transform faults that can offset the ridge by hundreds of metres to hundreds of kilometres. Active volcanism associated with spreading centres along the MAR has created a series of hydrothermal vent sites. Hydrothermal activity at these sites and resulting precipitation of sulphide minerals have formed hard substrate sulphide habitat and, in some places, metal-rich sediments. In some locations, sulphide habitat remains hydrothermally active, while in others, hydrothermal activity has ceased rendering the sulphides hydrothermally inactive. The MAR also hosts a variety of ecosystems controlled by multiple environmental factors, such as water depth,

food supply, seabed substrate and water mass characteristics. Due to its complex hydrographic and topographic setting, the MAR concentrates biomass over its flanks and summits, creating areas of high productivity in the pelagic environment. The pelagic assemblages of the MAR have a diverse fauna, including fishes, sharks, cephalopods (squid and octopus), crustaceans (shrimp) and surface animals, such as seabirds, sea turtles and marine mammals. The benthic environment of the MAR is a complex patchwork of habitats spanning thousands of metres and encompassing varied seabed geomorphologies. The linear nature of mid-ocean ridges and the intermittent occurrence of hydrothermally active areas pose challenges to specialized biological communities whose populations need to be able to interconnect from one hydrothermal vent site to another. Areas with low levels of hydrothermal venting and inactive vent sites are poorly characterized but may also support diverse and complex seafloor communities. Rocky substrates are common elsewhere along the MAR axis and can support habitat-forming species, such as corals and sponges, that, in turn, host larger complex biological communities. Benthic habitats of the MAR are dynamically connected over a range of spatial scales through dispersal processes and interactions with the pelagic ecosystem.

PMS are one of the three seabed mineral resources for which ISA has awarded contracts for exploration; the other

two include polymetallic nodules and cobalt-rich ferromanganese crusts. In the northern MAR, the distribution of 22 currently detected PMS deposits is rather heterogeneous. Distances between sites vary considerably. As of July 2021, three contracts have been signed by ISA for exploration on the northern MAR. Individual contract blocks in each contract area are closely tied to the ridge axis and cover both hydrothermally active and inactive areas. Exploitation for PMS has not started yet and will likely differ from exploitation for the other two mineral

resources. This technical study provides a robust scientific basis for understanding the specific characteristics of the environment and future exploitation practices for PMS, which have important implications for the development of the REMP in the northern MAR. It also shows the state of knowledge when the REMP was developed and may be used as a benchmark in determining when new scientific discoveries and information have been gathered to merit a review of the regional environmental assessment and an update to the REMP.

2. DOCUMENT PURPOSE AND SCOPE

This document represents a compilation of background information to support ISA Secretariat in facilitating the development of a REMP by ISA for the area of the seabed and ocean floor and subsoil thereof, beyond the limits of national jurisdiction (the Area) in the North Atlantic Ocean with a focus on PMS deposits. REMPs are a key component of ISA's strategy to ensure effective protection of the marine environment (ISA, 2019a). ISA is mandated, in accordance with article 145 of United Nations Convention on the Law of the Sea (UNCLOS), and with respect to activities in the Area, to take measures necessary to ensure effective protection of the marine environment from harmful effects that may arise from those activities, and to adopt appropriate rules, regulations and procedures for 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, the prevention of damage to the flora and fauna of the marine environment, and others. REMPs therefore form part of ISA's policy framework for environmental management, and 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 PMS (ISA, 2019c).

PMS are one of the three seabed mineral resources for which ISA has awarded contracts for exploration, the others being polymetallic nodules and cobalt-rich ferromanganese crusts. PMS have analogous deposits on land and can contain economically viable proportions of metals such as copper, zinc, lead, gold and silver. It is important to note that deep-sea exploitation 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 ISA is for the Clarion-Clipperton Zone in the Pacific Ocean, where exploration for polymetallic nodules is taking place (ISA, 2012). Polymetallic sulphides (PMS) are a very different resource to polymetallic nodules—with different mining practices—and 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 PMS resources in the Atlantic, which will be different from those of polymetallic nodule resources 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 between hydrothermal vent sites. In addition, areas with low levels of hydrothermal venting together with inactive vent sites are poorly understood 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 as a description of contract areas for exploration for mineral resources, mining processes 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 identification of area-based management approaches and

assessment of cumulative impacts, and inform the identification of elements for inclusion in the REMP for the MAR. This document should be of value beyond the development of the REMP, as it may provide information on the regional environment to inform the contractors' environmental impact assessments (EIAs) 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.

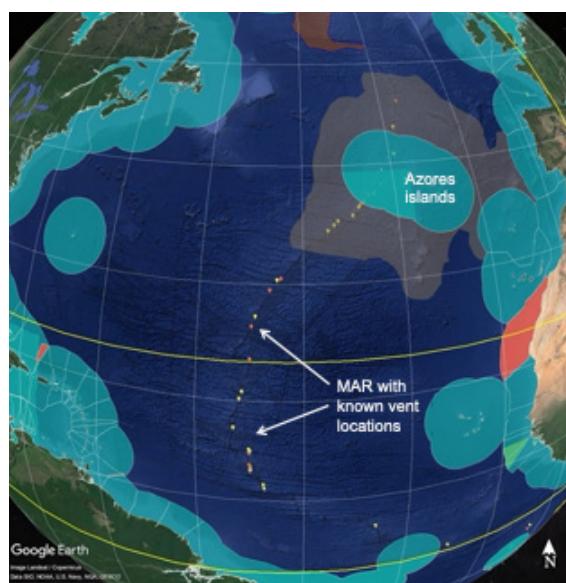
International Seabed Authority (2019b). Implementation of the Authority's strategy for the development of regional environmental management plans for the Area. ISBA/25/C/13.

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 a regional context for REMP development, it is necessary to understand physical processes and ecosystem distributions at full-basin scale rather than simply along the MAR and within the Area. Thus, the authors have taken a broad view by looking, 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 (ECS) claim on the MAR to the equator, exclusive of the Portuguese 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 extends along the MAR from the southern boundary of the Icelandic ECS claim (brown shading) to the equator, exclusive of the Portuguese ECS claim north and south of the Azores (grey shading) and the Brazilian 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 found at www.marineregions.org)



4. GEOLOGICAL OVERVIEW OF THE MID-ATLANTIC RIDGE OF THE NORTH ATLANTIC

4.1 Description of the Mid-Atlantic Ridge

The MAR 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, and creating new crust. This forms 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.

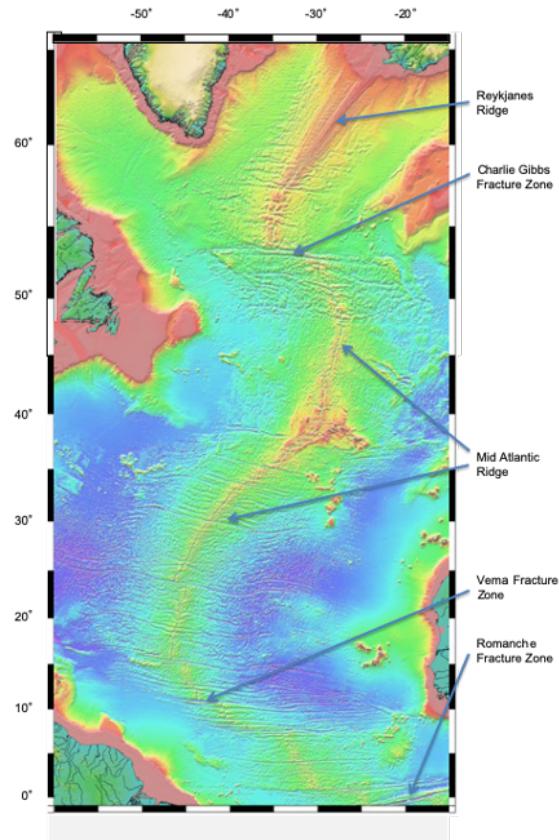
The ridge axis is broken into numerous segments by fracture zones that are formed by transform faults, and which can offset the ridge from hundreds of metres to hundreds of kilometres. The largest fracture zone in the Atlantic Ocean, located just south of the equator, is the Romanche Fracture Zone, which offsets the ridge axis by 900 km. Fracture zones appear as narrow, steep-sided valleys, which can be as deep as 7,761 m in the case of the

Romanche Fracture Zone. Other examples include the Charlie Gibbs Fracture Zone, another large feature located between Iceland and the Azores that creates an offset of 350 km (Figure 4.1) and is over 4,500 m deep at its deepest point, and the Vema Fracture Zone located at $10^{\circ} 46' N$, a narrow valley up to 5,000 m deep 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 albeit 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 National Oceanic and Atmospheric Administration Bathymetric Data Viewer website (<https://maps.ngdc.noaa.gov/viewers/bathymetry/>), and an example of data coverage is shown in Figure 4.2. The northern MAR (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 data availability varies from a few kilometres to 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. (Becker et al., 2019)



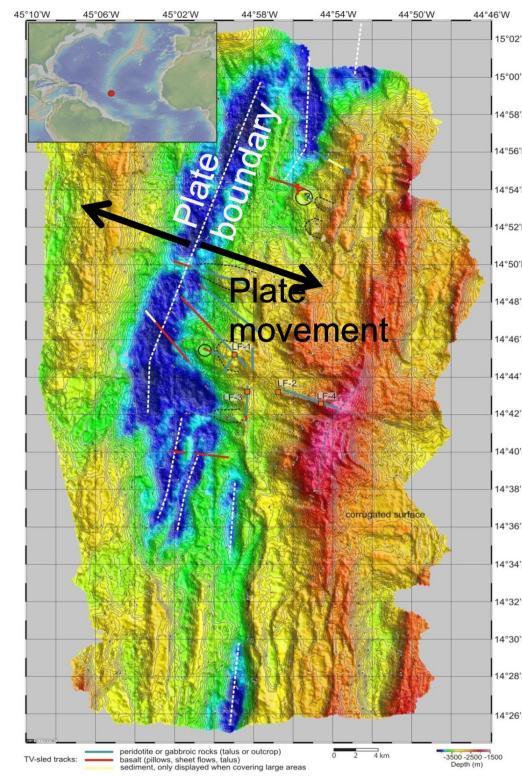
The highest-resolution data is obtained from multibeam echosounders operated close to the seabed either in remotely-operated or autonomous vehicles. Such deep-towed surveys are expensive and cover very small areas but can produce images with great clarity (Figure 4.3).

High-resolution bathymetry shows that the MAR comprises a middle or axial valley, often with steep sides (Figure 4.3), through which runs the plate boundary. Outside of the middle valley, there may be a series of ridges running parallel to the

Figure 4.2 Colour-shaded relief visualization of gridded multibeam bathymetric data from surveys archived at National Oceanic and Atmospheric Administration's National Centers for Environmental Information (NCEI). (<https://noaa.maps.arcgis.com/home/item.html?id=6b16e66ffd3740b5820875a-d0af25042>, accessed 22 August 2019)



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



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 by settling skeletons of plankton and wind-blown dust and progresses with time, eventually smoothing off the topography and forming layers that may 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 wide

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 smaller south of the Azores than at the equator.

Figure 4.4 Top: Geologic map with profile lines corresponding to the cross-sections presented in the bottom image. Bottom: Cross-sections (vertical exaggeration of 4x) 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 the top image. 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)

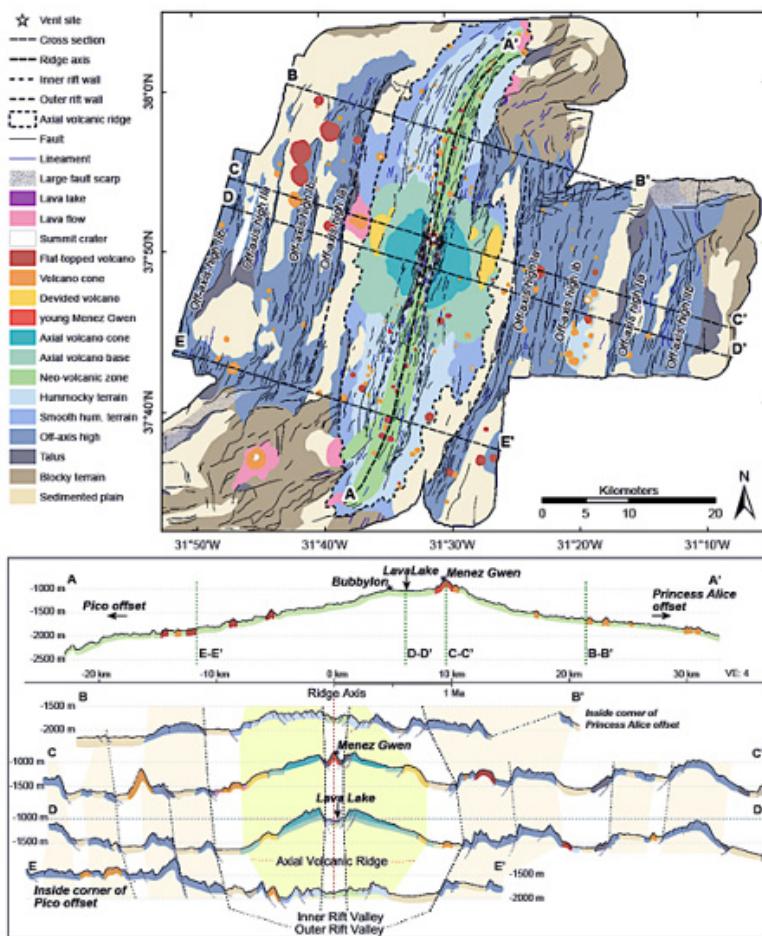


Figure 4.5 Top: Sediment thickness in the Atlantic Ocean (Straume et al., 2019). **Bottom:** Cross-section of the MAR showing increasing age of crust away from ridge axis and gradual sediment build-up away from the ridge axis.

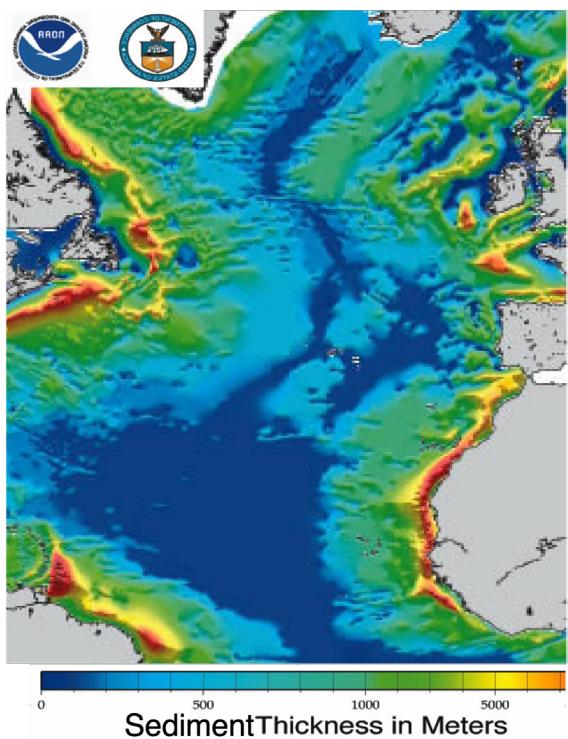
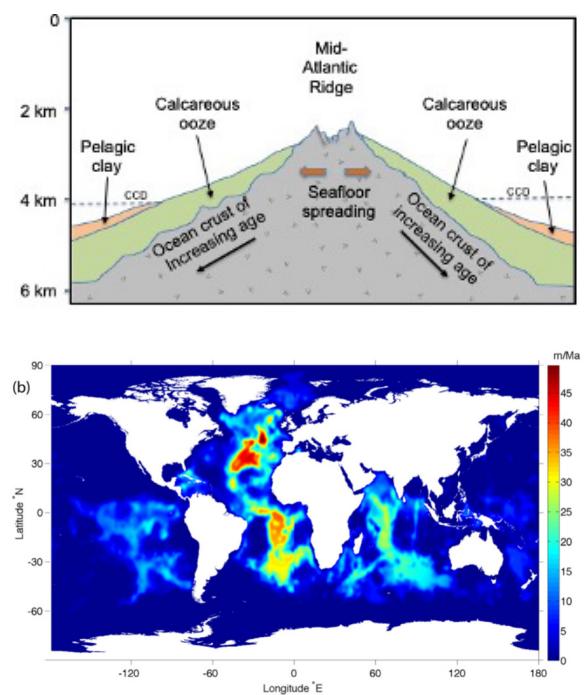


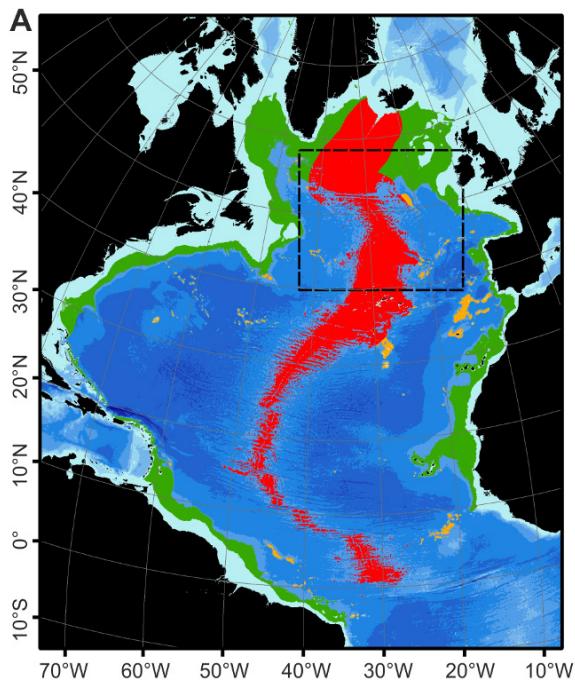
Figure 4.6 Present-day global ocean sediment accumulation rates. (Reproduced from Olson et al., 2016)



Niedzielski et al. (2013) carried out detailed surveys of sediment cover on the ecosystems of the Mid-Atlantic Ridge at the Sub-Polar Front and Charlie-Gibbs Fracture Zone (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 the 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 “[h]ard 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 are sedimented, although elevated outcrops that are swept clear of sediments by currents retain 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 per cent had slopes steeper than 30°, and 70 per cent of these steep slopes had hard substrates. Thus, Niedzielski concluded that the MAR (defined for this purpose as between water depths of 800 and 3,500 m and extending a maximum of 400 km either side of the ridge axis—see Figure 4.7) had 90 per cent 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 on sedimented ones at 45° N on the MAR. Gebruk and 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 Biology Chapters 8 and 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 and 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 800–3,500 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 sea floor since they are elevated above the local topography, often provide habitat for increased numbers of species nearby, 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 (Nalessa et al., 1995). In a study off of 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 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 1,000 m above the ocean floor. Features with elevations of 500–1,000 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 occur at a wide range of 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 lie partly in oxygen-minimum zones. Seamounts may be isolated, part of a cluster or part of a chain such as along the MAR axis. They are subject to varying levels of organic carbon flux that can influence faunal distributions, and have been classified into those receiving high, medium and low flux and through a proximity index in which seamounts are regarded as being close if they lie within 100 km of their nearest neighbour and distant if farther away (Clark et al., 2011).

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

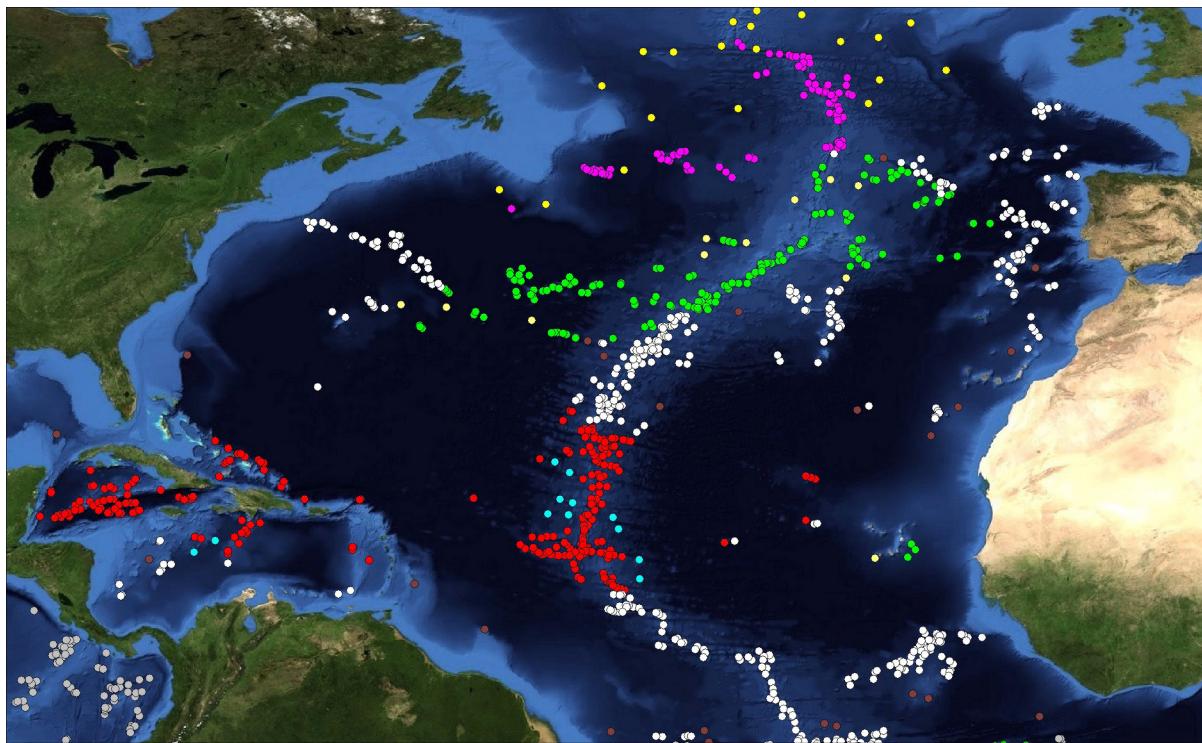


Figure 4.8 shows 1,197 seamounts with elevations greater than 1,500 m in the North Atlantic identified and grouped into 19 classes by Clark et al. (2011), who regarded the primary distinguishing features for these classes to be organic matter flux and proximity index. Seamounts of the New England chain (white) are similar to those of the central region of the MAR (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 are characterised by low organic matter flux.

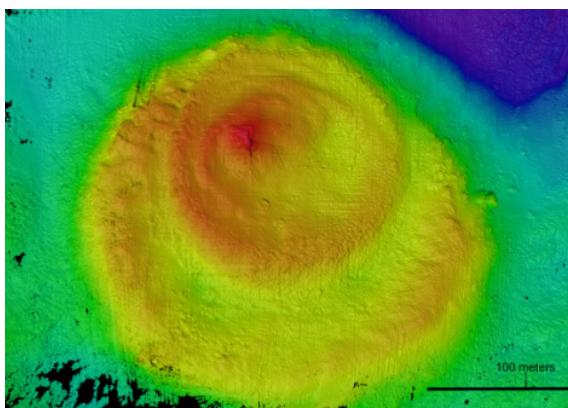
Yesson et al. (2011) identified over 1400 seamounts within the North Atlantic and listed an additional 7537 knolls that they believe could provide equally important habitat. One feature which is apparent in the datasets of both Clark et al. and Yesson et al. is the concentration of seamounts along the 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 that have buried some 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 zinc and lead sulphide minerals soluble at lower temperatures are deposited

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

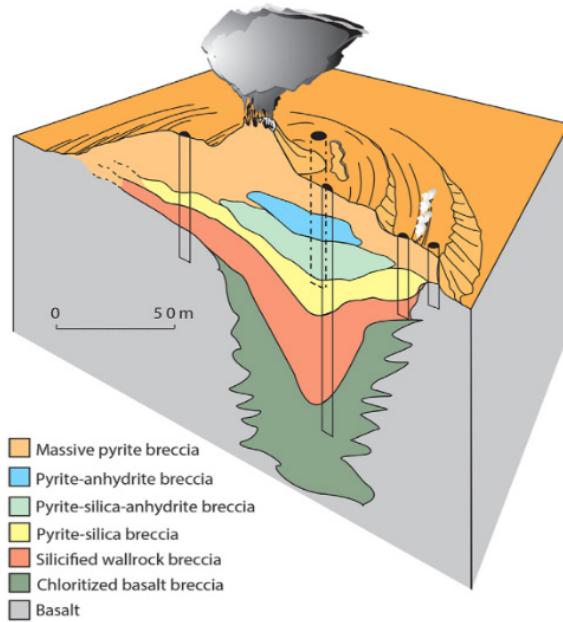


farther away. If conditions are favourable, polymetallic massive sulphide deposits are formed at or below the seafloor and are composed predominantly by iron sulphides (pyrite and/or pyrrhotite), sphalerite, chalcopyrite, and/or galena as the main sulphide phases. The chimneys are unstable and, over 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).

The Trans-Atlantic Geotraverse (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 at 3,600 m water depth, 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 emitting fluids at around 360°C. The TAG mound was drilled by the Ocean Drilling Programme Leg 158 in 1994 (Humphris et al., 1995), with seventeen holes drilled at five locations. Maximum depth of the drilling was 125 m. The drilling results

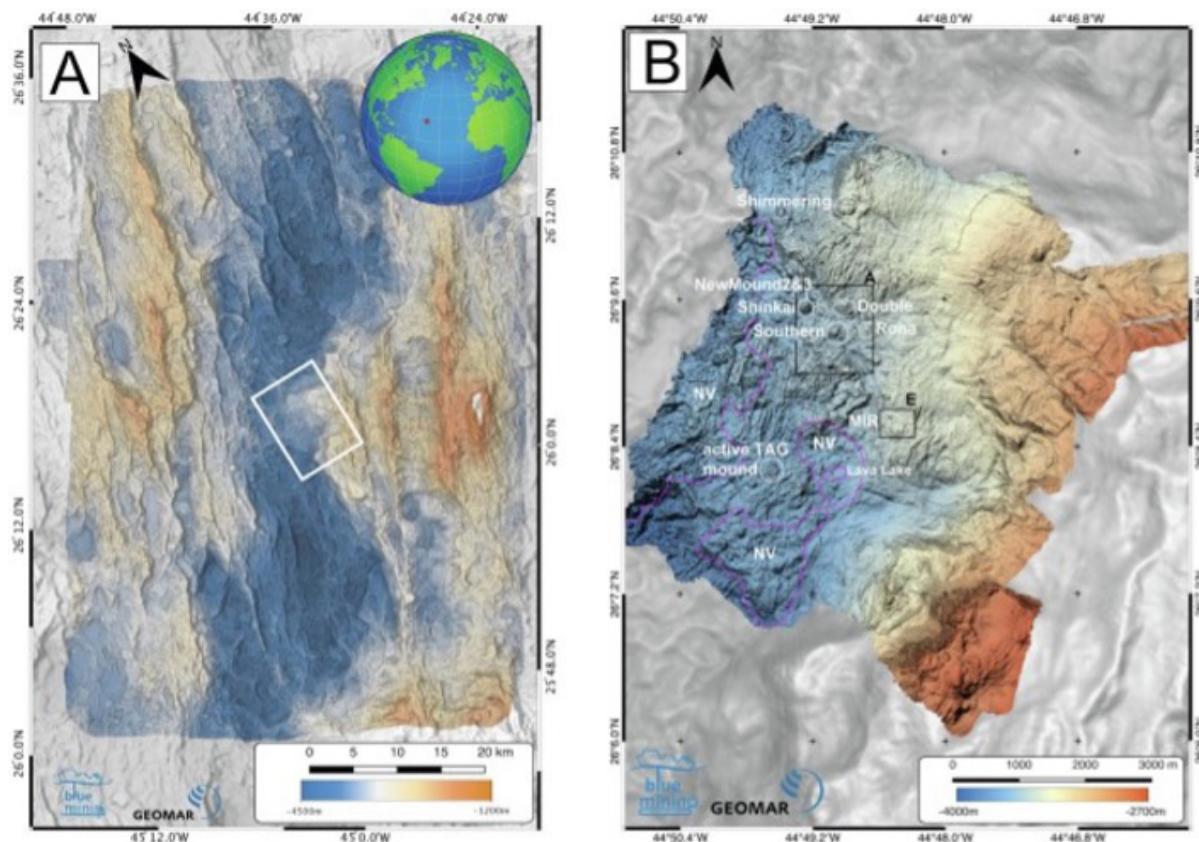
have enabled the subsurface structure of the mound to be determined (Humphris et al., 2015) as shown in Figure 4.10. It consists of a stockwork zone (denoted as silicified wallrock breccia and chloritized basalt breccia) that connects to a sulphide lens above (denoted as pyrite intervals).

Figure 4.10 The subsurface stratigraphy of the TAG active mound determined by drilling during Ocean Drilling Programme 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, for example, Krasnov, Peterburgskoe, Zenith-Victoria and Puy des Folles (Cherkashov et al., 2010). Other fields are comprised of a number of individual sites, such as Ashadze and Logatchev in Table 4.1. In some cases,

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



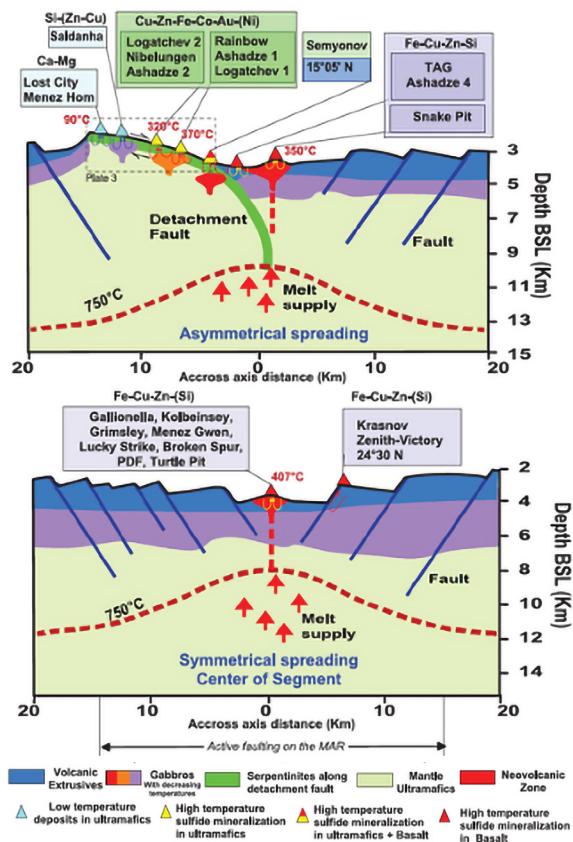
individual sites are hydrothermally active, whilst others within the same field are inactive, for example in the TAG mound, part of the TAG vent field, which includes a series of inactive vent sites (Murton et al., 2019).

It is important to note that deposits of PMS 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 form in a range of locations relative to the spreading plates (Fouquet et al., 2010). Some form at the plate boundary in the axial valley, where they are associated with volcanism and basaltic rocks and are known to have a predominantly magmatic setting. This type may also occur on top of the axial valley walls, where their location is determined by faults (Figure 4.12, lower panel). Other vents form away from the

plate boundary in locations where mantle rocks are exposed on the seabed due to the removal of the crust by detachment faults. These tectonically-controlled vents occur 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, upper panel), but are sustained by fluid flow through the upper crust driven by hot subsurface intrusions and/or exothermic reactions. Detachment faults can displace the vents away from the ridge axis by as much as 12 km in the case of the Logatchev 2 vent.

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

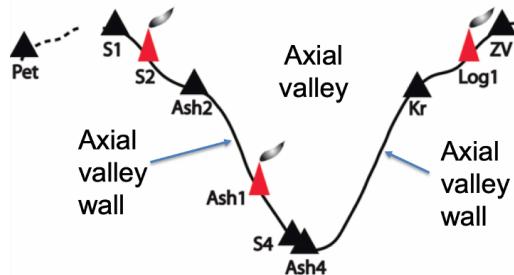
Figure 4.12 Schematic model for the location and composition of major hydrothermal deposits along the MAR. **Upper panel:** Cross-section of the MAR showing vent locations related to detachment faults (heavy green line). Positions of vents are at the scale of their distance from the axis—Lost City, 15 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-Victoria, 9 km. Note that black smokers with a temperature of 320°C are seen as far as 12 km from the ridge 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)



4.4 Relationship of active to inactive vent sites

Many vents on the MAR have been active for thousands of years—some for as long as 200,000 years (Cherkashov et al., 2017)—although all of them have experienced several discrete periods of active hydrothermalism interspersed with inactive periods (Figure 4.14). Active periods

Figure 4.13 Location of some known active and inactive vent sites with respect to the axial valley (active vent sites in red): Peterburgskoe (Pet); Semenov (S) 1, 2 and 4; Ashadze (Ash); Krasnov (Kr); Logatchev (Log); Zenith-Victoria (ZV). (Figure courtesy of A. Gebruk)

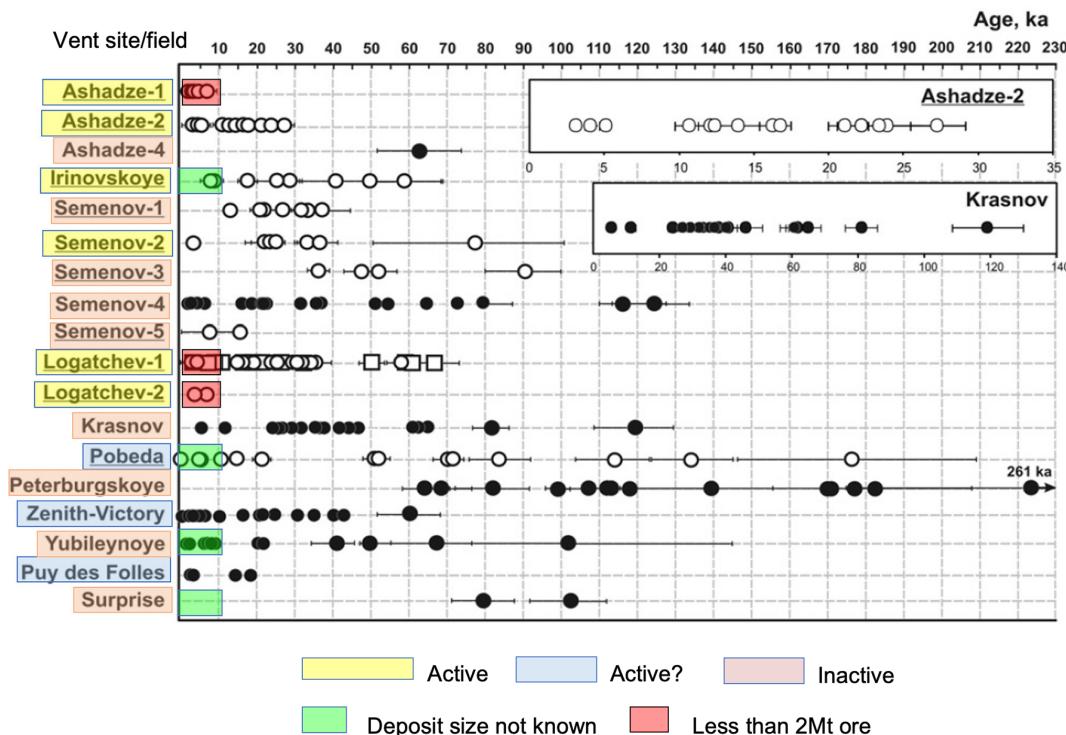


may end due to reductions in supply of hydrothermal fluids, obstructions to their flow – for example clogging of chimney conduits – or volcanic activity (Van Dover, 2019). Cherkashov et al. (2017) analysed data from several locations and concluded that there have been distinct periods when hydrothermal activity was at a peak, such as during the last glacial maximum.

Eventually, vent sites become permanently inactive due to movement of the plate away from the ridge axis and thus movement of the site away from the heat source, the site becoming covered with lava flow, or the vent fluids finding a new route to the seabed (Van Dover, 2019). Thus, there are three possible states for 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 the driving hydrothermal force, probably due to movement away from the ridge axis by plate tectonics or to being covered with lava flow (Van Dover, 2019)

Figure 4.14 Dating results with 1σ variability for SMS deposits in the contract area of the Government of the Russian Federation in the North Atlantic MAR. Symbols represent periods of activity. For further explanation, see Cherkashov et al., 2017. (Figure based on data from Cherkashov et al., 2017)



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

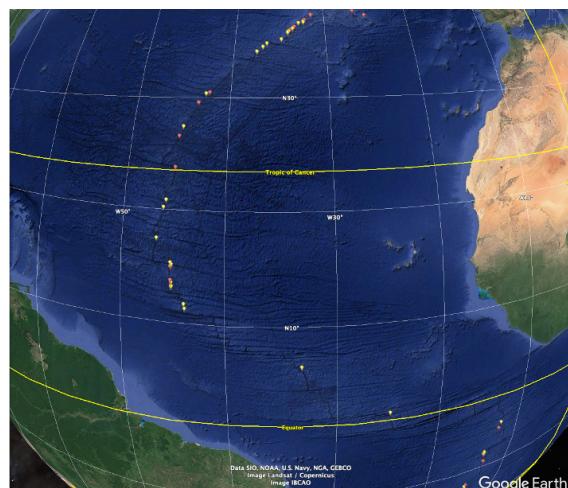
Extinct vents may become covered by thin layers of lava or may remain exposed on the seabed, where sediments will gradually cover them, although they are likely to remain exposed or shallowly-buried a few km to tens of km away from the ridge axis.

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 Interridge¹, 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

Figure 4.15 Location of vent sites listed in the Interridge database, plotted on a Google Earth map. Vent sites that are known to be active are coloured red, while those inferred but not proven to be active are yellow. (Beaulieu and Szafranski, 2019)



¹<https://vents-data.interridge.org/>

vent fields listed in the Interridge database in the Area between the southern boundary of the Icelandic ECS claim and the northern boundary of the Portuguese ECS claim.

The Interridge database lists 18 active hydrothermal vent sites on the North Atlantic MAR (including the Reykjanes Ridge), plus 28 which are inferred to be

active and 14 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. (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
Bubylon	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

Name ID	Activity	Latitude	Longitude	Maximum or single reported depth	Full spreading rate (mm/a)
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

Name ID	Activity	Latitude	Longitude	Maximum or single reported depth	Full spreading rate (mm/a)
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 ECS claim vent sites are more frequent (Figure 4.15; Table 4.1). Within the latter range, the average distance of separation between known active and active-inferred vent sites is 105 km, with a maximum distance of 322 km between Snake Pit and Puy de Folles. These calculations, however,

are likely to change with the discovery of new active vent sites based on further exploration and if active-inferred sites are eventually confirmed as active or inactive.

4.6 References

References for Chapter 4 are included in the References section of Chapter 5.

5. CONTRACT AREAS AND THE MINING PROCESS

5.1 Existing ISA contract areas on the northern MAR

The total area awarded for exploration by 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 PMS 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 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 six contiguous blocks lie across the ridge axis. This creates a corridor at least 30 km

wide on each side of the ridge axis where contract blocks have been identified for exploration. Several of the blocks cover known active hydrothermal vent sites, others cover known inactive vents, and many of them cover areas of ridge where active vents have not yet been detected.

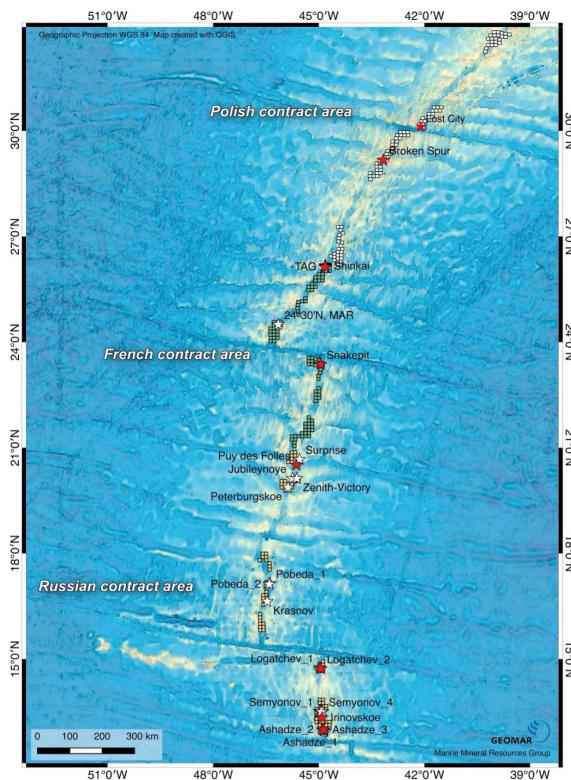
If the contractor has not contributed a reserved area (paragraph 4 above) but has an exploration contract for up to 100 blocks, then the relinquishment process operates as outlined in ISBA/25/LTC/8. Exploration contracts last for up to 15 years, during which time the contractor must relinquish parts 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 per cent of the original area allocated to it and
- b) by the end of the tenth year from the date of the contract, the contractor shall have relinquished at least 75 per cent 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 earlier, the contractor must nominate an area from the remaining area allocated to it to be retained for exploitation. Thus, exploited areas will be much smaller than explored areas.

ISBA/25/LTC/8 provides clarity on how relinquishment could occur. Each 10 km by 10 km block can be subdivided into 1 km by 1 km cells, and the requisite number of cells returned to ISA 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 $\leq 10 \text{ km} \times 10 \text{ km}$) approved for exploration by ISA in the North Atlantic (yellow blocks: Russian Federation; green blocks: France; white blocks: Poland) and 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 (for example, the young vent sites Ashadze 1 and Logatchev 2 in Figure 5.1 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. Overall, only a

small proportion of known vent sites have commercially-attractive accumulations of PMS deposits, although 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 and 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; Petersen et al., 2009), revealing 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 per cent), including virtually all of the zinc, silver, lead and gold plus 80–85 per cent of the copper, are concentrated in the upper 5 m of the mound, with 15–20 per cent of the total copper being located in the deeper stockwork. These metal concentrations compare to the range of copper 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. 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 that only the upper few metres of the mounds have economic potential.

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

Table 5.1 Estimates of resources for a range of hydrothermal fields in the contract area of the Government of the Russian Federation (Cherkashov et al., 2010; Cherkashov et al., 2013) and the TAG field (Hannington et al., 1998). Note most of these fields are located at active vent sites (column 1).

Deposit A = active I = inactive	Latitude N	Water depth m	Area km ²	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

It is likely that commercial mining practice will extract at least one Mt of ore per year, as 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. It is unclear what the lower cut-off will be for the volume of exploitable resources, 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).

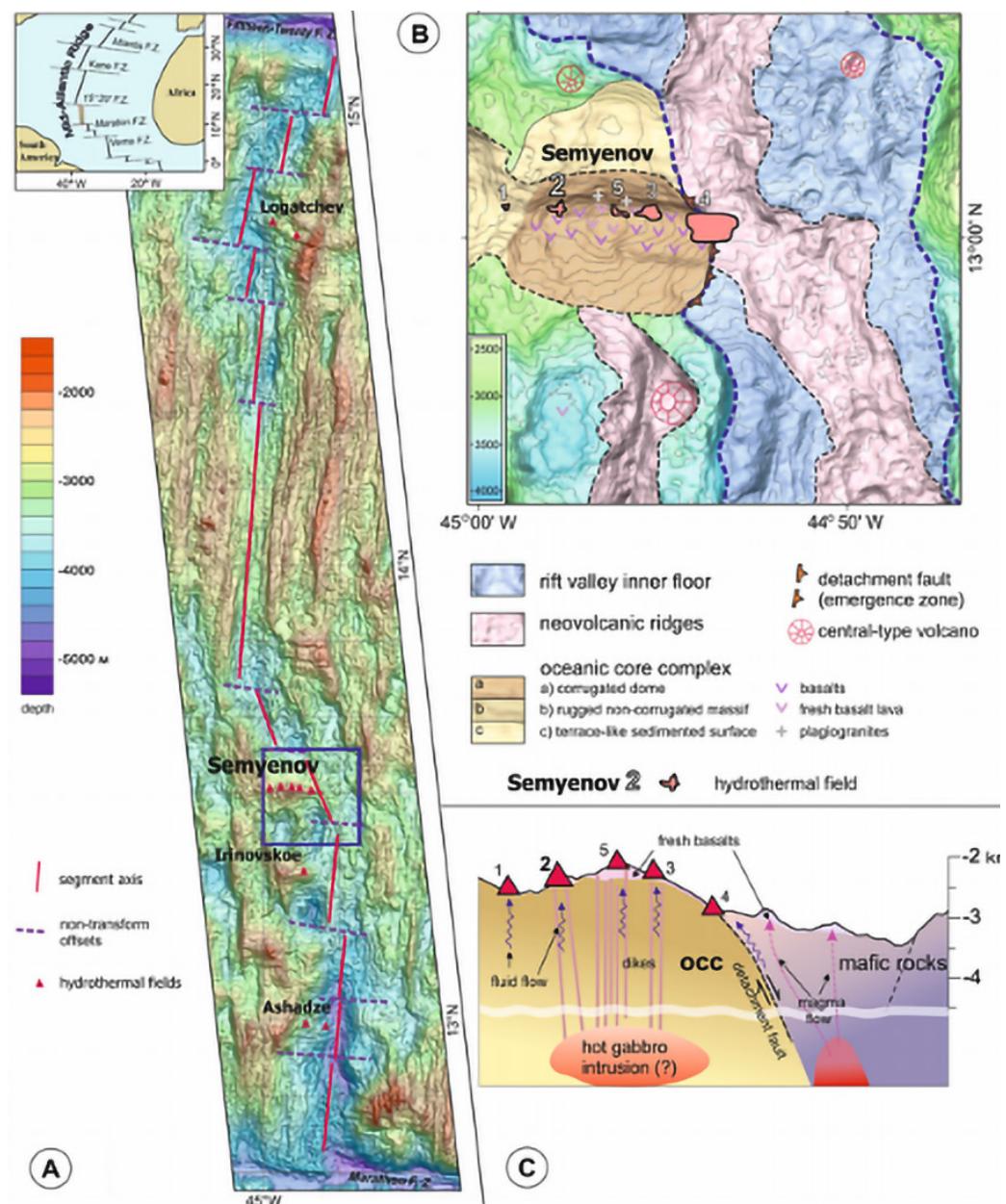
However, better targets for exploitation may be inactive and extinct vent sites. Extinct vent sites are likely to contain the largest amounts of resources since they have completed the whole cycle of metal formation, as opposed to active hydrothermal sites and inactive sites, which may continue to precipitate 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 (see Figure 5.2) contains five vent sites, only one of which is hydrothermally active (Cherkashov et al., 2017; Firstova et al., 2019). In such 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 are 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 for those farther away from the ridge axis where they are increasingly likely to be covered by sediment layers or basalt flows. For these sites, 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). It is not known 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 on 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.

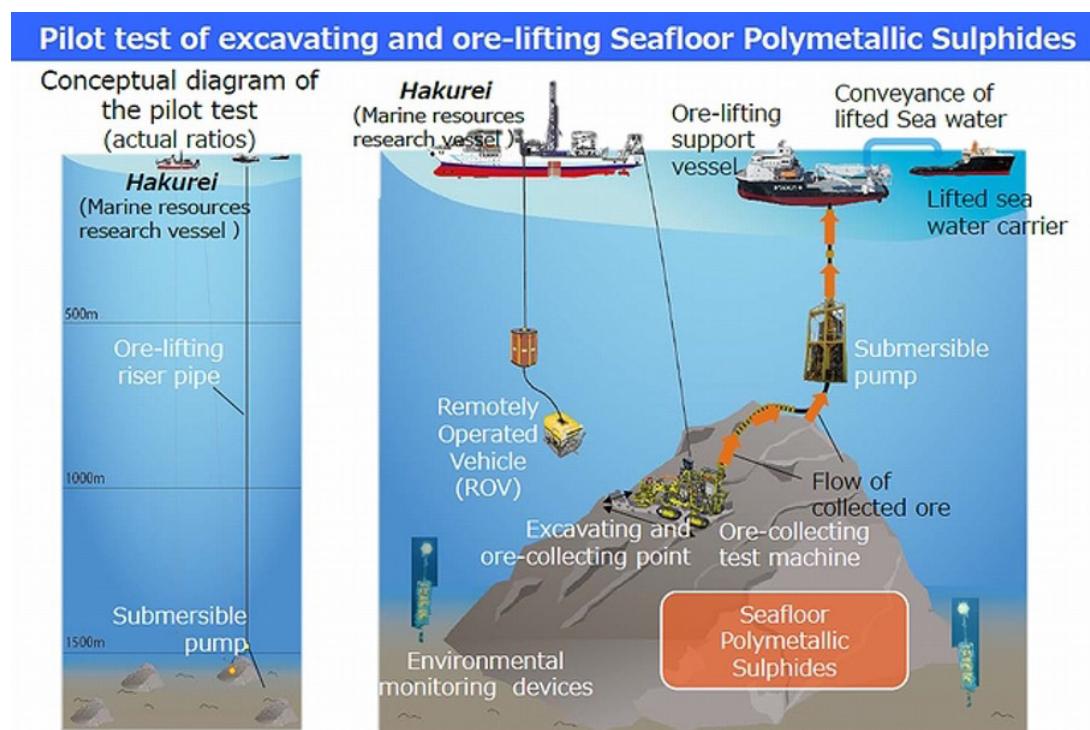
Figure 5.2 The Semenov vent field in the contract area of the Government of the Russian Federation. **(A)** Shaded-relief bathymetric map of the MAR between the Fifteen-Twenty Fracture Zone and the Marathon Fracture Zone, showing the location of the hydrothermal fields. The contour interval is 200 m. 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 from 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

Figure 5.3 Test mining carried out in Okinawa, Japan in 2017. (Reproduced from METI, 2018)



thick and 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 test cases

The exploitation phase of deep-sea exploitation for PMS has not begun yet, so there are no accounts of actual mining practices. 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 and 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).

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 (Gwyther, 2008). Nautilus Minerals developed three seafloor instruments for mining PMS: a bulk cutter, an auxiliary cutter and a 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. The mining process would involve the auxiliary cutter levelling the seabed in preparation for the bulk cutter, which would mine in a similar way to coal-cutting machines. The two cutting machines would disaggregate the rock, leaving it for the collecting machine to draw in as slurry and pass to the riser system. Ultimately a hole would 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 km². In addition, the overburden would need to be removed, which at Solwara 1 consists of an estimated 130,000 tons of unconsolidated sediment plus 115,000 tons of waste rock. 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 km².

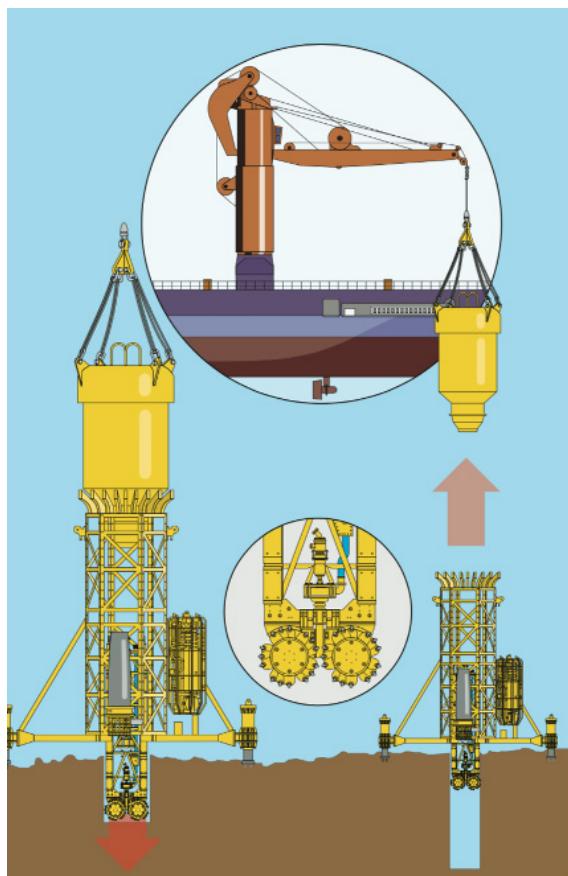
The mining, retrieval and shipping processes can be divided into the following actions (Ishiguro et al., 2013; Gwyther, 2008).

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 as in the Japanese test or it could leave crushed ore in swathes on the seabed waiting for a collector vehicle as in the Nautilus Minerals example, although the original Nautilus Minerals plan was for the riser pipe to be connected directly to the mining vehicles.
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 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 known as a Vertical Transport System (VTS) or Riser and Lift System (RALS). A discussion of various riser systems is given by 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 lift 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 a support vessel. The water will need to be removed from the slurry as soon as it arrives on 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, and 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 would visit 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 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 exploitation tool showing vertical cutting head and container lift system. (Reproduced from DSMA, n.d.)



5.5 Potential areas of impact

Deep-sea exploitation is likely to have impacts in at least 4 areas:

- 1. The mine site.** PMS deposits are three-dimensional and will involve mining a pit in the seabed. The size of the mine will depend 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 resources (Lipton, 2012), was planned to cover an area of 0.112 km². In addition to this, some overburden may be removed and relocated elsewhere on the seabed. If the mine site includes active hydrothermal vents with vent-obligate fauna, these will be destroyed. When active vents with vent-obligate fauna are located close to inactive vents with high mineral content, it may be difficult to avoid impacting vent communities, which will be affected by sediment plumes even if they are not destroyed directly by mining. For example, the Semenov field has an estimated 40 Mt of ore and comprises five sites, with site 2 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.** 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, but 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) in addition to 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 will rapidly release metals and metalloids into seawater. Thus, the mining plumes may contain contaminants (Fallon et al., 2018; Knight et al., 2018) that 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, an 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 of the smallest particles, and those smaller than a few tens of μm will be discharged with the returned water. In many cases, toxic metals attach preferentially to fine particles. Even though the discharge plume may be diluted very quickly into 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 its results are reported in Drazen et al., (2019). Recommendations include:

minimising effects in the mesopelagic zone by releasing water below 1,000 m depth; avoiding the production of a midwater haze due to enhanced suspended particle concentrations; further research on the bathypelagic and abyssopelagic zones (from around 1,000 m depth to just above the seafloor); and more modelling of plume behaviour and its biological effects.

- 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 as in the case for Solwara 1, which 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 no metal content may be similarly dumped nearby on the seabed.

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

5.6 References

- Augustin, N. (2007). *The Logatchev Hydrothermal Field (MAR, 15°N): High- and Low-Temperature Alteration of Ultramafic Oceanic Crust-Geology, Geochemistry, Mineralogy*. Christian-Albrechts Universität Kiel.
- Baker, E. T. (2017). Exploring the ocean for hydrothermal venting: New techniques, new discoveries, new insights. *Ore Geology Reviews*, 86, 55-69. <https://doi.org/10.1016/j.oregeorev.2017.02.006>
- Beaulieu S. E., Baker E. T. and German C. R. (2015). Where are the undiscovered hydrothermal vents on oceanic spreading ridges? *Deep-Sea Research Part II*, 121, 202-212. [doi:10.1016/j.dsrr.2015.05.001](https://doi.org/10.1016/j.dsrr.2015.05.001)

- Beaulieu, S. E. and Szafranski, K. (2019). *InterRidge Global Database of Active Submarine Hydrothermal Vent Fields, Version 3.4.* Available at <http://vents-data.interridge.org>, accessed 9 August 2019.
- Becker, J. J., D. T. Sandwell, W. H. F. Smith, J. Braud, B. Binder, J. Depner, D. Fabre, J. Factor, S. Ingalls, S-H. Kim, R. Ladner, K. Marks, S. Nelson, A. Pharaoh, R. Trimmer, J. Von Rosenberg, G. Wallace, P. Weatherall. (2009). Global Bathymetry and Elevation Data at 30 Arc Seconds Resolution: SRTM30_PLUS. *Marine Geodesy*, 32(4), 355-371.
- Brown, A., Thatje, S., and Hauton, C. (2017). The effects of temperature and hydrostatic pressure on metal toxicity: insights into toxicity in the deep sea. *Environmental Science and Technology*, 51, 10222-10231.
- Cherkashev, G. A., Ivanov, V. N., Bel'tenev, V. I., Lazareva, L. I., Rozhdestvenskaya, I. I., Samovarov, M. L., Poroshina, I. M., Sergeev, M. B., Stepanova, T. V., Dobretsova, I. G., and Kuznetsov, V.Yu. (2013). Massive sulfide ores of the northern equatorial Mid-Atlantic Ridge. *Oceanology*, 53(5), 607-619.
- Cherkashov G., Kuznetsov, V., Kuksa, K., Tabuns, E., Maksimov, F., and Bel, V. (2017). Sulfide geochronology along the Northern Equatorial Mid-Atlantic Ridge. *Ore Geology Reviews*, 87, 147-154. <http://doi.org/10.1016/j.oregeorev.2016.10.015>
- Cherkashov G., Poroshina, I., Stepanova, T., Ivanov, V., Bel'tenev, V., Lazareva, L., Rozhdestvenskaya, I., Samovarov, M., Shilov, V., Glasby, G. P., Fouquet, Y., and Kuznetsov, V. (2010). Seafloor massive sulfides from the northern equatorial Mid-Atlantic ridge: New discoveries and perspectives. *Marine Georesources and Geotechnology*, 28(3), 222-239. <http://doi.org/10.1080/1064119X.2010.483308>
- Clark, M. (2013). Biology Associated with Cobalt-rich Ferromanganese Crusts. In Baker E. and Beaudoin Y. (Eds.) *Deep Sea Minerals: Cobalt-rich Ferromanganese Crusts, a Physical, Biological, Environmental and Technical Review. Vol. 1C.* 15-22. Secretariat of the Pacific Community.
- Clark, M., and Smith S. (2013). Environmental management considerations. In Baker E. and Beaudoin Y. (Eds.) *Deep Sea Minerals: Cobalt-rich Ferromanganese Crusts, a Physical, Biological, Environmental and Technical Review. Vol. 1C.* 23-40. Secretariat of the Pacific Community.
- Clark, M. R., Watling, L., Rowden, A. A., Guinotte, J. M., and Smith, C. R. (2011). A global seamount classification to aid the scientific design of marine protected area networks. *Ocean and Coastal Management*, 54(1), 19-36. <https://doi.org/10.1016/j.ocecoaman.2010.10.006>
- DeepSea Mining Alliance e.V. (DSMA), n.d. *Our way towards the responsible exploitation of high-tech metals.* Available at <https://cdn.website-editor.net/5a6bb-be829ab42feb975732933e00a63/files/uploaded/Our%2520way%2520towards%2520the%2520responsible%2520exploitation%2520of%2520high-tech%2520metals%2520-%2520Facts%2520and%2520challenges%2520of%2520Deep-Sea%2520Mining.pdf>
- Drazen J., Smith C., Gjerde K., Au W., Black J., Carter G., Clark M., Durden J., Dutrieux P., Goetze E., Haddock S., Hatta M., Hauton C., Hill P., Koslow J., Leitner A., Measures C., Pacini A., Parrish F., Peacock T., Perelman J., Sutton T., Taymans C., Tunnicliffe V., Watling L., Yamamoto H., Young E., Ziegler A. (2019). Report of the workshop Evaluating the nature of midwater mining plumes and their potential effects on midwater ecosystems. *Research Ideas and Outcomes*, 5. e33527. <https://doi.org/10.3897/rio.5.e33527>
- Dutkiewicz, A., Müller, D., O'Callaghan, S., and Jónasson, H. (2015). Census of seafloor sediments in the world's ocean. *Geology*, 43(9), 795-798. <https://doi.org/10.1130/G36883.1>

- Fallon, E. K., Niehorster, E., Brooker, R. A., and Scott, T. B. (2018). Experimental leaching of massive sulphide from TAG active hydrothermal mound and implications for seafloor mining. *Marine Pollution Bulletin*, 126, 501-515.
- Firstova, A., Stepanova, T., Sukhanova, A., Cherkashov G. and Poroshina, I. (2019). Au and Te Minerals in Seafloor Massive Sulphides from Semyenov-2 Hydrothermal Field, Mid-Atlantic Ridge. *Minerals*, 9, 294.
- Fouquet, Y., Cambon, P., Etoubleau, J., Charlou, J. L., OndréAs, H., Barriga, F. J. A. S., Cherkashov G., Semkova, T., Poroshina, I., Bohn, M., Donval, J. P., Henry, K., Murphy, P. and Rouxel, O. (2010). Geodiversity of Hydrothermal Processes Along the Mid-Atlantic Ridge and Ultramafic-Hosted Mineralization: a New Type Of Oceanic Cu-Zn-Co-Au Volcanogenic Massive Sulfide Deposit. In P. A. Rona, C. W. Devey, J. Dymant and B.J. Murton (Eds.), *Diversity Of Hydrothermal Systems On Slow Spreading Ocean Ridges*. <https://doi.org/10.1029/2008GM000746>
- Frimanslund, E. K. T. (2016). Feasibility of Deep-Sea Mining Operation Within Norwegian Jurisdiction. Norwegian University of Science and Technology. (Unpublished thesis). Available at <https://brage.bibsys.no/xmlui/handle/11250/2410761>
- Fuchida S., Ishibashi J., Nozaki T., Matsushita Y., Kawachi M., and Koshikawa H. (2019). Metal Mobility from Hydrothermal Sulfides into Seawater During Deep Seafloor Mining Operations. In R. Sharma (Ed), *Environmental Issues of Deep-Sea Mining Impacts, Consequences and Policy Perspectives*. Springer International Publishing AG, Switzerland.
- Fuchida, S., Yokoyama, A., Fukuchi, R., Ishibashi, J., Kawagucci, S., Kawachi, M. and Koshikawa, H. (2017). Leaching of metals and metalloids from hydrothermal ore particulates and their effects on marine phytoplankton. *American Chemical Society Omega*, 2(7), 3175-3182. <http://doi.org/10.1021/acsomega.7b00081>
- Gebruk, A. and Krylova E. M. (2013). Megafauna of the Charlie -Gibbs Fracture Zone (northern Mid-Atlantic Ridge) based on video observations. *Journal of the Marine Biological Association of the United Kingdom*, 93(5). 1143-1150.
- Gwyther, D. (2008). *Environmental Impact Statement: Nautilus Minerals Niugini Limited, Solwara 1 Project*, Vol. A. Coffey Natural Systems, Queensland, Australia. <http://www.deepseaminingoutofourdepth.org/wp-content/uploads/Steiner-Independent-review-DSM1.pdf>
- Hannington, M., and Galley, A. (1998). Comparison of the TAG Mound and Stockwork Complex with Cyprus-Type Massive Sulfide Deposits. *Proceedings of the Ocean Drilling Program, Scientific Results*, 158.
- Hauton, C., Brown, A., Thatje, S., Mestre, N. C., Bebianno, M. J., Martins, I., Bettencourt, R., Canals, M., Sanchez-Vidal, A., Shillito, B., Ravaux, J., Zbinden, M., Duperron, S., Mevenkamp, L., Vanreusel, A., Gambi, C., Dell'Anno, A., Danovaro, R., Gunn, V. and Weaver, P. (2017). Identifying Toxic Impacts of Metals Potentially Released during Deep-Sea Mining—A Synthesis of the Challenges to Quantifying Risk. *Frontiers in Marine Science*, 4(368), <http://doi.org/10.3389/fmars.2017.00368>
- Hölz, S., Jegen, M., Petersen, S., and Hannington, M. (2015). How to find buried and inactive seafloor massive sulfides using transient electromagnetics. *Nearshore Underwater Mining: Critical Commodities for the Future, 44th Underwater Mining Conference 2015, Tampa Bay, Florida USA*.
- Humphris, S. E., and Kleinrock, M. C. (1996). Detailed morphology of the TAG active hydrothermal mound: insights into its

- formation and growth. *Geophys. Res. Lett.* 23, 3443–3446. doi: 10.1029/96gl03079
- Humphris, S. E., Herzig, P. M., Miller, D. J., Alt, J. C., Becker, K., Brown, D. and Zhao, X. (1995). The internal structure of an active sea-floor massive sulphide deposit. *Nature*, 377, 713–716.
- Humphris, S. E., Tivey, M. K. and Tivey, M. A. (2015). The Trans-Atlantic Geotraverse hydrothermal field: A hydrothermal system on an active detachment fault. *Deep Sea Research, Part II*, 121, 8–16.
- Ishiguro, S., Yamauchi, Y., Odaka, H. and Akiyama, S. (2013). Development of Mining Element Engineering Test Machine for Operating in Seafloor Hydrothermal Deposits. *Mitsubishi Heavy Industries Technical Review*, 50(2), 21–26.
- Kastens, K., Bonatti, E., Caress, D., Carrara, G., Dauteuil, O., Frueh-Green, G. and Tartarotti, P. (1998). The Vema Transverse Ridge(CentralAtlantic). *Marine Geophysical Researches*, 20(6), 533–556. <https://doi.org/10.1023/A:1004745127999>
- Kawada, Y. and Kasaya, T. (2017). Marine self-potential survey for exploring seafloor hydrothermal ore deposits. *Scientific Reports*, 7, 13552. <https://doi.org/10.1038/s41598-017-13920-0>
- Kawada, Y. and Kasaya, T. (2018). Self-potential mapping using an autonomous underwater vehicle for the Sunrise deposit, Izu-Ogasawara arc, southern Japan. *Earth, Planets and Space*, 70(142). <https://doi.org/10.1186/s40623-018-0913-6>
- Klischies, M., Petersen, S., and Devey, C. W. (2019). Geological mapping of the Menez Gwen segment at 37°50'N on the Mid-Atlantic Ridge: Implications for accretion mechanisms and associated hydrothermal activity at slow-spreading mid-ocean ridges. *Marine Geology*, 412, 107–122. doi:10.1016/j.margeo.2019.03.012
- Knight, R. D., Roberts, S. and Cooper, M. J. (2018). Investigating monomineralic and polymetallic reactions during the oxidation of sulphide minerals in seawater: Implications for mining seafloor massive sulphide deposits. *Applied Geochemistry*, 90, 63–74.
- Lalou, C., Reyss, J. L. and Brichet, E. (1998). Age of sub-bottom sulfide samples at the TAG active mound. In: P. M. Herzig, S. E. Humphris, D. J. Miller and R. A. Zierenberg (Eds.), *Proceedings of the Ocean Drilling Program-Scientific Results* (pp. 111–117). Texas A&M University, College Station, Texas.
- Lehrmann, B., Stobbs, I. J., Lusty, P. A. J. and Murton, B. J. (2018). Insights into Extinct Seafloor Massive Sulfide Mounds at the TAG, Mid-Atlantic Ridge. *Minerals*, 302. doi:10.3390/min8070302
- Levin, L. A., Baco, A. R., Bowden, D. A., Colaco, A., Cordes, E. E., Cunha, M. R., Demopoulos, A. W. J., Gobin, J., Grupe, B. M., Le, J., Metaxas, A., Netburn, A. N., Rouse, G. W., Thurber, A. R., Tunnicliffe, V., Van Dover, C. L., Vanreusel, A. and Watling, L. (2016). Hydrothermal vents and methane seeps: Rethinking the sphere of influence. *Frontiers in Marine Science*, 3(72). <https://doi:10.3389/fmars.2016.00072>
- Lipton, I. (2012). *Mineral Resource Estimate: Solwara Project, Bismarck Sea, PNG*. Technical Report compiled under NI43-101. Golder Associates, for Nautilus Minerals Niugini Inc.
- Ministry of Economy, Trade and Industry of Japan (METI) (2018). *World's First Success in Continuous Ore Lifting test for Seafloor Polymetallic Sulphides: Pilot test of excavating and ore lifting conducted for seafloor polymetallic sulphides under the sea area near Okinawa Prefecture*. [Press release]. Retrieved from http://www.meti.go.jp/english/press/2017/0926_004.html

- Morris, K., Tyler, P.A., Murton, B. and Rogers, A. D. (2012). Lower bathyal and abyssal distribution of coral in the axial volcanic ridge of the Mid-Atlantic Ridge at 451N. *Deep Sea Research Part I: Oceanographic Research Papers*, 62, 32-39.
- Murton, B. J., Lehrmann, B., Dutrieux, A. M., Martins, S., de la Iglesia, A. G., Stobbs, I. J., Barriga, F. J. A. S., Bialas, J., Dannowski, A., Vardy, M. E., North, L. J., Yeo, I., Lusty, P., and Petersen, S. (2019). Geological fate of seafloor massive sulphides at the TAG hydrothermal field (Mid-Atlantic Ridge). *Ore Geology Reviews*, 107, 903-925. <http://doi.org/10.1016/j.oregeorev.2019.03.005>
- Nalessø, R. C., Duarte, L. F. L., Rierozzi, I. and Enomo, E.F. (1995). Tube epifauna of the polychaete *Phyllochaetopterus socialis* Claparede. *Estuarine and Coastal Shelf Science*, 41, 91-100.
- Niedzielski, T., Høines, Å., Shields, M.A., Linley, T. and Priede, I. G. (2013). A multi-scale investigation on seafloor topography of the northern Mid-Atlantic Ridge based on Geographic Information System analysis. *Deep Sea Research Part II: Topical Studies in Oceanography*, 98, 231-243.
- Okamoto, N., Igarashi, Y., and, Matsui, T. (2019). Preliminary results of environmental monitoring of seafloor massive sulphide excavation and lifting tests in the Okinawa Trough. *Proceedings of the Twenty-ninth International Ocean and Polar Engineering Conference*, 78-84.
- Olson, P., Reynolds, E., Hinnov, L. and Goswami A. (2016). Variation of ocean sediment thickness with crustal age. *Geochemistry, Geophysics, Geosystems*, 17, 1349-1369. doi:10.1002/2015GC006143.
- Pertsev, A. N.; Bortnikov, N. S.; Vlasov, E. A.; Bel'tenev, V. E.; Dobretsova, I. G. and Ageeva, O. A. (2012). Recent massive sulphide deposits of the Semenov ore district, Mid-Atlantic Ridge, 13°31' N: Associated rocks of the oceanic core complex and their hydrothermal alteration. *Geology of Ore Deposits*, 54, 334-346.
- Petersen, S., Augustin, N., Cherkashov G., Fisher, S., Franz, L., Han, X., Klien, F., Maggiulli, M., Ockert, C., Perner, M., Peters, M., Rahders, E., Rudzitis, E., Smith, D., Stepanova, T., Storm, S., Strauss, H. and Zhou, N. (2007). Shallow-drilling of the ultramafic-hosted Logatchev hydrothermal field at 14°45'N on the Mid-Atlantic Ridge using a new lander-type seafloor drill. *InterRidge News*, 16, 11-13.
- Petersen, S., Hannington, M. and Krätschell A. (2017). Technology developments in the exploration and evaluation of deep-sea mineral resources. *Responsabilité & Environnement*, 85, 14-18.
- Petersen, S., Krätschell, A., Augustin, N., Jamieson, J., Hein, J. R. and Hannington, M. D. (2016). News from the seabed—Geological characteristics and resource potential of deep-sea mineral resources. *Marine Policy*, 70, 175-187.
- Petersen, S., Kuhn, K., Kuhn, T., Augustin, N., Hékinian, R., Franz, L. and Borowski, C. (2009). The geological setting of the ultramafic-hosted Logatchev hydrothermal field (14°45'N , Mid-Atlantic Ridge) and its influence on massive sulfide formation. *Lithos*, 112(1-2), 40-56. <https://doi.org/10.1016/j.lithos.2009.02.008>
- Priede et al. (2013). Does Presence of a Mid-Ocean Ridge Enhance Biomass and Biodiversity? *PLOS one* 8(5), e61550.
- Rowden, A. A., Schlacher, T. A., Williams, A., Clark, M. R., Stewart, R., Althaus, F., Bowden, D. A., Consalvey, M., Robinson, W. and Dowdney, J. (2010). A test of the seamount oasis hypothesis: seamounts support higher epibenthic megafaunal biomass than adjacent slopes. *Marine Ecology 31 (Suppl. 1)*, 1-12.
- Schmid, F., Peters, M., Walter, M., Devey, C., Petersen, S., Yeo, I., Köhler, J., Jamieson, J.

- W., Walker, S. and Süttenfuß, J. (2019). Physico-chemical properties of newly discovered hydrothermal plumes above the Southern Mid-Atlantic Ridge(13°-33°S). *Deep-Sea Research Part I: Oceanographic Research Papers*, 148, 34-52. <https://doi.org/10.1016/j.dsr.2019.04.010>
- Simpson, S. L., and Spadaro, D. A. (2016). Bioavailability and Chronic Toxicity of Metal Sulfide Minerals to Benthic Marine Invertebrates: Implications for Deep Sea Exploration, Mining and Tailings Disposal. *Environmental Science and Technology*, 50, 4061–4070.
- Spagnoli, G., Miedema, S. A., Herrmann, C., Rongau, J., Weixler, L. and Denegre, J. (2015). Preliminary design of a trench cutter system for deep-sea mining applications under hyperbaric conditions. *IEEE Journal of Oceanic Engineering*, 41, 930-943.
- St. Laurent L. C. and Thurnherr A. M. (2007). Intense mixing of lower thermocline water on the crest of the Mid-Atlantic Ridge. *Nature*, 448, 680-683.
- Straume, E. O., Gaina, C., Medvedev, S., Hochmuth, K., Gohl, K., Whittaker, J. M., et al. (2019). GlobSed: Updated total sediment thickness in the world's oceans. *Geochemistry, Geophysics, Geosystems*, 20. doi: 10.1029/2018GC008115
- Van Dover C. L. (2019). Inactive Sulfide Ecosystems in the Deep Sea: A Review. *Frontiers in Marine Science*, 6(461). doi: 10.3389/fmars.2019.00461
- Van Dover, C. L., Arnaud-Haond, S., Gianni, M., Helmreich, S., Huber, J., Jaeckel, A., et al. (2018). Scientific rationale and international obligations for protection of active hydrothermal vent ecosystems from deep-sea mining. *Marine Policy*, 90, 20-28. doi: 10.1016/j.marpol.2018.01.020
- Weaver P. P. E. and Billett, D. S .M. (2019). Environmental impacts of nodule, crust and sulphide mining - an overview. In R. Sharma(Ed). *Environmental Issues of Deep-Sea Mining: Impacts, Consequences and Policy Perspectives* (pp. 27-62). Springer International Publishing AG, Switzerland.
- Yesson, C., Clark, M. R., Taylor, M. L. and Rogers, A. D. (2011). The global distribution of seamounts based on 30 arc seconds bathymetry data. *Deep-Sea Research Part I: Oceanographic Research Papers*, 58(4), 442-453. <https://doi.org/10.1016/j.dsr.2011.02.004>

6. PHYSICAL OCEANOGRAPHY OF THE NORTH ATLANTIC

6.1 Introduction and scope

This chapter 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 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 scantily 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 (Figure 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

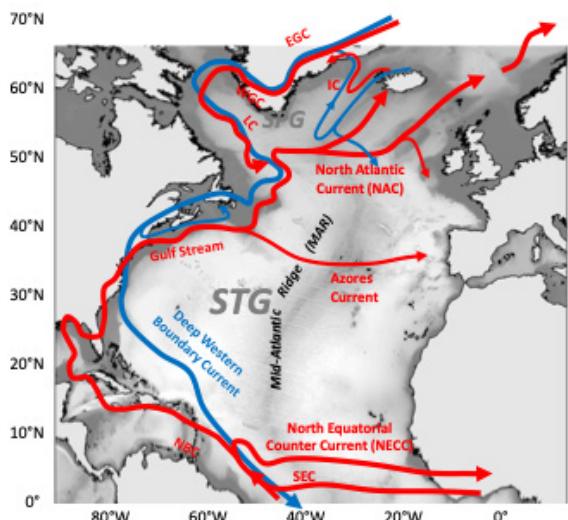
Greenland and Scotland, which must be traversed by newly-formed deep waters.

Flows can, for convenience, be broadly split into surface, intermediate and deep/bottom layers, based on loosely defined 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 in the lower water column, since most forcing occurs at the surface (winds and the effects of heating and cooling). Significant flows do exist at depth, however, with a global average of measured near-bottom current speed in depths over 1,500 m of 8–9 cm/s (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 (NAC).



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. Deep flows are therefore 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 (Figure 6.2) is steadier in time because it is locked to invariant topography (Xu et al., 2010).

6.2.2 Surface layer currents

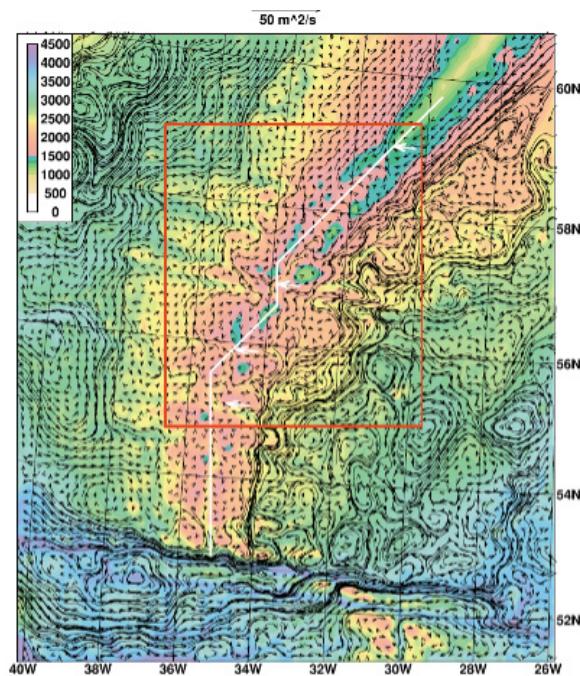
The broad pattern of surface flows in the Atlantic consists of a pair of large, rotary gyre circulations: the clockwise subtropical gyre and the anti-clockwise sub-polar gyre to the north of 45–50°N (Figure 6.1) (Fratantoni, 2001; Reverdin et al., 2003).

The subtropical gyre is strongly intensified against its western boundary to form the Gulf Stream (Fofonoff, 1981), which originates in the Caribbean and follows the North American shelf until 20°N, where it heads broadly to the east and 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 m/s, 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 35°N 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 (the 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). 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 is broad and shallow (100 m), forming the northern limb of the South Atlantic subtropical gyre. Its northern branch, the northern South Equatorial Current, extends north of the equator to around 4°N, feeding the North Brazil Current flowing to the northwest along the Brazilian coast. Much of the North Brazil Current "retroflects", turning back on itself to return eastward as the North Equatorial Counter Current between 4°N and 10°N, which effectively forms a tropical gyre

with the South Equatorial Current. The broad west-flowing North Equatorial Current between 10°N and 20°N forms the southern limb of the northern hemisphere subtropical gyre but is considerably weaker than the northern South Equatorial Current and North Equatorial Counter Current.

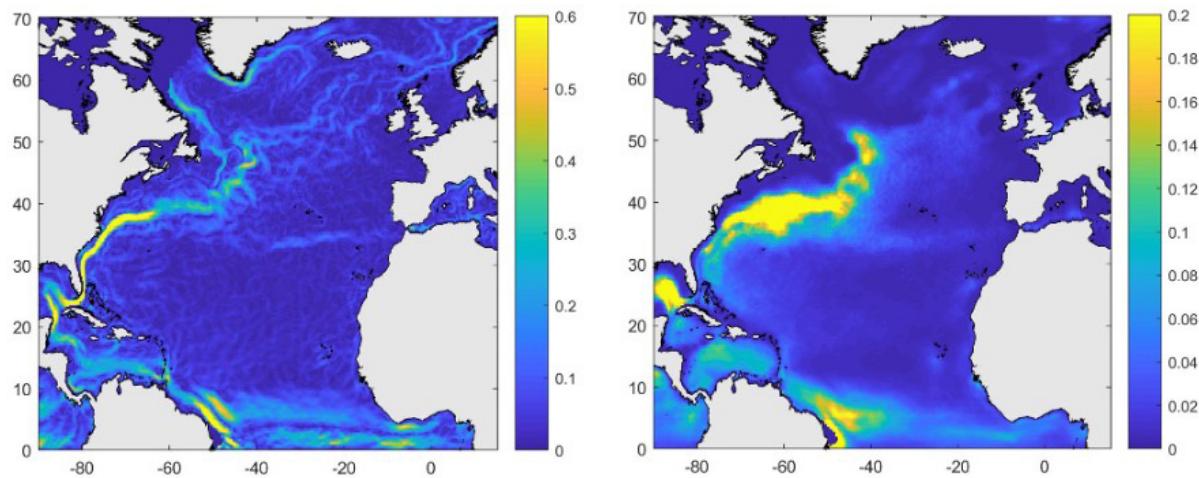
Where surface circulations are persistent and sufficiently intense, they are clear in satellite altimetry (Figure 6.3). These more persistent flows cross the MAR in three key regions corresponding to the NAC north of 45°N, the Azores Current around 35°N, and the equatorial current system south of 10°N. 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, 52–53°N), the Faraday Fracture Zone (50–51°N) and the area around 49°N, 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).

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, however, are more difficult to obtain, 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 from subsurface floats

Figure 6.3 (a) Mean surface geostrophic flow speed (m/s) 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)



(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 the CGFZ to 45°N (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 and dominated by mesoscale eddying, but convergence of the flow at the CGFZ elevated the mean there to 5 cm/s. A similarly extensive dataset of floats tracking pressure surfaces at 400, 700 or 1500 decibars (approximately equal to metres) provided excellent coverage north of 44°N and partial coverage to 25°N, 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. Strong flows not exceeding 5 cm/s 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, or 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 were used to identify and track Labrador Sea Water at 1,000–2,000 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.

Farther south, floats released at 700 m on the flanks of the MAR to the SE of the Azores, in clusters at 33°N on the eastern flank and 36°N on the western flank, dispersed widely in both eastern and western basins (Ollitrault and Colin de Verdier 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 30°N and 55°N, 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, the Antarctic Bottom Water (AABW) found in depths in excess of 4,000 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 8–16°N 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 at 0–2°N, but this component remains topographically restricted from spreading more widely in the North Atlantic. More significant in this respect is the Vema Fracture Zone at 11°N (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 the 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 in the case of the Denmark Strait

Overflow Water, and between Iceland and Scotland in the case of the 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 (Figure 6.1).

The component of the deep flow that most influences the MAR is the 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 CGFZ (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, the ISOW turns to flow north along the western flank of the MAR and circulates around the Irminger Basin.

Model simulations of the flow of the ISOW in the vicinity of the Northern MAR suggest that a highly complex, topographically-steered pattern is superimposed on the large-scale transport (Xu et al., 2010) (Figure 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 (see 6.3 below), 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 lack the resolution needed to grasp the full complexity of the topography.

6.3 Distribution of water properties

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

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 northeast Atlantic, Irminger Sea, southern Labrador Sea and along the path of the NAC. Depths in excess of 100 m develop in October to November and reach a peak of 500 m or more in places, before being much reduced during April and May, and largely erased by June. These mixing depths set the depth of the permanent pycnocline.

Figure 6.4 West-east sections of: (a) potential temperature (°C); (b) practical salinity; and (c) oxygen concentration ($\mu\text{mol/kg}$) across the North Atlantic at 36°N (WOCE line A03). (Reproduced from Koltermann et al., 2011, based on 1990s data)

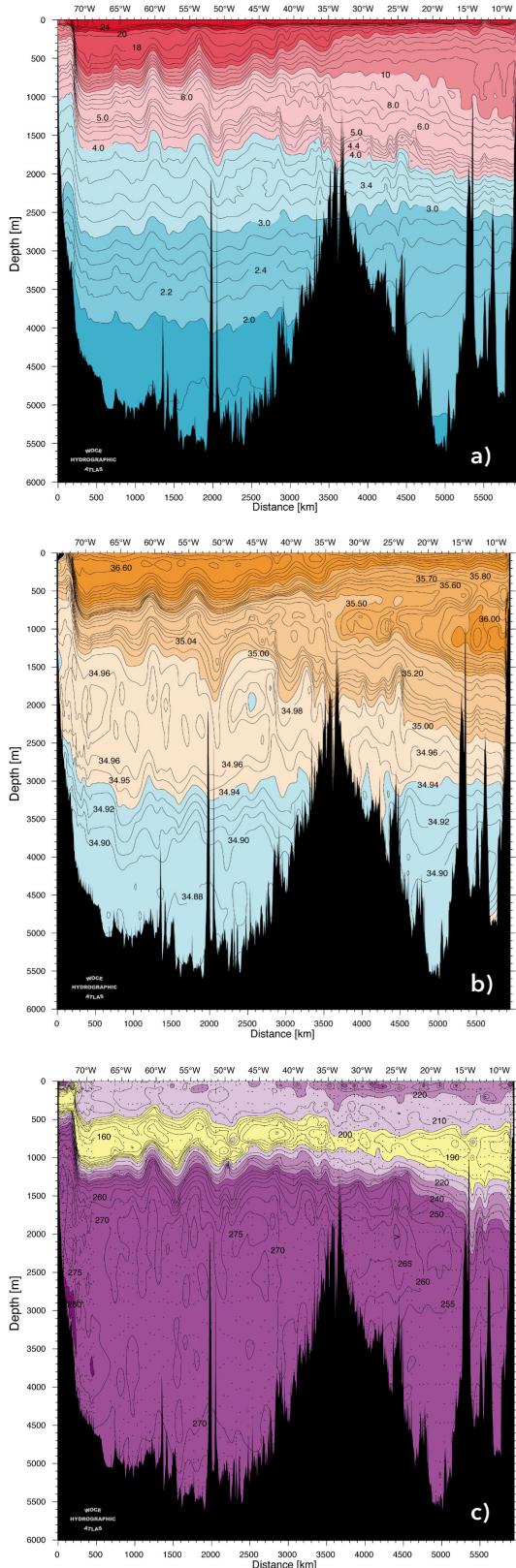
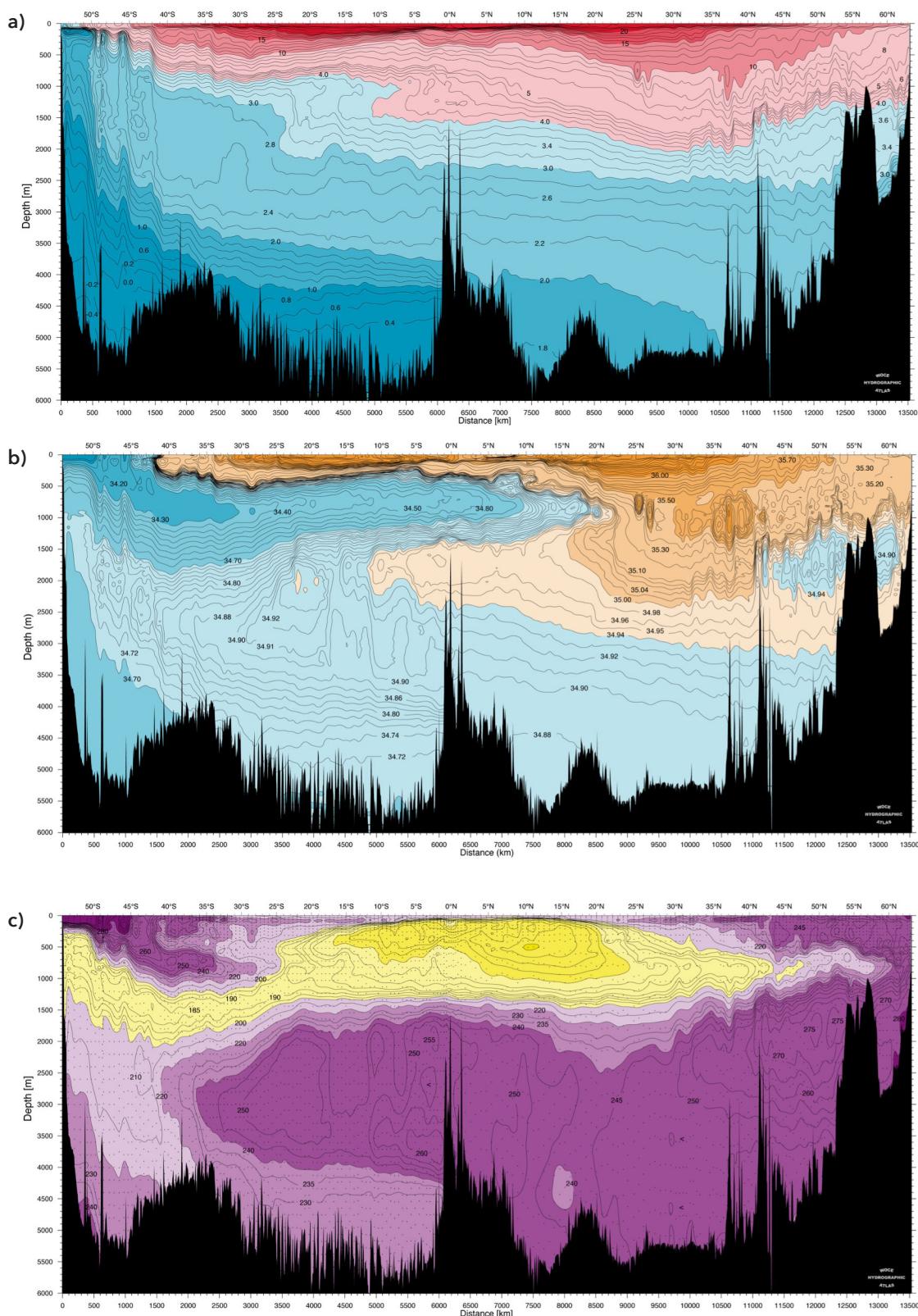


Figure 6.5 South-north sections of: (a) potential temperature ($^{\circ}\text{C}$); (b) practical salinity; and (c) oxygen concentration ($\mu\text{mol/kg}$) in the eastern basins of the Atlantic (WOCE line A16). (Reproduced from Koltermann et al., 2011)



A feature of the North Atlantic at intermediate depths is the inflow of the 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 (Figure 6.5). This spreading is initially at around 1,000 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 above, the 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 different 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.

AABW differs from 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. The coolest AABW, with a potential temperature of less than 0°C, is therefore in the western basin near the equator, and temperatures increase from there to the north, 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 that retain their oxygen signature from their formation regions (Figure 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 4,000 m (Figure 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 higher 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 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 of over 1,000 $\mu\text{g}/\text{cm}^2$ 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 of up to 27 cm/s 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 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, and could reasonably be described roughly as a series of basins separated by sills (Thurnherr, 2000). These chains of basins can be further grouped into disjointed segments with varying 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 to be 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. In the well-studied

segment from 35.5°N to 36.7°N, a mean flow of 0.01–0.03 m/s to the northeast in the bottom few hundred metres was found to compensate an along-valley density gradient of -0.9×10^{-5} kg/m³/km (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-average flow recorded of 0.14 m/s near the Rainbow hydrothermal vent site (see 5.3 above).

6.4.2 Ridge flanks: mixing-driven upslope flow

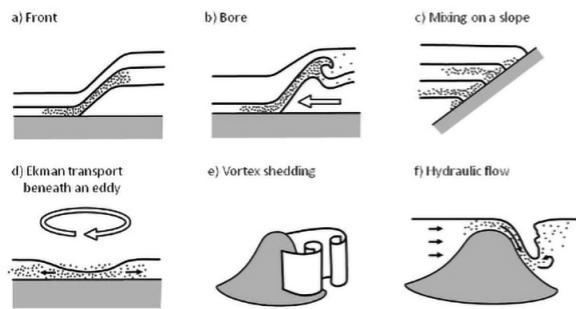
Mixing against a sloping boundary can also create a horizontal density gradient which drives a compensating upslope flow (Phillips et al., 1986). In many areas, the flanks of the MAR are incised by canyons perpendicular to the ridge axis, with the base of these canyons rising towards the ridge crest. 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 (Figure 6.6). In the Lucky Strike segment of the axial valley at 37.3°N, two-week averaged velocities at the sill crest and instantaneous velocities in

the bottom 200 m downstream exceeded 0.1 m/s, 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 (36.2°N), intensified and unidirectional near-bed flows reaching 0.14 m/s have been recorded over a sill (Thurnherr, 2006), and high levels of mixing can be 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. (Richards, 1990)



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

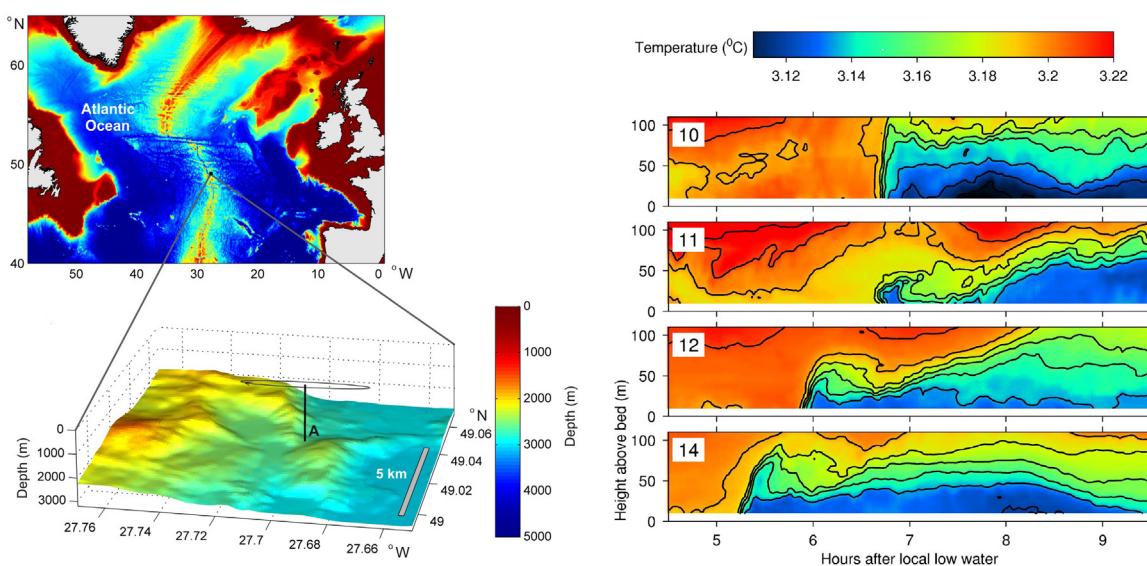
Depth-averaged tidal current speeds away from coastal and shelf areas are low, typically a few cm/s. Topographic effects, however, can greatly enhance tidal effects locally, extracting energy from the back-and-forth motion of the water column as a whole (Egbert and Ray, 2000) and feeding a range of more 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 this turbulence 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 49°N (Figures 6.6 and 6.7), 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). Away from the MAR, highly

turbulent, similar upslope-propagating fronts have also been observed at around 500 m depth on the flanks of the Great Meteor Seamount (van Haren, 2005), at 470 m on the continental slope in the Faeroe-Shetland Channel (Hosegood and van Haren, 2004) and at 1,400 m on the Biscay continental slope (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 3,000m 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. 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. (Dale and Inall, 2015)



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 ocean-basin scale (Speer and Helfrich, 1995). A vent plume is initially warmer and more buoyant than its surroundings so it 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, to 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 hundreds of metres in vertical extent (German et al., 1996). As plume waters spread after reaching equilibrium with ambient waters, they veer due to 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 m/s (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, as 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 that 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 it 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, meaning scales on the order of 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, although 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 NAC, the Azores Current and in the tropics south of 10°N (Figure 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 (Frantoni, 2001; Reverdin et al., 2003) and at intermediate depths (Ollitrault and Colin de Verdière, 2002; Lavender et al.,

2005), 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 4–5°N, 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 exploitation 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 (Figure 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 by 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 (Figure 6.7). Predictions of plume behaviour are highly dependent on the exact nature, or 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 NAC crosses the MAR in a broad and variable zone between 49°N and 53°N; in the Azores current at around 35°N; and in the equatorial current system south of 10°N (Figure 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 the 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 4,000 m there is also flow of 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

- Biscaye, P. E. and Eittreim, S. L. (1977). Suspended particulate loads and transports in the nepheloid layer of the abyssal Atlantic Ocean. *Marine Geology*, 23, 155-72.
- Bonnin, J., Van Haren, H., Hosegood, P. and Brummer G-J. A. (2006). Burst resuspension of seabed material at the foot of the continental slope in the Rockall Channel. *Marine Geology*, 226, 167-84.
- Bower, A. S., Lozier, S., Biastoch, A., Drouin, K., Foukal, N., Furey, H., Lankhorst, M., Rühs, S. and Zou, S. (2019). Lagrangian views of the pathways of the Atlantic Meridional Overturning Circulation. *Journal of Geophysical Research: Oceans*, 124, 5313-35.
- Bower, A. S., Le Cann, B., Rossby, T., Zenk, W., Gould, J., Speer, K., Richardson, P. L., Prater, M. D., and Zhang, H-M. (2002). Directly measured mid-depth circulation in the northeastern North Atlantic Ocean. *Nature*, 419, 603.
- Bower, A. S., and von Appen, W-J. (2008). Interannual variability in the pathways of the North Atlantic Current over the Mid-Atlantic Ridge and the impact of topography. *Journal of Physical Oceanography*, 38, 104-20.
- Buckley, M. W. and Marshall, J. (2016). Observations, inferences, and mechanisms of the Atlantic Meridional Overturning Circulation: A review. *Reviews of Geophysics*, 54, 5-63.
- D'Asaro, E., Walker, S. and Baker, E. (1994). Structure of two hydrothermal megaplumes. *Journal of Geophysical Research: Oceans*, 99, 20361-73.
- Dale, A. C. and Inall. M. E. (2015). Tidal mixing processes amid small-scale, deep ocean topography. *Geophysical Research Letters*, 42, 484-91.
- de Boyer Montégut, C., Madec, G., Fischer, A. S., Lazar, A. and Iudicone, D. (2004). Mixed layer depth over the global ocean: An examination of profile data and a profile-based climatology. *Journal of Geophysical Research: Oceans*, 109.
- Dickson, R. R. and Brown, J. (1994). The production of North Atlantic Deep Water: sources, rates, and pathways. *Journal of Geophysical Research: Oceans*, 99, 12319-41.
- Dobrolyubov, S. A., Lappo, S. S., Morozov, E. G. and Sokov, A. V. (2003). Water transport through the Charlie-Gibbs fracture zone. In *Doklady Earth Sciences C/C of Doklady-Akademiiia Nauk* (pp. 903-05). Interperiodica Publishing.
- Dziak, R. P., Smith, D. K., Bohnenstiehl, D. R., Fox, C. G., Desbruyeres, D., Matsumoto, H., Tolstoy, M. and Fornari, D. J. (2004). Evidence of a recent magma dike intrusion at the slow spreading Lucky Strike segment, Mid-Atlantic Ridge. *Journal of Geophysical Research: Solid Earth*, 109.

- Eden, C. and Jung, T. (2001). North Atlantic interdecadal variability: oceanic response to the North Atlantic Oscillation (1865–1997). *Journal of Climate*, 14, 676–91.
- Egbert, G. D., and Ray, R. D. (2000). Significant dissipation of tidal energy in the deep ocean inferred from satellite altimeter data. *Nature*, 405, 775.
- Eittreim, S. L., Biscaye, P. E. and Jacobs, S. S. (1983). Bottom water observations in the Vema fracture zone. *Journal of Geophysical Research: Oceans*, 88, 2609–14.
- Eittreim, S., Thorndike, E. M. and Sullivan, L. (1976). Turbidity distribution in the Atlantic Ocean. In *Deep Sea Research and Oceanographic Abstracts* (pp. 1115–27). Elsevier.
- Fehn, U., Siegel, M. D., Robinson, G. R., Holland, H. D., Williams, D. L., Erickson, A. J. and Green, K. E. (1977). Deep-water temperatures in the FAMOUS area. *Geological Society of America Bulletin*, 88, 488–94.
- Fofonoff, N. P. (1981). The Gulf Stream. In B. A. Warren and C. Wunsch (Eds.) *Evolution of Physical Oceanography: Scientific Surveys in Honor of Henry Stommel* (pp. 112–39). MIT Press, Cambridge.
- Frajka-Williams, E., J Ansorge, I. J., Baehr, J., Bryden, H. L., Chidichimo, M. P., Cunningham, S. A., Danabasoglu, G., Dong, S., Donohue, K. A. and Eliot, S. (2019). Atlantic Meridional Overturning Circulation: Observed transports and variability. *Frontiers in Marine Science*, 6, 260.
- Fratantoni, D. M. (2001). North Atlantic surface circulation during the 1990's observed with satellite tracked drifters. *Journal of Geophysical Research: Oceans*, 106, 22067–93.
- Gardner, W. D., Tucholke, B. E., Richardson, M. J. and Biscaye, P. E. (2017). Benthic storms, nepheloid layers, and linkage with upper ocean dynamics in the western North Atlantic. *Marine Geology*, 385, 304–27.
- German, C. R., Klinkhammer, G. P. and Rudnicki, M. D. (1996). The Rainbow hydrothermal plume, 36° 15°N, MAR. *Geophysical Research Letters*, 23, 2979–82.
- Helfrich, K. R. (1994). Thermals with background rotation and stratification. *Journal of fluid mechanics*, 259, 265–80.
- Helfrich, K. R. and Battisti, T. M. (1991). Experiments on baroclinic vortex shedding from hydrothermal plumes. *Journal of Geophysical Research: Oceans*, 96, 12511–18.
- Hollister, C. D. and McCave, I. N. (1984). Sedimentation under deep-sea storms. *Nature*, 309, 220.
- Hosegood, P. and van Haren, H. (2004). Near-bed solibores over the continental slope in the Faeroe-Shetland Channel. *Deep Sea Research Part II: Topical Studies in Oceanography*, 51, 2943–71.
- Isley, A. E., Pillsbury, R. D. and Laine E. P. (1990). The genesis and character of benthic turbid events, northern Hatteras Abyssal Plain. *Deep Sea Research Part A: Oceanographic Research Papers*, 37, 1099–119.
- Jia, Y. (2000). Formation of an Azores Current due to Mediterranean overflow in a modeling study of the North Atlantic. *Journal of Physical Oceanography*, 30, 2342–58.
- Kanzow, T. and Zenk, W. (2014). Structure and transport of the Iceland Scotland Overflow plume along the Reykjanes Ridge in the Iceland Basin. *Deep Sea Research Part I: Oceanographic Research Papers*, 86, 82–93.
- Karstensen, J., Stramma, L. and Visbeck, M. (2008). Oxygen minimum zones in the eastern tropical Atlantic and Pacific oceans. *Progress in Oceanography*, 77, 331–50.

- Klein, H. and Mittelstaedt, E. (1992). Currents and dispersion in the abyssal Northeast Atlantic. Results from the NOAMP field program. *Deep Sea Research Part A: Oceanographic Research Papers*, 39, 1727-45.
- Koltermann, K. P., Gouretski, V. and Jancke, K. (2011). *Hydrographic Atlas of the World Ocean Circulation Experiment (WOCE): Volume 3: Atlantic Ocean*. National Oceanography Centre.
- Kuhlbrodt, T., Griesel, A., Montoya, M., Levermann, A., Hofmann, M. and Rahmstorf, S. (2007). On the driving processes of the Atlantic meridional overturning circulation. *Reviews of Geophysics*, 45.
- Lavender, K. L., Owens, W. B. and Davis, R. E. (2005). The mid-depth circulation of the subpolar North Atlantic Ocean as measured by subsurface floats. *Deep Sea Research Part I: Oceanographic Research Papers*, 52, 767-85.
- Ledwell, J. R., Watson, A. J. and Law, C. S. (1993). Evidence for slow mixing across the pycnocline from an open-ocean tracer-release experiment. *Nature*, 364, 701.
- Lozier, M. S., Li, F., Bacon, S., Bahr, F., Bower, A. S., Cunningham, S. A., De Jong, M. F., De Steur, L., Deyoung, B. and Fischer, J. (2019). A sea change in our view of overturning in the subpolar North Atlantic. *Science*, 363, 516-21.
- Lumpkin, R. and Garzoli, S. L. (2005). Near-surface circulation in the tropical Atlantic Ocean. *Deep Sea Research Part I: Oceanographic Research Papers*, 52, 495-518.
- McCartney, M. S., Bennett, S. L. and Woodgate-Jones, M. E. (1991). Eastward flow through the Mid-Atlantic Ridge at 11 N and its influence on the abyss of the eastern basin. *Journal of Physical Oceanography*, 21, 1089-121.
- Miller, P. I., Read, J. F. and Dale, A. C. (2013). Thermal front variability along the North Atlantic Current observed using microwave and infrared satellite data. *Deep Sea Research Part II: Topical Studies in Oceanography*, 98, 244-56.
- Ollitrault, M., and Colin de Verdière, A. (2002). SOFAR floats reveal midlatitude intermediate North Atlantic general circulation. Part I: A Lagrangian descriptive view. *Journal of Physical Oceanography*, 32, 2020-33.
- Özgökmen, T. M., Chassignet, E. P. and Rooth, C. G. H. (2001). On the connection between the Mediterranean outflow and the Azores Current. *Journal of Physical Oceanography*, 31, 461-80.
- Philander, S. G. (2001). *Atlantic Ocean equatorial currents*. Academic Press.
- Phillips, O. M., Shyu, J-H. and Salmun, H. (1986). An experiment on boundary mixing: mean circulation and transport rates. *Journal of fluid mechanics*, 173, 473-99.
- Polzin, K.L., Toole, J. M., Ledwell, J. R. and Schmitt, R. W. (1997). Spatial variability of turbulent mixing in the abyssal ocean. *Science*, 276, 93-96.
- Read, J. F., Pollard, R. T., Miller, P. I. and Dale, A. C. (2010). Circulation and variability of the North Atlantic Current in the vicinity of the Mid-Atlantic Ridge. *Deep Sea Research Part I: Oceanographic Research Papers*, 57, 307-18.
- Reverdin, G., Niiler, P. P. and Valdimarsson H. (2003). North Atlantic ocean surface currents. *Journal of Geophysical Research: Oceans*, 108, 2-1-2-21.
- Richards, K.J. (1990). Physical processes in the benthic boundary layer. *Philosophical Transactions of the Royal Society of London. Series A, Mathematical and Physical Sciences*, 331, 3-13.
- Rona, P. A., Klinkhammer, G., Nelsen, T. A., Trefry, J. H and Elderfield, H. (1986). Black smokers, massive sulphides and vent biota at the Mid-Atlantic Ridge. *Nature*, 321, 33.

- Saunders, P. M. (1994). The flux of overflow water through the Charlie-Gibbs Fracture Zone. *Journal of Geophysical Research: Oceans*, 99, 12343-55.
- Saunders, P. M. (1996). The flux of dense cold overflow water southeast of Iceland. *Journal of Physical Oceanography*, 26, 85-95.
- Saunders, P. M. and Francis, T. J. G. (1985). The search for hydrothermal sources on the Mid-Atlantic Ridge. *Progress in Oceanography*, 14, 527-36.
- Schott, F., Lothar, S., and Fischer, J. (1999). Interaction of the North Atlantic current with the deep Charlie Gibbs Fracture Zone throughflow. *Geophysical Research Letters*, 26, 369-72.
- Scott, R. B., Arbic, B. K., Chassignet, E. P., Coward, A. C., Maltrud, M., Merryfield, W. J., Srinivasan, A. and Varghese, A. (2010). Total kinetic energy in four global eddying ocean circulation models and over 5000 current meter records. *Ocean Modelling*, 32, 157-69.
- Speer, K. G. (1989). A forced baroclinic vortex around a hydrothermal plume. *Geophysical Research Letters*, 16, 461-64.
- Speer, K. G. and Helfrich, K. R. (1995). Hydrothermal plumes: a review of flow and fluxes. *Geological Society, London, Special Publications*, 87, 373-85.
- Speer, K. G. and Marshall, J. (1995). The growth of convective plumes at seafloor hot springs. *Journal of marine research*, 53, 1025-57.
- Speer, K. G. and Rona, P. A. (1989). A model of an Atlantic and Pacific hydrothermal plume. *Journal of Geophysical Research: Oceans*, 94, 6213-20.
- St. Laurent, L. C. and Thurnherr, A. M. (2007). Intense mixing of lower thermocline water on the crest of the Mid-Atlantic Ridge. *Nature*, 448, 680.
- St. Laurent, L. C., John M Toole, and Raymond W Schmitt. 2001. 'Buoyancy forcing by turbulence above rough topography in the abyssal Brazil Basin', *Journal of Physical Oceanography*, 31: 3476-95.
- Stendardo, I. and Gruber, N. (2012). Oxygen trends over five decades in the North Atlantic. *Journal of Geophysical Research: Oceans*, 117.
- Stramma, L. and Schott, F. (1999). The mean flow field of the tropical Atlantic Ocean. *Deep Sea Research Part II: Topical Studies in Oceanography*, 46, 279-303.
- Stramma, L., Visbeck, M., Brandt, P., Tanhua, T. and Wallace, D. (2009). Deoxygenation in the oxygen minimum zone of the eastern tropical North Atlantic. *Geophysical Research Letters*, 36.
- Sy, A., Rhein, M., Lazier, J. R. N., Koltermann, K. P., Meincke, J., Putzka, A. and Bersch, M. (1997). Surprisingly rapid spreading of newly formed intermediate waters across the North Atlantic Ocean, *Nature*, 386, 675-79.
- Thurnherr, A. M. (2006). Diapycnal mixing associated with an overflow in a deep submarine canyon. *Deep Sea Research Part II: Topical Studies in Oceanography*, 53, 194-206.
- Thurnherr, A. M. and Richards, K. J. (2001). Hydrography and high-temperature heat flux of the Rainbow hydrothermal site (36°14'N, Mid-Atlantic Ridge). *Journal of Geophysical Research: Oceans*, 106, 9411-26.
- Thurnherr, A. M., Richards, K. J., German, C. R., Lane-Serff, G. F. and Speer, K. G. (2002). Flow and mixing in the rift valley of the Mid-Atlantic Ridge. *Journal of Physical Oceanography*, 32, 1763-78.
- Thurnherr, A. M., St. Laurent, L. C., Speer, K. G., Toole, J. M. and Ledwell, J. R. (2005).

- Mixing associated with sills in a canyon on the midocean ridge flank. *Journal of Physical Oceanography*, 35, 1370-81.
- Thurnherr, A. M. (2000). *Hydrography and flow in the rift valley of the Mid-Atlantic Ridge*. University of Southampton.
- Tomczak, M. and Godfrey, J. (2003). *Regional Oceanography: An introduction. 2nd Edition*. Daya Publishing House.
- Trenary, L and DelSole, T. (2016). Does the Atlantic Multidecadal Oscillation get its predictability from the Atlantic Meridional Overturning circulation? *Journal of Climate*, 29, 5267-80.
- Turnewitsch, R., Falahat, S., Nycander, J., Dale, A., Scott, R. B. and Furnival, D. (2013). Deep-sea fluid and sediment dynamics—Influence of hill-to seamount-scale seafloor topography. *Earth-Science Reviews*, 127, 203-41.
- van Haren, H. (2005). Details of stratification in a sloping bottom boundary layer of Great Meteor Seamount. *Geophysical Research Letters*, 32.
- van Haren, H. (2006). Nonlinear motions at the internal tide source. *Geophysical Research Letters*, 33.
- van Haren, H. (2019). Off-bottom turbulence expansions of unbounded flow over a deep-ocean ridge. *Tellus A: Dynamic Meteorology and Oceanography*, 71, 1-10.
- van Haren, H., Duineveld, G. and de Stigter, H. (2017). Prefrontal bore mixing. *Geophysical Research Letters*, 44, 9408-15.
- van Haren, H., Gostiaux, L., Morozov, E. and Tarakanov, R. (2014). Extremely long Kelvin-Helmholtz billow trains in the Romanche Fracture Zone. *Geophysical Research Letters*, 41, 8445-51.
- Von Schuckmann, K., Brandt, P. and Eden, C. (2008). Generation of tropical instability waves in the Atlantic Ocean. *Journal of Geophysical Research: Oceans*, 113.
- Warren, B. A. (1981). Deep circulation of the world ocean. *Evolution of physical oceanography*, 6-41.
- Weaver, A. J., Bitz, C. M., Fanning, A. F. and Holland, M. M. (1999). Thermohaline circulation: High-latitude phenomena and the difference between the Pacific and Atlantic. *Annual Review of Earth and Planetary Sciences*, 27, 231-85.
- Woods, A. W. and Bush, J. W. M. (1999). Dimensions and dynamics of megaplumes. *Journal of Geophysical Research: Oceans*, 104, 20495-507.
- Xu, X., Bower, A., Furey, H. and Chassignet, E. P. (2018). Variability of the Iceland-Scotland Overflow Water Transport Through the Charlie-Gibbs Fracture Zone: Results From an Eddying Simulation and Observations. *Journal of Geophysical Research: Oceans*, 123, 5808-23.
- Xu, X., Schmitz Jr, W. J., Hurlburt, H. E., Hogan, P. J. and Chassignet, E. P. (2010). Transport of Nordic Seas overflow water into and within the Irminger Sea: An eddy resolving simulation and observations. *Journal of Geophysical Research: Oceans*, 115.
- Yeager, S. G. and Robson, J. I. (2017). Recent progress in understanding and predicting Atlantic decadal climate variability. *Current Climate Change Reports*, 3, 112-27.
- Zilberman, N. V., Becker, J. M., Merrifield, M. A. and Carter, G. S. (2009). Model estimates of M 2 internal tide generation over Mid-Atlantic Ridge topography. *Journal of Physical Oceanography*, 39, 2635-51.

7. CUMULATIVE IMPACTS

This chapter describes potential cumulative impacts from future exploitation of PMS mineral resources in the study area. It should be noted that such exploitation activities have not started yet. Currently, how such exploitation activities will take place in time and space in the future is largely unknown, as is the likelihood of multiple exploitation activities.

Current scientific understanding and prediction are that the metal content from more than 90 per cent of all known (Beaulieu et al., 2020) seafloor PMS occurrences is only a small fraction of past production and current geological resources of similar type of massive sulfide deposits from the geological record on land. Although potential exploitation of deep-sea PMS resources is different from that for PMN deposits and may potentially be technically feasible, the current debate must consider the resource size and its economic viability of future recovery of metals from potential seafloor PMS deposits (Hannington et al., 2010, 2011).

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 ISA to be used for addressing cumulative impacts through the REMP process. Contractors to 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 (LTC). There is, therefore, an 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 is commonly attempted in Europe, and this provides some relevant information for assessment and management. Assessment of cumulative impacts was first required by a European Economic Community EIA Directive (85/337/EEC, since amended by further Directives) and by an EC Habitats Directive (92/43/EEC, 1992), where they are called "in-combination" impacts. More recently, a European Strategic Environmental Assessment 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 EC Habitats Directive requires consideration of "in-combination" impacts (Article 6.3), which are taken to be synonymous with cumulative impacts.

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

Additive impacts are equal to the sum of all 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.

Cumulative impacts can occur to a greater extent in space and time than the sum of all individual impacts. 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 could 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).

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 prediction 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 on communities (Kirby et al., 2009). The interplay of different environments, impacts and scales gives 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 the 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 exploitation of mineral resources, 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 exploitation, including: 1) multiple potential multiple exploitation activities, 2) interactions with other activities, such as fishing, other commercial harvesting, scientific research, tourism, marine debris or litter, bioprospecting, and cables and 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 concern about the vulnerability of ridge habitats to cumulative impacts resulting from potential multiple exploitation activities and fishing activities (Levin et al., 2016; Washburn et al., 2019).

Here, we describe and evaluate the potential cumulative impacts that could occur from deep-sea exploitation of mineral resources. For the purpose of this description, we focus on the northern MAR between the southern boundary of the Icelandic ECS claim south of Iceland to the equator, exclusive of the Portuguese ECS claim north and south of the Azores and Brazilian EEZ around the islands of St. Peter and St. Paul (Figure 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 individual 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 history, 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 location of exploitation activities as well as the magnitude, duration and spatial extent of impacts resulting from them. The location of exploitation activities will be driven by the resource availability, legal framework and potential technological, economic and environmental considerations (Jones et al., 2018a; Lusty and Murton, 2018). The impacts of exploitation activities could vary greatly dependent on technology and mitigation measures put in place (Cuvelier et al., 2018).

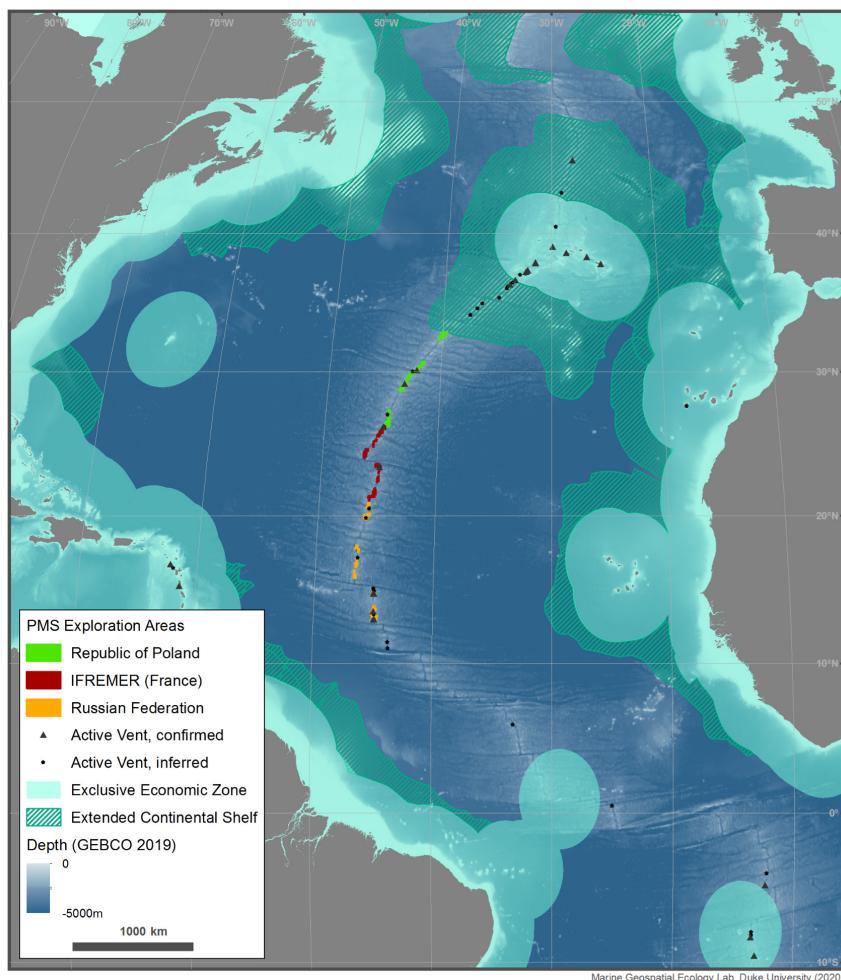
7.2.1 Direct impacts

Many of the most severe impacts from exploitation (Table 7.2), such as direct disturbance to the sea floor from seabed collection, only occur at the mine site, and the same area of sea floor 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—potentially, hydrothermal vent communities and others—to lead to cumulative effects including impacts on connectivity between populations.

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-lagged or delayed effects	Effects over time
Cross-boundary movement	Impacts occur elsewhere
Fragmentation	Fragmentation of habitats
Compounding/synergistic effects	Effects from multiple causes and processes; interaction of impacts and policies
Indirect effects; secondary or higher order effects	Indirect and secondary impacts
Nibbling effects	Continued small-scale impacts over area or time

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 exclusive of the Portuguese ECS claim north and south of the Azores and the Brazilian EEZ around the islands of St. Peter and St. Paul. Existing French, Polish, and Russian Federation exploration contracts with 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.



7.2.2 Indirect impacts

The most likely contribution to cumulative impacts from exploitation are impacts that extend over wider areas than the mine site itself. These impacts are mostly associated with plumes that are enriched by suspended particles or chemicals (Boschen et al., 2013). Modelling of the MAR 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 (0–200 m), pelagic (200–50 m off-bottom) and benthic (seabed to 50 m off-bottom) environments.

7.3 Types of cumulative impacts

7.3.1 Potential multiple exploitation activities

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 MAR, 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 exploitation operations, deposits, the potential impacts of plumes

Figure 7.2 Conceptual figure showing the scale of possible impacts and habitats on the MAR (Weaver; scales based on Cherkashov et al. 2010 and Niedzielski et al., 2013)

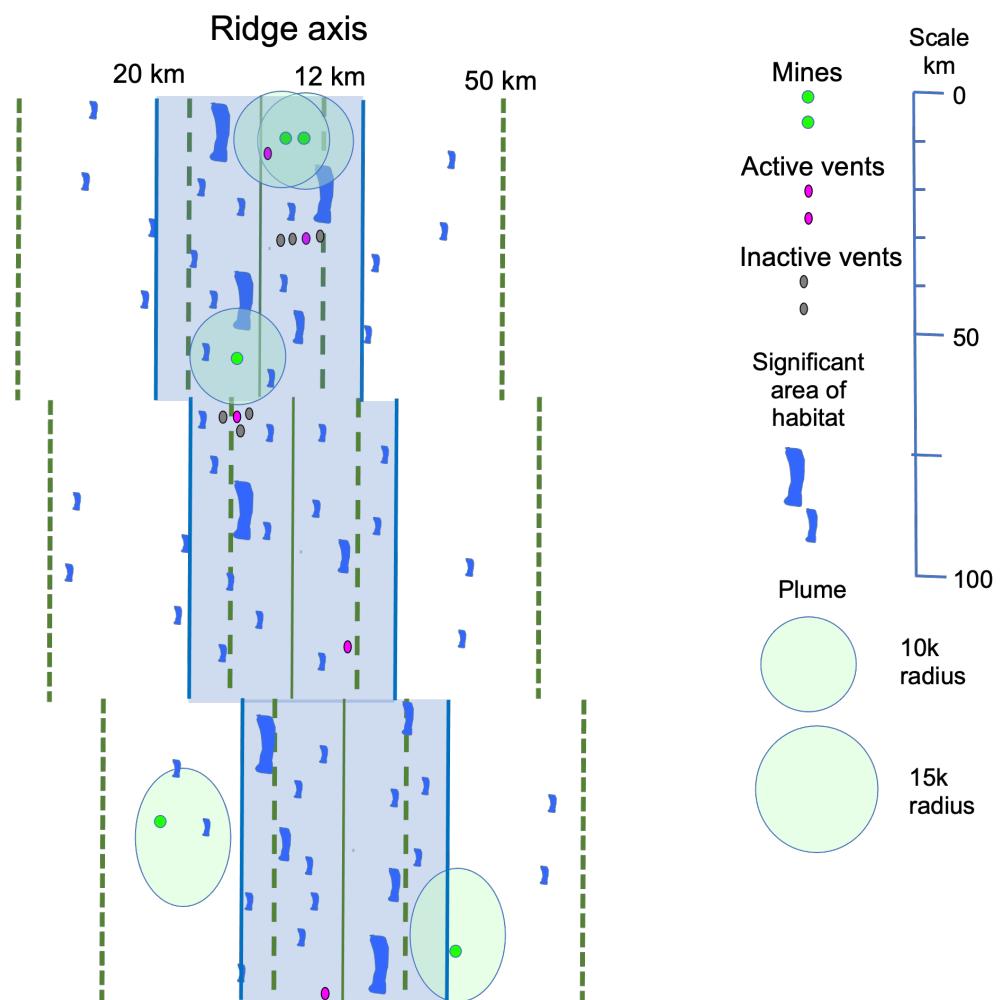
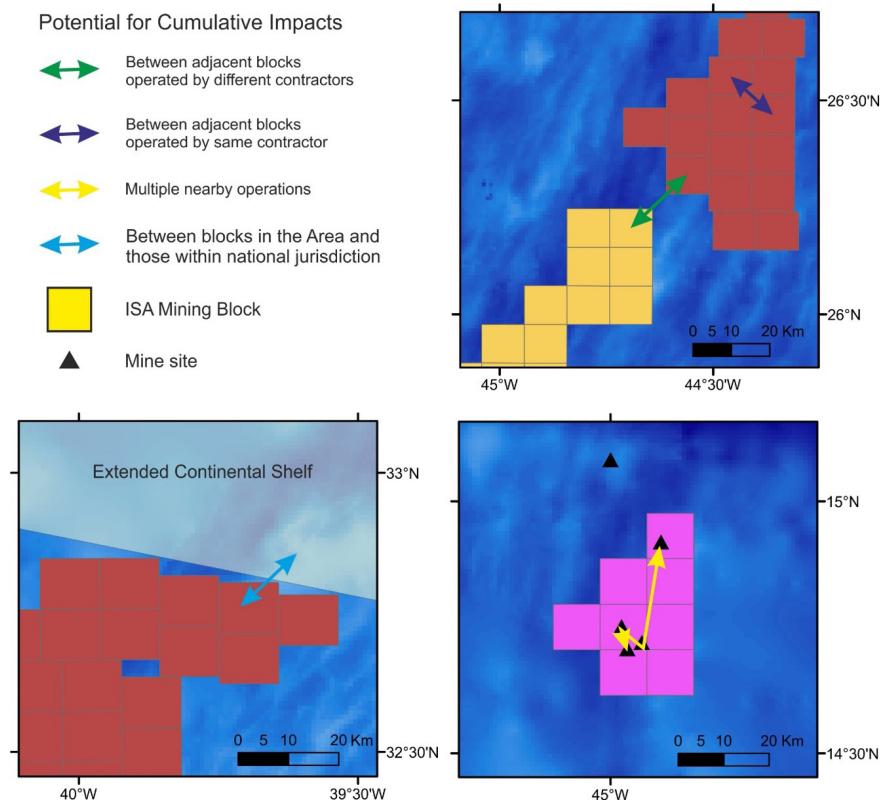


Figure 7.3 Maps showing potential for cumulative impacts. Maps are based on the spatial location of actual ISA exploration blocks (10 x 10 km) and vent sites (as potential mining areas) for scaling. However, the figures do not imply any real mine location information or planned impact scenarios. The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



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 exploitation operations are from adjacent ongoing exploitation operations. Ecosystem resilience will influence the impact of adjacent ongoing exploitation 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 and Russia, or France and Poland)

4. between blocks in the Area and those within national jurisdiction (transboundary issues). For example, Polish exploration blocks are adjacent to the Portuguese ECS around the Azores, which may be subject to future mining activities under national jurisdiction.

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 to deep-sea exploitation. Different approaches will likely lead to different impacts (Table 7.1) and may affect the potential for cumulative impacts, particularly on nearby operations.

Profitable exploitation on the MAR may target numerous and relatively small SMS deposits (Lusty and Murton, 2018). Given that efficient exploitation activities might target only the highest-grade resources, each area may be fully exploited within months (Petersen et al., 2016). This presents the potential for cumulative impacts from single operations that move rapidly. The impacts of rapidly targeting 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 sea-floor environment from deep-sea exploitation 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 exploitation activities are not expected to arrest the hydrothermal system, but activities near vent systems will

Table 7.2 Expected impacts and effects of exploitation on the MAR (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 sea-floor 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

probably alter the distribution of venting activity on a local scale of 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 exploitation 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, hindering recovery. Habitat loss or degradation attributable to cumulative exploitation events seems likely to be associated with chronic reductions 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 exploitation or other disturbances more likely to cause ecosystem-scale consequences.

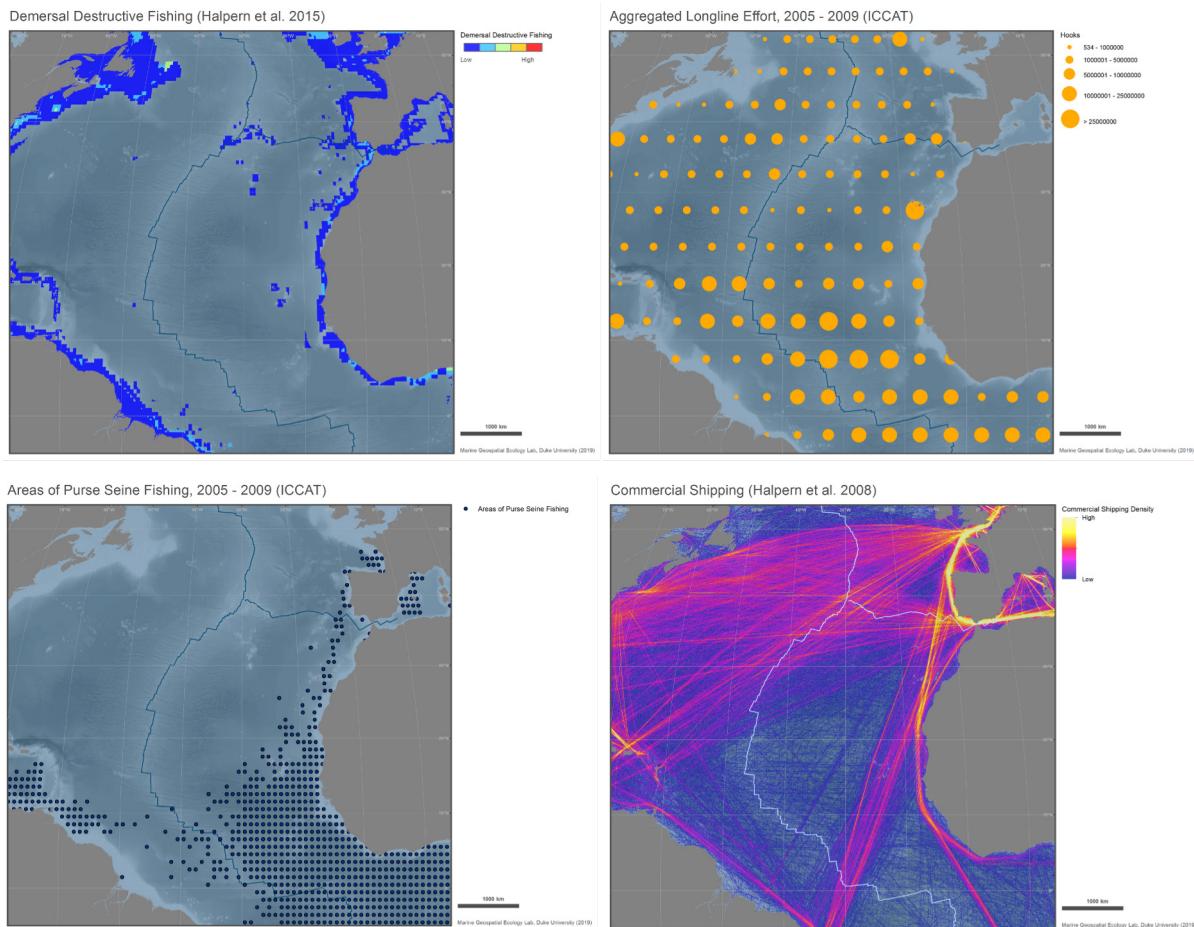
7.3.2 Fishing and other harvesting

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 MAR 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 of years 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 and 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 exploitation and either demersal or pelagic fisheries is still to be determined. Even without direct overlap, there could be potential for cumulative impacts between exploitation and fishing activities. Potential effects may be one-sided, only affecting the fishery and not the exploitation 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 exploitation 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 also possible that two-way potential synergistic effects of exploitation 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 sea floor, such as habitat alteration and plume formation (Jennings and Kaiser, 1998), act in combination with the effects

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/dataproduct-19nov-lowres.pdf>)



of exploitation to exceed a particular ecological threshold that was not exceeded by each impact individually, or even that a three-way potential cumulative impact could occur between fishing, climate change and exploitation activities.

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 sea floor (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 exploitation, including the MAR (Sweetman et al., 2017). The impacts of climate change will lead to effects on deep-sea life, including direct impacts to key biological processes such as 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 disturbances will interact.

Present projections suggest that the bathyal Atlantic (200–3,000 m depth), of which a significant proportion is on the MAR, is expected to experience dissolved-oxygen changes of –0.68 to 2.05 per cent and changes in the flux of particulate organic carbon (food supply) to the sea floor of –36.27 to 4.79 per cent between present conditions and the year 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 sea-floor biomass (Jones et al., 2014).

In the coming decades, climate-induced changes will affect all areas of exploitation 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, that are 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 exploitation impacts. Incorporating climate change into the management process for exploitation 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 exploitation activities (Benn et al., 2010). These include scientific research and bioprospecting, marine debris or litter, and cables and communication infrastructure. Civilian and military disposal activities occur in the

deep sea, but typically not in the area of the MAR (Benn et al., 2010).

Marine scientific research uses a range of equipment to sample the marine environment, including dredges and trawls, grabs, corers, submersibles and 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 MAR (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 exploitation.

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 exploitation 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 MAR may receive cumulative pressures from fishing, climate change and pollution. Such additive analyses may underestimate true cumulative impacts, particularly with the addition of mining pressure. The

effects of exploitation could exacerbate other changes. Exploitation could affect deep-sea biota, with resulting feedbacks on other ecosystem processes, functions and services. Disturbance of microbes and removal of animals, combined with changing temperature, and oxygen depletion caused by sediment plumes, are likely to affect carbon sinks. These 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 a different regime (Holling, 1973; Petraitis et al., 2009; Scheffer and Carpenter, 2003). Tipping points result from a nonlinear relationship between ecosystem conditions 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 modes 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 exploitation activities as well as the combined impacts of exploitation and other anthropogenic pressures on the marine environment, including climate change.
- There is potential for a wide range of cumulative impacts to occur during exploitation operations on the MAR.
- Marine ecosystem responses to individual, additive or synergistic stressors can be large, abrupt and surprising.

7.6 References

- Aleynik, D., Dale, A. C. and Inall, M. E. (2015). Near-field hydrodynamic modelling of two case study sites. *MIDAS Deliverable 2.2*, 21.
- Amorim, P., Perán, A. D., Pham, C. K., Juliano, M., Cardigos, F., Tempera, F. and Morato, T. (2017). Overview of the Ocean Climatology and Its Variability in the Azores Region of the North Atlantic Including Environmental Characteristics at the Seabed. *Frontiers in Marine Science* 4(56).
- Ardron, J. A. and Warner, R. (2015). International Marine Governance and Protection of Biodiversity. In: Smith, H. D., Suarez de Vivero, J. L. and Agardy, T. S. (Eds.), Chapter 4, *Handbook of Ocean Resources and Management*. Taylor & Francis/Routledge, London, UK.
- Beaulieu, S. E., Baker, E. T., German, C. R. and Maffei, A. (2013). An authoritative global database for active submarine hydrothermal vent fields. *Geochemistry, Geophysics, Geosystems* 14(11), 4892-4905.
- Benn, A. R., Weaver, P. P., Billett, D. S. M., van den Hove, S., Murdock, A. P., Doneghan, G. B. and Le Bas, T. (2010). Human Activities on the Deep Seafloor in the North East Atlantic: An Assessment of Spatial Extent. *PLoS ONE* 5(9), e12730.
- Bensch, A., Gianni, M., Gréboval, D., Sanders, J. S. and Hjort, A. (2009). Worldwide review of bottom fisheries in the high seas. FAO Fisheries and Aquaculture Technical Paper. No. 522, Rev.1, Rome, 145.
- Bergstad, O. A., Menezes, G. and Høines, Å. S. (2008). Demersal fish on a mid-ocean ridge: Distribution patterns and structuring factors. *Deep-Sea Research* 2(55), 185-202.
- Boschen, R. E., Rowden, A. A., Clark, M. R. and Gardner, J. P. A. (2013). Mining of deep-sea seafloor massive sulfides: A review of the deposits, their benthic communities, impacts from mining, regulatory frameworks and management strategies. *Ocean & Coastal Management* 84, 54-67.
- Beaulieu, S. E., Szafrański, K. M. (2020). InterRidge Global Database of Active Submarine Hydrothermal Vent Fields Version 3.4. PANGAEA, <https://doi.org/10.1594/PANGAEA.917894>
- Boyd, P. W. and Brown, C. J. (2015). Modes of interactions between environmental drivers and marine biota. *Frontiers in Marine Science* 2(9).
- Breitburg, D., Levin, L. A., Oschlies, A., Grégoire, M., Chavez, F. P., Conley, D. J., Garçon, V., Gilbert, D., Gutiérrez, D., Isensee, K., Jacinto, G. S., Limburg, K. E., Montes, I., Naqvi, S. W. A., Pitcher, G. C., Rabalaïs, N. N., Roman, M. R., Rose, K. A., Seibel, B. A., Telszewski, M., Yasuhara, M. and Zhang, J. (2018). Declining oxygen in the global ocean and coastal waters. *Science* 359(6371), eaam7240.
- Brown, C. J., Saunders, M. I., Possingham, H. P. and Richardson, A. J. (2013). Managing for Interactions between Local and Global Stressors of Ecosystems. *PLoS ONE* 8(6), e65765.
- Cherkashov, G., Poroshina, I., Stepanova, T., Ivanov, V., Bel'tenev, V., Lazareva, L., Rozhdestvenskaya, I., Samovarov, M., Shilov, V., Glasby, G.P., Fouquet, Y. and Kuznetsov, V. (2010). Seafloor Massive Sulfides from the Northern Equatorial Mid-Atlantic Ridge: New Discoveries and Perspectives. *Marine Georesources & Geotechnology* 28 (3), 222-239.
- Christensen, V., Guénette, S., Heymans, J. J., Walters, C. J., Watson, R., Zeller, D. and Pauly, D. (2003). Hundred-year decline of North Atlantic predatory fishes. *Fish and Fisheries* 4(1), 1-24.
- Cleary, J. S., DeLand, E., Mennini, S., McCrory, K., Ismail, P. N. and Halpin, P. N. (2019). *Data Report: Workshop on the*

Regional Environmental Management Plan for the Area of the Northern Mid-Atlantic Ridge, 151 pp. Atlantic REMP Project.

Cooper, L. M. and Sheate, W. R. (2004). Integrating cumulative effects assessment into UK strategic planning: implications of the European Union SEA Directive. *Impact Assessment and Project Appraisal* 22(1), 5-16.

Cuvelier, D., Gollner, S., Jones, D. O. B., Kaiser, S., Arbizu, P. M., Menzel, L., Mestre, N. C., Morato, T., Pham, C., Pradillon, F., Purser, A., Raschka, U., Sarrazin, J., Simon-Lledó, E., Stewart, I. M., Stuckas, H., Sweetman, A. K. and Colaço, A. (2018). Potential Mitigation and Restoration Actions in Ecosystems Impacted by Seabed Mining. *Frontiers in Marine Science* 5(467).

Doak, D. F., Estes, J. A., Halpern, B. S., Jacob, U., Lindberg, D. R., Lovvorn, J., Monson, D. H., Tinker, M. T., Williams, T. M., Wootton, J. T., Carroll, I., Emmerson, M., Micheli, F. and Novak, M. (2008). Understanding and predicting ecological dynamics: are major surprises inevitable. *Ecology* 89(4), 952-961.

Duarte, C. M. (2014). Global change and the future ocean: a grand challenge for marine sciences. *Frontiers in Marine Science* 1(63).

Dunn, D. C., Van Dover, C. L., Etter, R. J., Smith, C. R., Levin, L. A., Morato, T., Colaço, A., Dale, A. C., Gebruk, A. V., Gjerde, K. M., Halpin, P. N., Howell, K. L., Johnson, D., Perez, J. A. A., Ribeiro, M. C., Stuckas, H., Weaver, P. P. E. and the SEMPIA Workshop Participants (2018). A strategy for the conservation of biodiversity on mid-ocean ridges from deep-sea mining. *Science Advances* 4(7), eaar4313. doi:10.1126/sciadv.aar4313

Dunstan, P. K., Dambacher, J. M., Thornborough, K., Marshall, N. and Stuart-Smith, R. (2019). *Draft Guidelines for analysis of cumulative impacts and risks to the Great Barrier Reef. Project E1: Guidelines for*

analysis of cumulative impacts and risks to the Great Barrier Reef. Report to the National Environmental Science Program, Marine Biodiversity Hub, 84.

Durden, J. M., Lallier, L. E., Murphy, K., Jaeckel, A., Gjerde, K. and Jones, D. O. B. (2018). Environmental Impact Assessment process for deep-sea mining in 'the Area'. *Marine Policy* 87, 194-202.

Fock, H. O., Matthiessen, B., Zidowitz, H. and Westernhagen, H. V. (2002). Diel and habitat-dependent resource utilisation by deep-sea fishes at the Great Meteor Seamount: Niche overlap and support for the sound scattering layer interception hypothesis. *Marine Ecology Progress Series* 244, 219-233.

Foley, M. M., Mease, L. A., Martone, R. G., Prahler, E. E., Morrison, T. H., Clarke Murray, C. and Wojcik, D. (2017). The challenges and opportunities in cumulative effects assessment. *Environmental Impact Assessment Review* 62, 122-134.

Fuller, K. and Sadler, B. (1999). EC guidance on cumulative effects assessment. *Environmental Assessment* 7(2), 33-35.

Garibaldi, L. and Limongelli, L. (2003). *Trends in Oceanic Captures and Clustering of Large Marine Ecosystems: Two Studies Based on the FAO Capture Database*. Technical Paper No. 435. FAO Fisheries, Rome, 71.

Gehlen, M., Séférian, R., Jones, D. O. B., Roy, T., Roth, R., Barry, J., Bopp, L., Doney, S. C., Dunne, J. P., Heinze, C., Joos, F., Orr, J. C., Resplandy, L., Segschneider, J. and Tjiputra, J. (2014). Projected pH reductions by 2100 might put deep North Atlantic biodiversity at risk. *Biogeosciences* 11(23), 6955-6967.

Gianni, M. (2004). *High Seas Bottom Trawl Fisheries and Their Impacts on the Biodiversity of Vulnerable Deep-Sea Ecosystems*. IUCN, Gland, Switzerland, 90.

- Gjerde, K. M., Weaver, P., Billett, D., Paterson, G., Colaco, A., Dale, A., Greinert, J., Hauton, C., Jansen, F., Jones, D., Arbizu, P. M., Murphy, K. and Sweetman, A. (2016). *Implications of MIDAS results for policy makers: recommendations for future regulations*. Seascapes Consultants, Romsey.
- Gollner, S., Kaiser, S., Menzel, L., Jones, D. O. B., Brown, A., Mestre, N. C., van Oevelen, D., Menot, L., Colaço, A., Canals, M., Cuvelier, D., Durden, J. M., Gebruk, A., Egho, G. A., Haeckel, M., Marcon, Y., Mevenkamp, L., Morato, T., Pham, C. K., Purser, A., Sanchez-Vidal, A., Vanreusel, A., Vink, A. and Martinez-Arbizu, P. (2017). Resilience of benthic deep-sea fauna to mining activities. *Marine Environmental Research* 129, 76-101.
- Griffith, G. P., Fulton, E. A., Gorton, R. and Richardson, A. J. (2012). Predicting Interactions among Fishing, Ocean Warming, and Ocean Acidification in a Marine System with Whole-Ecosystem Models. *Conservation Biology* 26(6), 1145-1152.
- Halpern, B. S., Walbridge, S., Selkoe, K. A., Kappel, C. V., Micheli, F., D'Agrosa, C., Bruno, J. F., Casey, K. S., Ebert, C., Fox, H. E., Fujita, R., Heinemann, D., Lenihan, H. S., Madin, E. M. P., Perry, M. T., Selig, E. R., Spalding, M., Steneck, R. and Watson, R. (2008). A Global Map of Human Impact on Marine Ecosystems. *Science* 319(5865), 948-952.
- Hannington, M.D., Jamieson, J., Monecke, T., and Petersen, S. (2010). Modern Sea-Floor Massive Sulfides and Base Metal Resources: Toward an Estimate of Global Sea-Floor Massive Sulfide Potential. *Soc. Economic Geologist, Spec. Publ.* 16, p. 317-338.
- Hannington, M., Jamieson, J., Monecke, T., Petersen, S. and Beaulieu, S. (2011). The abundance of seafloor massive sulfide deposits. *Geology* 39(12), 1155-1158.
- Hauton, C., Brown, A., Thatje, S., Mestre, N. C., Bebianno, M. J., Martins, I., Bettencourt, R., Canals, M., Sanchez-Vidal, A., Shillito, B., Ravaux, J., Zbinden, M., Duperron, S., Mevenkamp, L., Vanreusel, A., Gambi, C., Dell'Anno, A., Danovaro, R., Gunn, V. and Weaver, P. (2017). Identifying Toxic Impacts of Metals Potentially Released during Deep-Sea Mining—A Synthesis of the Challenges to Quantifying Risk. *Frontiers in Marine Science* 4(368).
- Holling, C. S. (1973). Resilience and Stability of Ecological Systems. *Annual Review of Ecology and Systematics* 4(1), 1-23.
- Humphris, S. E., Alt, J. C., Teagle, D. A. H. and Honnorez, J. J. (1998). Geochemical changes during hydrothermal alteration of basement in the stockwork beneath the active TAG hydrothermal mound. In: Herzig, P. M., Humphris, S. E., Miller, D. J. and Zierenberg, R. A. (Eds.), *Proceedings of the Ocean Drilling Program, Scientific Results, Vol. 15*, 255.
- Jackson, J. B. C., Kirby, M. X., Berger, W. H., Bjorndal, K. A., Botsford, L. W., Bourque, B. J., Bradbury, R. H., Cooke, R., Erlandson, J., Estes, J. A., Hughes, T. P., Kidwell, S., Lange, C. B., Lenihan, H. S., Pandolfi, J. M., Peterson, C. H., Steneck, R. S., Tegner, M. J. and Warner, R. R. (2001). Historical Overfishing and the Recent Collapse of Coastal Ecosystems. *Science* 293(5530), 629-637.
- Jennings, S. and Kaiser, M. J. (1998). The Effects of Fishing on Marine Ecosystems. In: Blaxter, J. H. S., Southward, A. J. and Tyler, P. A. (Eds.), *Advances in Marine Biology*. Academic Press, 201-352.
- Johnson, C. J. (2013). Identifying ecological thresholds for regulating human activity: Effective conservation or wishful thinking? *Biological Conservation* 168, 57-65.
- Johnson, C. J. (2016). *Defining and Identifying Cumulative Environmental, Health, and Community Impacts*.

- The Integration Imperative Springer International Publishing, 21-45.
- Jones, D. O. B., Amon, D. J. and Chapman, A. S. A. (2018a). Mining Deep-Ocean Mineral Deposits: What are the Ecological Risks? *Elements* 14(5), 325-330.
- Jones, D. O. B., Ardron, J. A., Colaço, A. and Durden, J. M. (2018b). Environmental considerations for impact and preservation reference zones for deep-sea polymetallic nodule mining. *Marine Policy*.
- Jones, D. O. B., Durden, J. M., Murphy, K., Gjerde, K. M., Gebicka, A., Colaço, A., Morato, T., Cuvelier, D. and Billett, D. S. M. (2019). Existing environmental management approaches relevant to deep-sea mining. *Marine Policy* 103, 172-181.
- Jones, D. O. B., Yool, A., Wei, C.-L., Henson, S. A., Ruhl, H. A., Watson, R. A. and Gehlen, M. (2014). Global reductions in seafloor biomass in response to climate change. *Global Change Biology* 20(6), 1861-1872.
- Kane, I. A. and Clare, M. A. (2019). Dispersion, Accumulation, and the Ultimate Fate of Microplastics in Deep-Marine Environments: A Review and Future Directions. *Frontiers in Earth Science* 7(80).
- Kirby, R. R., Beaugrand, G. and Lindley, J. A. (2009). Synergistic Effects of Climate and Fishing in a Marine Ecosystem. *Ecosystems* 12(4), 548-561.
- Koslow, J. A., Boehlert, G. W., Gordon, J. D. M., Haedrich, R. L., Lorance, P. and Parin, N. (2000). Continental slope and deep-sea fisheries: implications for a fragile ecosystem. *ICES Journal of Marine Science* 57(3), 548-557.
- Law, K. L. (2017). Plastics in the Marine Environment. *Annual Review of Marine Science* 9(1), 205-229.
- Levin, L. A., Mengerink, K., Gjerde, K. M., Rowden, A. A., Van Dover, C. L., Clark, M. R., Ramirez-Llodra, E., Currie, B., Smith, C. R., Sato, K. N., Gallo, N., Sweetman, A. K., Lily, H., Armstrong, C. W. and Brider, J. (2016). Defining "serious harm" to the marine environment in the context of deep-seabed mining. *Marine Policy* 74, 245-259.
- Levin, L. A., Wei, C.-L., Dunn, D. C., Amon, D., Ashford, O., Cheung, W., Colaço, A., Escobar, E., Guilloux, B., Harden-Davies, H., Drazen, J. C., Gjerde, K., Ismail, K., Jones, D., Johnson, D., Le, J., Lejzerowicz, F., Mitarai, S., Morato, T., Mulsow, S., Snelgrove, P., Sweetman, A. K. and Yasuhara, M. (2019). *Climate Change Considerations are Fundamental to Sustainable Management of Deep-Seabed Mining*. DOSI Policy Brief, 4.
- Levitus, S., Antonov, J. I., Boyer, T. P. and Stephens, C. (2000). Warming of the World Ocean. *Science* 287(5461), 2225-2229.
- Lusty, P. A. J. and Murton, B. J. (2018). Deep-Ocean Mineral Deposits: Metal Resources and Windows into Earth Processes. *Elements* 14(5), 301-306.
- Morato, T., Hoyle, S. D., Allain, V. and Nicol, S. J. (2010). Seamounts are hotspots of pelagic biodiversity in the open ocean. *Proceedings of the National Academy of Sciences of the United States of America* 107(21), 9707-9711.
- Morato, T., Watson, R., Pitcher, T. J. and Pauly, D. (2006). Fishing down the deep. *Fish and Fisheries* 7(1), 24-34.
- Myers, R. A. and Worm, B. (2003). Rapid worldwide depletion of predatory fish communities. *Nature* 423(6937), 280-283.
- Nakajima, R., Yamamoto, H., Kawagucci, S., Takaya, Y., Nozaki, T., Chen, C., Fujikura, K., Miwa, T. and Takai, K. (2015). Post-Drilling Changes in Seabed Landscape and Megabenthos in a Deep-Sea Hydrothermal System, the Iheya North Field, Okinawa Trough. *PLoS ONE* 10(4), e0123095.
- Niedzielski, T., Høines, Å., Shields, M. A., Linley, T. D. and Priede, I. G. (2013). A multi-

- scale investigation into seafloor topography of the northern Mid-Atlantic Ridge based on geographic information system analysis. *Deep Sea Research Part II: Topical Studies in Oceanography* 98, Part B, 231–243.
- Pauly, D., Alder, J., Bennett, E., Christensen, V., Tyedmers, P. and Watson, R. (2003). The Future for Fisheries. *Science* 302(5649), 1359–1361.
- Petersen, S., Krätschell, A., Augustin, N., Jamieson, J., Hein, J. R. and Hannington, M. D. (2016). News from the seabed – Geological characteristics and resource potential of deep-sea mineral resources. *Marine Policy* 70 (Supplement C), 175–187.
- Petraitis, P. S., Methratta, E. T., Rhile, E. C., Vidargas, N. A. and Dudgeon, S. R. (2009). Experimental confirmation of multiple community states in a marine ecosystem. *Oecologia* 161(1), 139–148.
- Pham, C. K., Ramirez-Llodra, E., Alt, C. H. S., Amaro, T., Bergmann, M., Canals, M., Company, J. B., Davies, J., Duineveld, G., Galgani, F., Howell, K. L., Huvenne, V. A. I., Isidro, E., Jones, D. O. B., Lastras, G., Morato, T., Gomes-Pereira, J. N., Purser, A., Stewart, H., Tojeira, I., Tubau, X., Van Rooij, D. and Tyler, P.A. (2014). Marine Litter Distribution and Density in European Seas, from the Shelves to Deep Basins. *PLoS ONE* 9(4), e95839.
- Pitcher, T. J. (2001). Fisheries Managed to Rebuild Ecosystems? Reconstructing the Past to Salvage the Future. *Ecological Applications* 11(2), 601–617.
- Queiroz, N., Humphries, N. E., Mucientes, G., Hammerschlag, N., Lima, F. P., Scales, K. L., Miller, P. I., Sousa, L. L., Seabra, R. and Sims, D. W. (2016). Ocean-wide tracking of pelagic sharks reveals extent of overlap with longline fishing hotspots. *Proceedings of the National Academy of Sciences* 113(6), 1582–1587.
- Rabalais, N. N., Díaz, R. J., Levin, L. A., Turner, R. E., Gilbert, D. and Zhang, J. (2010). Dynamics and distribution of natural and human-caused hypoxia. *Biogeosciences* 7(2), 585–619.
- Salter, I., Schiebel, R., Ziveri, P., Movellan, A., Lampitt, R. and Wolff, G. A. (2014). Carbonate counter pump stimulated by natural iron fertilization in the Polar Frontal Zone. *Nature Geoscience* 7, 885.
- Scheffer, M., Bascompte, J., Brock, W. A., Brovkin, V., Carpenter, S. R., Dakos, V., Held, H., van Nes, E. H., Rietkerk, M. and Sugihara, G. (2009). Early-warning signals for critical transitions. *Nature* 461(7260), 53–59.
- Scheffer, M. and Carpenter, S. R. (2003). Catastrophic regime shifts in ecosystems: linking theory to observation. *Trends in Ecology & Evolution* 18(12), 648–656.
- Selkoe, K. A., Blenckner, T., Caldwell, M. R., Crowder, L. B., Erickson, A. L., Essington, T. E., Estes, J. A., Fujita, R. M., Halpern, B. S., Hunsicker, M. E., Kappel, C. V., Kelly, R. P., Kittinger, J. N., Levin, P. S., Lynham, J. M., Mach, M. E., Martone, R. G., Mease, L. A., Salomon, A. K., Samhouri, J. F., Scarborough, C., Stier, A. C., White, C. and Zedler, J. (2015). Principles for managing marine ecosystems prone to tipping points. *Ecosystem Health and Sustainability* 1(5), 1–18.
- Spaling, H. (1994). Cumulative effects assessment: concepts and principles. *Impact Assessment* 12, 231–251.
- Steinacher, M., Joos, F., Frölicher, T. L., Bopp, L., Cadule, P., Cocco, V., Doney, S. C., Gehlen, M., Lindsay, K., Moore, J. K., Schneider, B. and Segschneider, J. (2010). Projected 21st century decrease in marine productivity: a multi-model analysis. *Biogeosciences* 7(3), 979–1005.
- Stephenson, R. L., Hobday, A. J., Cvitanovic, C., Alexander, K. A., Begg, G. A., Bustamante, R. H., Dunstan, P. K., Frusher, S., Fudge, M., Fulton, E. A., Haward, M., Macleod, C., McDonald, J., Nash, K. L., Ogier, E., Pecl, G., Plagányi, É. E., van Putten, I., Smith, T. and Ward, T. M. (2019). A practical framework for

implementing and evaluating integrated management of marine activities. *Ocean & Coastal Management* 177, 127-138.

Stockwell, C. A., Hendry, A. P., Kinnison, M. T. (2003). Contemporary evolution meets conservation biology. *Trends in Ecology & Evolution* 18(2), 94-101.

Sweetman, A. K., Thurber, A. R., Smith, C. R., Levin, L. A., Mora, C., Wei, C.-L., Gooday, A. J., Jones, D. O. B., Rex, M. A., Yasuhara, M., Ingels, J., Ruhl, H. A., Frieder, C. A., Danovaro, R., Würzberg, L., Baco, A. R., Grupe, B. M., Pasulka, A., Meyer, K. S., Dunlop, K. M., Henry, L. A. and Roberts, J. M. (2017). Major impacts of climate change on deep-sea benthic ecosystems. *Elementa Science of the Anthropocene* 5(4).

Synnes, M. (2007). Bioprospecting of organisms from the deep sea: scientific and environmental aspects. *Clean Technologies and Environmental Policy* 9(1), 53-59.

The Royal Society (2005). *Ocean acidification due to increasing atmospheric carbon dioxide*. The Royal Society, London, 60.

Therivel, R. (2010). *Strategic Environmental Assessment in Action*. Earthscan, London.

Toggweiler, J. R. and Russell, J. (2008). Ocean circulation in a warming climate. *Nature* 451(7176), 286-288.

Travis, J., Coleman, F. C., Auster, P. J., Cury, P. M., Estes, J. A., Orensanz, J., Peterson, C. H., Power, M. E., Steneck, R. S. and Wootton, J. T. (2014). Integrating the invisible fabric of nature into fisheries management. *Proceedings of the National Academy of Sciences* 111(2), 581-584.

Uthicke, S., Fabricius, K., De'ath, G., Negri, A., Warne, M., Smith, R., Noonan, S., Johansson, C., Gorsuch, H. and Anthony, K. (2016). *Multiple and cumulative impacts on the GBR: assessment of current status and development of improved approaches for management: Final Report Project*

1.6. *Report to the National Environmental Science Programme*. Reef and Rainforest Research Centre Limited, Cairns p. 144.

Van Dover, C. L. (2011). Mining seafloor massive sulphides and biodiversity: what is at risk? *ICES Journal of Marine Science: Journal du Conseil* 68(2), 341-348.

Van Dover, C. L. (2014). Impacts of anthropogenic disturbances at deep-sea hydrothermal vent ecosystems: A review. *Marine Environmental Research* 102, 59-72.

Van Dover, C. L. (2019). Inactive Sulfide Ecosystems in the Deep Sea: A Review. *Frontiers in Marine Science* 6(461).

Van Dover, C. L., Arnaud-Haond, S., Gianni, M., Helmreich, S., Huber, J. A., Jaeckel, A. L., Metaxas, A., Pendleton, L. H., Petersen, S., Ramirez-Llodra, E., Steinberg, P. E., Tunnicliffe, V. and Yamamoto, H. (2018). Scientific rationale and international obligations for protection of active hydrothermal vent ecosystems from deep-sea mining. *Marine Policy* 90, 20-28.

Vecchione, M., Bergstad, O. A., Byrkjedal, I., Falkenhaug, T., Gebruk, A. V., Godø, O. R., Gislason, A., Heino, M., Høines, Å. S., Menezes, G. M., Piatkowski, U., Priede, I. G., Skov, H., Søiland, H., Sutton, T. and de Lange Wenneck, T. (2010). Biodiversity Patterns and Processes on the Mid-Atlantic Ridge. In: McIntyre, A. D. (Ed.), *Life in the World's Oceans*. Wiley, 103-122.

Walker, L. J. and Johnston, J. (1999). *Guidelines for the assessment on indirect and cumulative impacts as well as impact interactions*. Office for Official Publications of the European Communities, Luxembourg, 169.

Washburn, T. W., Turner, P. J., Durden, J. M., Jones, D. O. B., Weaver, P. and Van Dover, C. L. (2019). Ecological risk assessment for deep-sea mining. *Ocean & Coastal Management* 176, 24-39.

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 (pelagic) 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 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 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 the sea floor) and benthic (sea floor to 50 m above) environments (Figure 8.1). The REMP for the nMAR is only anticipated to address the area of the seabed beyond national jurisdiction (the Area) along the nMAR. However, the inclusion of the surface and mid-water environments within the EIS template supports the inclusion of these environments in the biological chapters, to support the establishment of regional environmental baselines from the surface to the sea floor, 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, although 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 restricted to the "surface", 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.

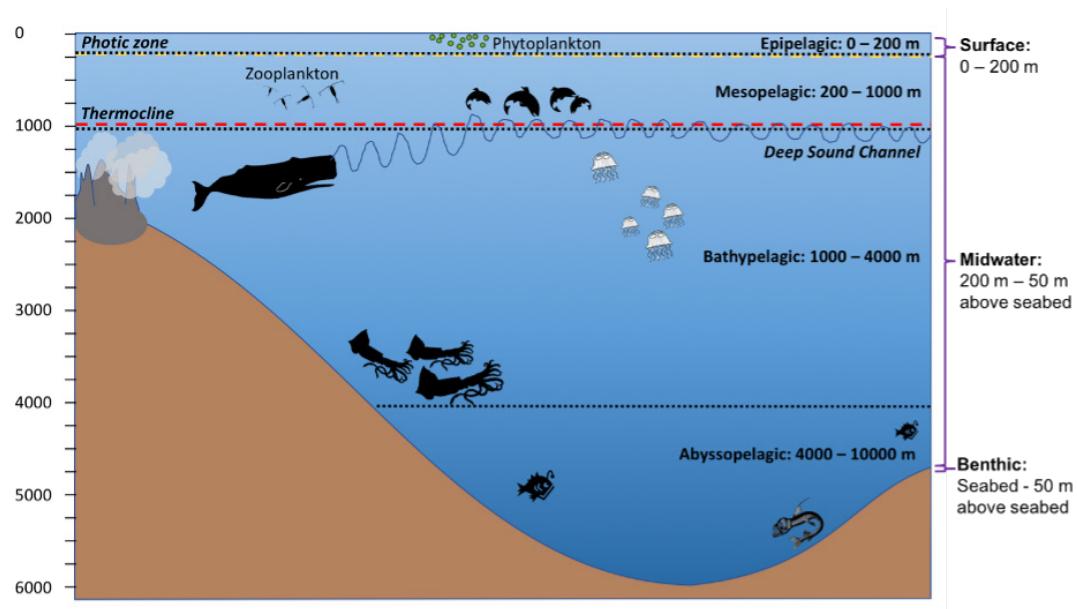
Within the benthic and combined surface and midwater environments, an attempt has been made to cover the range of biological components included within the EIS template of ISBA/25/C/WP.1, and the required aspects of their biology, such as regional distribution, temporal variation, trophic relationships, 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 sea floor 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, and where this is the case it 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, such as Patterns and processes of the ecosystems of the northern mid-Atlantic (MAR-ECO) and ECOMAR which focussed on the nMAR.

The information provided within this section focuses on studies conducted along the northern MAR between the

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



southern extent of the Icelandic ECS 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. This 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.

9. BIOLOGY OF THE SURFACE AND MID-WATER ENVIRONMENT

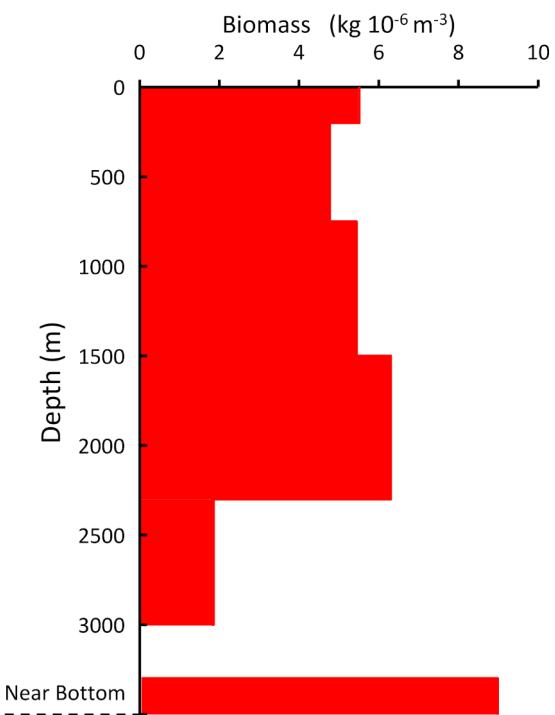
The MAR has a profound role in the circulation of the water masses in the North Atlantic Ocean (Bower et al., 2002a; Heger et al., 2008; Keller et al., 1975; Rossby, 1999; Søiland et al., 2008; Sy et al., 1992), as discussed in Chapter 6 on its physical oceanography. The complex hydrographic setting 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 ocean circulation, creating regions of high biomass that may arise from topographic influences on water circulation (St. Laurent and 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, subtropical 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 sea floor) 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. In addition to 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 2,000 m increase in depth (Priede, 2017) in both the benthic and pelagic realms. Over the MAR, there is an important difference in that there is a fish biomass maximum at 1,500-2,300 m, and within 200 m of

Figure 9.1 The vertical distribution of deep-pelagic biomass (wet weight) over the nMAR (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)



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, meaning fishes, sharks, cephalopods (squid and octopus) and crustaceans (shrimp); and air-breathing fauna made up of 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.

9.1 Regional distribution

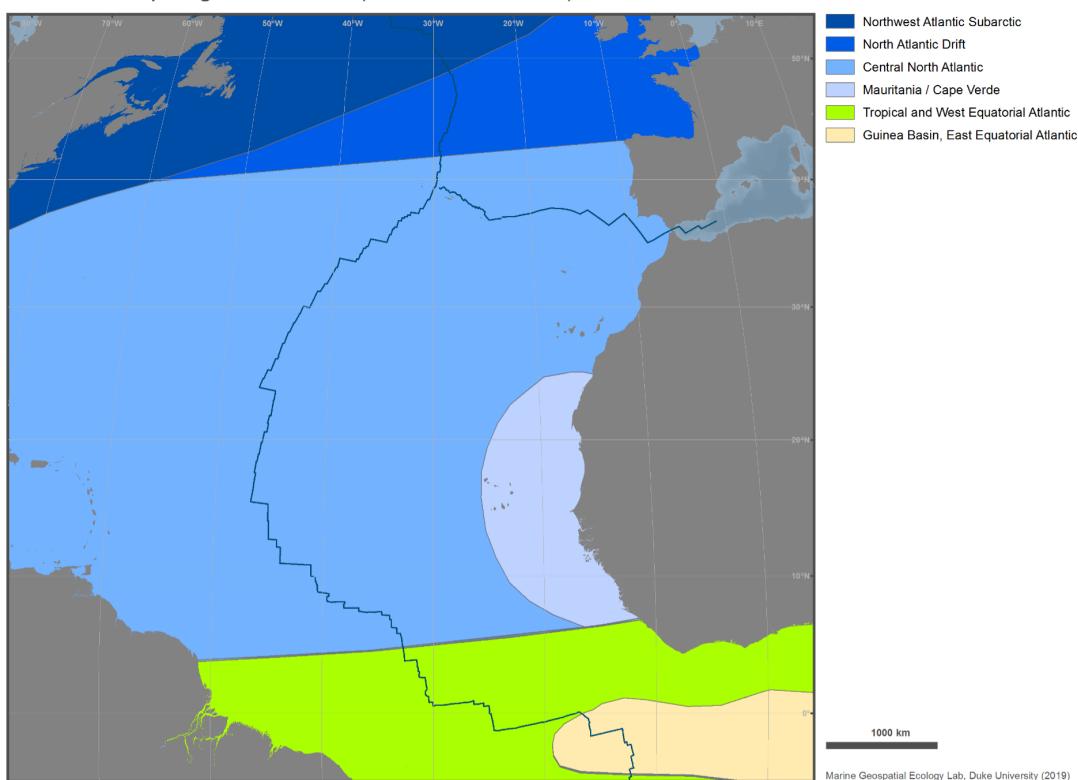
9.1.1 Biogeography

The pelagic environment of the nMAR under consideration (south of the Iceland ECS 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 CGFZ. Acoustic surveys of the MAR show a maximum of back scattering associated with the Sub-Polar front, the CGFZ 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 which 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 and 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

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 at <https://ran-s3.s3.amazonaws.com/isa.org.jm/s3fs-public/files/documents/datreport-19nov-lowres.pdf>)

Global Mesopelagic Provinces (Sutton et al. 2017)



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.

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 (Sternopychidae) 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 lanternfish *Benthosema glaciale*, accounting for over 90 per cent of the catch in large trawls (Sutton and Sigurðsson, 2008). The bristlemouth *Cyclothona microdon* is also important but has been less well sampled (Sutton et al., 2008).

Other myctophid lanternfish 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 rissoii*, *Serrivomer beanii*, *Paralepis coregonoides*, *Stomias boa ferox*, *Xenodermichthys copei*, *Argyropelecus hemigymnus*, *Maurolicus muelleri*, *Holtbyrnia anomala*, *Linophryne lucifer*, *Holtbyrnia macrops* and *Scopelogadus beanii* (Priede, 2017). Judkins and Haedrich (2018) identify a total of 140 fish species in the ecoregion with the species grouping *Benthosema glaciale*, *Bathylagus euryops*, *Lampanyctus macdonaldi*, *Cyclothona microdon*, *Maurolicus weitzmani*, *Borostomias antarcticus*, and *Melamphaes suborbitalis* considered to characterise the fauna having the highest geometric mean of the proportion of joint occurrences.

On the Reykjanes Ridge to the north of the CGFZ, Sutton and 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 *Cyclothona microdon* (Sutton et al., 2008). Other important myctophids

are *Protomyctophum arcticum* and *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 and 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 750–2,300 m depth dominated by three species; the bristlemouth *Cyclothona microdon*, deep-sea smelt *Bathylagus euryops* and sawtooth eel *Serrivomer beanii*, making up more than 50 per cent of the fish biomass. At depths of 200–750 m, the myctophid *Benthosema glaciale* makes up more than 25 per cent 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 (*Cyclothona microdon*).

The Central North Atlantic ecoregion is a vast area extending from north of the Azores to almost the equator in which Judkins and 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 and 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 lanternfish, 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 750–1,500 m depth, the pelagic assemblage was dominated by the bristlemouth *Cyclothona microdon*, loosejaw dragonfish *Malacosteus niger* and three large melamphaid species *Serrivomer beanii*, *Scopeloberyx robustus* and *Poromitra megalops*. At depths greater than 1,500 m there is a continuation of the same assemblage as found beneath the North Atlantic Drift comprising the bristlemouth *Cyclothona microdon*, the deep-sea smelt *Bathylagus euryops*, the sawtooth eel *Serrivomer beanii*, two melamphaid species *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 less than 1,500 m but relatively little species turnover at greater depths.

Judkins and 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 per cent 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 per cent 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 and 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* and *Astronesthes gudrunae* that rarely occur elsewhere, and species that also occur in the Central North Atlantic, the lanternfish *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 Kobylansky *et al.*,

(2010) the most abundant myctophid species in rank order are: *Ceratoscopelus warmingii*, *Bolinichthys photothorax*, *Lepidophanes gausi*, *Lepidophanes guentheri*, *Nannobrachium cuprarium* and *Lampanyctus photonotus*. The lightfish *Vinciguerria nimbaria*, bristlemouths *Cyclothona* sp., and hatchetfishes *Sternopyx 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 per cent of the total catch. Therefore, more than half the species present account for less than 1 per cent 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, but 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 in Table 9.1, are quite abundant, while 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 1,000 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* species (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 MAR. Abundance (N) and Biomass are totals obtained in the survey of the nMAR. 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)	Northwest Atlantic Subarctic	North Atlantic Drift	Central North Atlantic
Anguilliformes	Derichthyidae (longneck eels)	<i>Derichthys serpentinus</i>	16	466	Y	Y	Y
		<i>Nessorhamphus ingolfianus</i>	5	345	Y	Y	Y
	Nemichthyidae (snipe eels)	<i>Nemichthys scolopaceus</i>	9	449	Y	Y	Y
		<i>Avocettina infans</i>	1	33		Y	
	Serrivomeridae (sawtooth eels)	<i>Serrivomer beanii</i>	1062	78218	Y	Y	Y
		<i>Serrivomer lanceolatus</i>	8	526			Y
	Eurypharyngidae (gulper eels)	<i>Eurypharynx pelecanoides</i>	95	7396	Y	Y	Y
	Saccopharyngidae (swallowers)	<i>Saccopharynx ampullaceus</i>	4	757		Y	
Argentiniiformes	Opisthoproctidae (spookfishes)	<i>Opisthoproctus soleatus</i>	3	20		Y	Y
		<i>Bathylychnops exilis</i>	2	89		Y	Y
		<i>Opisthoproctus grimaldii</i>	2	2			Y
		<i>Dolichopteryx longipes</i>	1	7	Y		
	Microstomatidae (pencil smelts)	<i>Bathylagus eryops</i>	4543	190027	Y	Y	Y
		<i>Bathylagichthys greyae</i>	100	700			Y
		<i>Melanolagus bericoides</i>	15	308		Y	Y
		<i>Nansenia</i> sp.	14	886	Y	Y	Y
		<i>Dolicholagus longirostris</i>	4	40			Y
		<i>Nansenia tenera</i>	3	49		Y	Y
	<i>Nansenia atlantica</i>		2	61			Y

Order	Family	Species	Abundance (N)	Biomass wet weight (g)	Northwest Atlantic Subarctic	North Atlantic Drift	Central North Atlantic
		<i>Microstoma microstoma</i>	1	31			Y
	Platytroctidae (tubeshoulders)	<i>Maulisia microlepis</i>	931	96481	Y	Y	Y
		<i>Holtbyrnia anomala</i>	283	11545	Y	Y	Y
		<i>Normichthys operosus</i>	261	5089	Y	Y	Y
		<i>Holtbyrnia macrops</i>	32	970	Y	Y	Y
		<i>Searsia koefoedi</i>	10	410	Y	Y	Y
		<i>Sagamichthys schnakenbecki</i>	4	51	Y	Y	
		<i>Maulisia argipalla</i>	2	121		Y	Y
		<i>Maulisia mauli</i>	2	132	Y	Y	Y
	Bathylaconidae	<i>Herwigia krefftii</i>	5	1167			Y
		<i>Bathyaco nigricans</i>	2	375			Y
	Alepocephalidae (slickheads)	<i>Xenodermichthys copei</i>	43	1001	Y	Y	Y
		<i>Bajacalifornia megalops</i>	35	2461	Y	Y	Y
		<i>Bathyroctes microlepis</i>	8	1060		Y	Y
		<i>Mirognathus normani</i>	3	55		Y	
		<i>Bathyprion danae</i>	2	119		Y	Y
		<i>Einara macrolepis</i>	2	162			Y
		<i>Photostylylus pycnopterus</i>	2	18	Y		
		<i>Bathyroctes macrolepis</i>	1	33		Y	
		<i>Rouleina attrita</i>	1	73.3	Y		
Stomiiformes	Gonostomatidae (bristlemouths)	<i>Cyclothona microdon</i>	7430	6557	Y	Y	Y
		<i>Sigmops bathophilum</i>	564	10939	Y	Y	Y

Order	Family	Species	Abundance (N)	Biomass wet weight (g)	Northwest Atlantic Subarctic	North Atlantic Drift	Central North Atlantic
		<i>Sigmops elongatus</i>	112	1973	Y	Y	Y
		<i>Cyclothona braueri</i>	82	34	Y	Y	Y
		<i>Bonapartia pedaliota</i>	71	151		Y	Y
		<i>Cyclothona pallida</i>	53	39	Y	Y	Y
		<i>Margrethia obtusirostra</i>	33	84			Y
		<i>Gonostoma denudatum</i>	18	207			Y
		<i>Cyclothona pseudopallida</i>	10	3	Y	Y	Y
	Sternopychidae (hatchetfish & pearlsides)	<i>Maurolicus muelleri</i>	3379	4470	Y	Y	Y
		<i>Argyropelecus hemigymnus</i>	329	246	Y	Y	Y
		<i>Sternopyx diaphana</i>	261	473		Y	Y
		<i>Argyropelecus aculeatus</i>	116	394	Y	Y	Y
		<i>Argyropelecus olfersii</i>	25	144	Y	Y	
		<i>Sternopyx pseudobscura</i>	14	36	Y	Y	Y
		<i>Valenciennellus tripunctulatus</i>	6	1			Y
		<i>Argyropelecus gigas</i>	1	2			Y
	Phosichthyidae (lightfishes)	<i>Vinciguerria poweriae</i>	281	190		Y	Y
		<i>Ichthyococcus ovatus</i>	13	15		Y	Y
		<i>Vinciguerria attenuata</i>	5	3			Y
		<i>Pollichthys mauli</i>	2	1		Y	Y
		<i>Chauliodus sloani</i>	897	21701	Y	Y	Y
		<i>Stomias boa ferox</i>	256	5963	Y	Y	Y

Order	Family	Species	Abundance (N)	Biomass wet weight (g)	Northwest Atlantic Subarctic	North Atlantic Drift	Central North Atlantic
Perciformes	Stomiidae	<i>Malacosteus niger</i>	235	9453	Y	Y	Y
		<i>Borostomias antarcticus</i>	139	11496	Y	Y	Y
		<i>Melanostomias bartonbeani</i>	11	381		Y	Y
		<i>Photostomias guernei</i>	8	40			Y
		<i>Pachystomias microdon</i>	5	189		Y	Y
		<i>Astronesthes niger</i>	4	30			Y
		<i>Flagellostomias boureei</i>	4	134		Y	Y
		<i>Neonesthes capensis</i>	4	65	Y	Y	Y
		<i>Leptostomias sp.</i>	2	64		Y	Y
		<i>Aristostomias tittmanni</i>	1	9			Y
		<i>Astronesthes gemmifer</i>	1	12			Y
		<i>Bathophilus longipinnis</i>	1	3			Y
		<i>Bathophilus vallanti</i>	1	3			Y
		<i>Melanostomias macrophotus</i>	1	12			Y
		<i>Photonectes margarita</i>	1	40			Y
		<i>Trigonalampa miriceps</i>	1	393	Y		
Aulopiformes	Notosudidae (waryfishes)	<i>Scopelosaurus lepidus</i>	6	356	Y	Y	
		<i>Ahliesaurus berryi</i>	2	30			Y
		<i>Scopelosaurus schmidtii</i>	1	3			Y
	Scopelarchidae (pearleyes)	<i>Benthalbella infans</i>	4	48		Y	Y
		<i>Scopelarchus analis</i>	2	9			Y
		<i>Scopelarchus guentheri</i>	1	4			Y

Order	Family	Species	Abundance (N)	Biomass wet weight (g)	Northwest Atlantic Subarctic	North Atlantic Drift	Central North Atlantic
Perciformes	Evermannellidae (sabretooth fishes)	<i>Evermannella balbo</i>	11	91	Y	Y	
	Alepisauridae (lancetfishes)	<i>Alepisaurus bre-virostris</i>	8	137		Y	Y
	Paralepididae (barracudinas)	<i>Omosudis lowei</i>	1	15			Y
		<i>Lestidiops sphyrenoides</i>	81	202		Y	Y
	Carangidae	<i>Arctozenus risso</i>	65	1048	Y	Y	
		<i>Anopterus pharao</i>	27	5886	Y	Y	Y
		<i>Lestidiops jay-akari</i>	14	143		Y	Y
		<i>Magnisudis atlantica</i>	8	60		Y	Y
		<i>Paralepis brevi-rostris</i>	5	44			Y
		<i>Paralepis core-gonooides</i>	2	19.7	Y	Y	Y
Myctophiformes	Myctophidae (lanternfishes)	<i>Benthosema glaciale</i>	16640	24503	Y	Y	Y
		<i>Lampanyctus macdonaldi</i>	4095	101685	Y	Y	Y
		<i>Notoscopelus kroyeri</i>	3630	28919	Y	Y	Y
		<i>Myctophum punctatum</i>	2418	11217	Y	Y	Y
		<i>Protomyctophum arcticum</i>	1289	1246	Y	Y	Y
		<i>Lobianchia do-fleini</i>	406	355		Y	Y
		<i>Diaphus rafinesquii</i>	315	711		Y	Y
		<i>Hygophum hy-gomii</i>	309	629			Y
		<i>Diaphus holti</i>	281	472			Y
		<i>Electrona risso</i>	237	789	Y	Y	Y
		<i>Lobianchia ge-mellarii</i>	216	1708		Y	Y
		<i>Hygophum ben-otti</i>	214	310			Y

Order	Family	Species	Abundance (N)	Biomass wet weight (g)	Northwest Atlantic Subarctic	North Atlantic Drift	Central North Atlantic
		<i>Symbolophorus veranyi</i>	191	672		Y	Y
		<i>Notoscopelus bolini</i>	145	736		Y	Y
		<i>Nannobrachium atrum</i>	139	967	Y	Y	Y
		<i>Lampanyctus crocodilus</i>	124	926	Y	Y	Y
		<i>Ceratoscopelus maderensis</i>	102	270		Y	Y
		<i>Lampadена speculigera</i>	94	2387	Y	Y	Y
		<i>Bolinichthys indicus</i>	52	66			Y
		<i>Bolinichthys supralateralis</i>	34	171	Y	Y	Y
		<i>Lampanyctus intricarius</i>	34	360	Y	Y	Y
		<i>Lampanyctus pusillus</i>	32	50			Y
		<i>Lampadena anomala</i>	30	844			Y
		<i>Diaphus metopoclampus</i>	28	111			Y
		<i>Diaphus effulgens</i>	18	201		Y	Y
		<i>Lampanyctus photonotus</i>	15	67			Y
		<i>Lampadena urophaeos atlantica</i>	14	226		Y	Y
		<i>Gonichthysocco</i>	13	12			Y
		<i>Lampanyctus festivus</i>	10	42			Y
		<i>Hygophum reinhardti</i>	9	7			Y
		<i>Lampadena chavesi</i>	7	28			Y
		<i>Diaphus mollis</i>	5	6			Y
		<i>Lepidophanes guentheri</i>	4	6			Y
		<i>Nannobrachium lineatum</i>	3	25			Y

Order	Family	Species	Abundance (N)	Biomass wet weight (g)	Northwest Atlantic Subarctic	North Atlantic Drift	Central North Atlantic
		<i>Taaningichthys bathyphilus</i>	3	7		Y	Y
		<i>Notolychnus valdiviae</i>	2	0		Y	Y
		<i>Benthosema suborbitale</i>	1	2			Y
		<i>Ceratoscopelus warmingii</i>	1	1			Y
		<i>Diaphus bertelsenii</i>	1	14			Y
		<i>Diogenichthys atlanticus</i>	1	2			Y
		<i>Lepidophanes gaussi</i>	1	4			Y
		<i>Loweina interrupta</i>	1	7			Y
		<i>Nannobrachium achirus</i>	1	8	Y		
		<i>Nannobrachium cuprarium</i>	1	1			Y
	Gadiformes	Macrouridae (grenadiers, rat-tails)	<i>Coryphaenoides rupestris</i>	12	92	Y	Y
			<i>Bathygadus melanobranchus</i>	3	6		Y
			<i>Odontomacrus murrayi</i>	1	4		Y
	Moridae (deep-sea cods)		<i>Halargyreus johnsonii</i>	1	35	Y	
	Melanonidae (pelagic cods)		<i>Melanonus zugmayeri</i>	12	56	Y	Y
	Merlucciidae (hakes)		<i>Lyconus brachycolus</i>	1	62		Y
	Ophidiiformes	Ophidiidae (cusk eels)	<i>Brotulotaenia crassa</i>	2	914		Y
Lophiiformes (Anglerfishes)	Melanocetidae (black sea devils)		<i>Melanocetus johnsonii</i>	3	333	Y	Y
	Oneirodidae (dreamers)		<i>Lophodolos acanthognathus</i>	10	105	Y	Y
			<i>Leptacanthichthys gracilispinis</i>	4	24		Y

Order	Family	Species	Abundance (N)	Biomass wet weight (g)	Northwest Atlantic Subarctic	North Atlantic Drift	Central North Atlantic
Lophiiformes		<i>Chaenophryne draco</i>	1	225	Y		
		<i>Danaphryne nigrofilis</i>	1	54	Y		
		<i>Dolopichthys longicornis</i>	1	4			Y
		<i>Microlophichthys microlophus</i>	1	70		Y	
		<i>Oneirodes eschrichtii</i>	1	156		Y	
		<i>Oneirodes macrosteus</i>	1	24			Y
		<i>Phyllorhinichthys micractis</i>	1	33			Y
		<i>Ceratias holboelli</i>	2	98		Y	Y
Gymnophioniformes		<i>Cryptopsaras couesi</i>	1	99		Y	
		<i>Gigantactis vanhoeffeni</i>	1	166		Y	
		<i>Linophrynidae</i> (leftvent seadevils)	<i>Linophryne macrodon</i>	1	1		Y
		<i>Melamphaidae</i> (bigscale fishes)	<i>Scopelogadus beanii</i>	2152	47264	Y	Y
			<i>Melamphaes microps</i>	255	5668	Y	Y
			<i>Scopeloberyx robustus</i>	239	1159	Y	Y
			<i>Poromitra crassiceps</i>	215	9456	Y	Y
			<i>Scopelogadus m. mizolepis</i>	96	336		Y
Stephanoberyciformes			<i>Poromitra megalops</i>	82	325	Y	Y
			<i>Poromitra capito</i>	58	670		Y
			<i>Scopeloberyx opisthopterus</i>	11	7	Y	Y
			<i>Melamphaes suborbitalis</i>	7	102	Y	Y

Order	Family	Species	Abundance (N)	Biomass wet weight (g)	Northwest Atlantic Subarctic	North Atlantic Drift	Central North Atlantic
		<i>Melamphaes typhlops</i>	1	1			Y
	Rondeletiidae (redmouth whalefishes)	<i>Rondeletia loricata</i>	5	84		Y	Y
	Cetomimidae (flabby whalefishes)	<i>Gyrinomimus meyersi</i>	3	260		Y	
		<i>Cetomimus</i> sp.	2	101	Y	Y	
		<i>Cetostoma regani</i>	1	15			Y
		<i>Proctichthys kreffti</i>	1	73		Y	
	Megalomycteridae (bignose fishes)	<i>Ataxolepis apus</i>	1	0			Y
Beryciformes	Anoplogastridae (fangtooth)	<i>Anoplogaster cornuta</i>	26	2767	Y	Y	Y
	Diretmidae (spinyfins)	<i>Diretmus argenteus</i>	9	191		Y	Y
Gasterosteiformes	Syngnathidae (pipefishes)	<i>Entelurusaequoreus</i>	160	775	Y	Y	
Scorpaeniformes	Scorpaenidae (scorpionfishes)	<i>Sebastesmentella</i>	4	8014	Y		
		<i>Sebastes</i> sp.	4	3264	Y		
	Liparidae (snailfishes)	<i>Psednos</i> sp.	1	1		Y	
Perciformes	Percichthyidae (oceanic basslets)	<i>Howella brodiei</i>	18	139		Y	Y
	Epigonidae (deepwater cardinal fish)	<i>Epigonus constanciae</i>	1	1			Y
		<i>Microichthys coccoi</i>	1	0			Y
	Carangidae (jacks)	<i>Trachurus picturatus</i>	1	16			Y
	Caristiidae (manefishes, veilfins)	<i>Caristius madeirensis</i>	1	34		Y	
		<i>Platyberyx opalescens</i>	1	319		Y	

Order	Family	Species	Abundance (N)	Biomass wet weight (g)	Northwest Atlantic Subarctic	North Atlantic Drift	Central North Atlantic
	Zoarcidae (eelpouts)	<i>Melanostigma atlanticum</i>	5	18	Y	Y	
	Anarhichadidae (wolffishes)	<i>Anarhichas minor</i>	1	1056		Y	
	Chiasmodontidae (swallowers)	<i>Chiasmodon niger</i>	91	1838	Y	Y	Y
		<i>Pseudoscopelus altipinnis</i>	9	266			Y
		<i>Kali macrodon</i>	5	413		Y	Y
		<i>Dysalotus alcocki</i>	4	130	Y	Y	Y
		<i>Kali indica</i>	4	270		Y	
		<i>Kali macrurus</i>	2	214		Y	Y
		<i>Pseudoscopelus obtusifrons</i>	1	68			Y
		<i>Pseudoscopelus scutatus</i>	2	35			Y
		<i>Pseudoscopelus sp.1</i>	1	68			Y
	Gempylidae (snake mackerels)	<i>Diplospinus multistriatus</i>	1	4			Y
	Trichiuridae (hairtails)	<i>Benthodesmus elongatus</i>	1	13		Y	
		<i>Lepidopus caudatus</i>	1	4			Y
	Centrolophidae (medusafishes)	<i>Schedophilus medusophagus</i>	1	639		Y	
	Nomeidae (driftfishes)	<i>Cubiceps gracilis</i>	99	1616		Y	Y
	Tetragonuridae (squaretails)	<i>Tetragonurus cuvieri</i>	9	155			Y
	Caproidae (boarfishes)	<i>Capros aper</i>	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 to 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), which 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 and 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 stenorhynchus* (Armhook squid), followed by *Teuthowenia megalops* (Glass squid) and small numbers of *Chiroteuthis veranyi* (Long-armed squid). Seven other wide-ranging species of squid and one octopus were also recorded in 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 *Brachioleuthis 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 the mid-water not favouring niche separation and a high number of species.

Table 9.2 Pelagic cephalopods of the MAR. (After Vecchione et al., 2010a)

Order	Family	Species	Northwest Atlantic Sub-Arctic	North Atlantic Drift	Central North Atlantic
Sepioidea	Sepiolidae	<i>Heteroteuthis dispar</i> (Odd bobtail squid)		Y	Y
Oegopsida	Bathyteuthidae	<i>Bathyteuthis</i> sp. (Deep-sea squid)	Y	Y	Y
	Brachioteuthidae	<i>Brachioteuthis beanii</i>		Y	Y
	Chiroteuthidae	<i>Chiroteuthis mega</i> <i>Chiroteuthis veranyi</i> (Long-armed squid)			Y
		<i>Grimalditeuthis bonplandi</i>			Y
		<i>Planctoteuthis levimana</i>	Y	Y	Y
	Chtenopterygidae	<i>Chtenopteryx sicula</i> (Comb-finned squid)			Y
	Cranchiidae	<i>Bathothauma lyromma</i> (Lyre cranch squid)			Y
		<i>Galiteuthis armata</i> (Armed cranch squid)	Y	Y	Y
		<i>Helicocranchia pfefferi</i> (Banded piglet squid)		Y	Y
		<i>Leachia atlantica</i> (Glass squid)			Y
		<i>Taonius pavo</i> (Glass squid)	Y	Y	Y
		<i>Teuthowenia megalops</i> (Glass squid)	Y	Y	Y

Order	Family	Species	Northwest Atlantic Sub-Arctic	North Atlantic Drift	Central North Atlantic
	Cycloteuthidae	<i>Discoteuthis laciniosa</i>			Y
	Enoplateuthidae	<i>Abraaliopsis morisii</i>			Y
	Gonatidae	<i>Gonatus steenstrupi</i> (Armhook squid)	Y	Y	
	Histioteuthidae	<i>Histioteuthis bonnellii</i> (Umbrella squid) <i>Histioteuthis corona</i> (Cock-eyed squid)	Y	Y	Y
		<i>Histioteuthis meleagroteuthis</i> (Cock-eyed squid)			Y
		<i>Histioteuthis reversa</i> (Elongate jewel squid)		Y	Y
	Joubiniteuthidae	<i>Joubiniteuthis portieri</i> (Joubin's squid)			Y
	Lepidoteuthidae	<i>Pholidoteuthis massyae</i> (Coffeebean scaled squid)			
	Lycoteuthidae	<i>Lampadioteuthis megaleia</i> (Firefly squid)		Y	Y
	Magnapinnidae	<i>Magnapinna</i> sp.			Y
	Mastigoteuthidae	<i>Mastigoteuthis agassizii</i> (Whiplash squid) <i>Mastigoteuthis horti</i> (Whiplash squid)	Y	Y	Y
		<i>Mastigoteuthis magna</i> (Whiplash squid)			Y

Order	Family	Species	Northwest Atlantic Sub-Arctic	North Atlantic Drift	Central North Atlantic
Cephalopoda	Octopoteuthidae	<i>Octopoteuthis sicula</i> (Octopus squid)		Y	Y
	Ommastrephidae	<i>Todarodes sagittatus</i> (Flying squid)	Y		Y
	Onychoteuthidae	<i>Ancistroteuthis lichtensteinii</i> (Angel squid)			Y
		<i>Onychoteuthis</i> sp. (Club hook squid)			Y
	Pro-machoteuthidae	<i>Promachoteuthis sloani</i>			
	Pyroteuthidae	<i>Pterygioteuthis gemmate</i> (Enope squid)			Y
		<i>Pyroteuthis marginifera</i> (Jewel enope squid)			Y
	Stauroteuthidae	<i>Stauroteuthis syrtensis</i> (Glowing sucker octopus)	Y	Y	Y
	Alloposidea	<i>Haliphron atlanticus</i> (Seven-armed octopus)		Y	Y
	Bolitaenidae	<i>Bolitaena pygmaea</i>			Y
		<i>Japetella diaphana</i>			Y
	Ocythoidae	<i>Ocythoe tuberculata</i> (Football octopus)		Y	Y
Vampyroteuthidae	Vampyroteuthidae	<i>Vampyroteuthis infernalis</i> (Vampire squid)	Y	Y	Y

Table 9.3 Pelagic cephalopods of the Central North Atlantic Ecoregion, MAR

Central North Atlantic Ecoregion, not found further North	Central North Atlantic & North Atlantic Drift Ecoregions
<i>Abraaliopsis morisii</i>	<i>Bathyteuthis abyssicola</i>
<i>Ancistroteuthis lichtensteinii</i>	<i>Brachiotheuthis beanii</i>
<i>Bolitaena pygmaea</i>	<i>Haliphron atlanticus</i>
<i>Chiroteuthis mega</i>	<i>Helicocranchia pfefferi</i>
<i>Chtenopteryx sicula</i>	<i>Heteroteuthis dispar</i>
<i>Grimalditeuthis bonplandi</i>	<i>Histioteuthis reversa</i>
<i>Histioteuthis corona</i>	<i>Lampadioteuthis megaleia</i>
<i>Histioteuthis meleagroteuthis</i>	<i>Octopoteuthis sicula</i>
<i>Japetella diaphana</i>	
<i>Joubiniteuthis portieri</i>	
<i>Leachia atlantica</i>	
<i>Mastigoteuthis hjorti</i>	
<i>Mastigoteuthis magna</i>	
<i>Ocythoe tuberculata</i>	
<i>Pholidoteuthis massyae</i>	
<i>Pterygioteuthis gemmata</i>	
<i>Pyroteuthis margaritifera</i>	

9.1.2.3 Shrimps

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, *Parapasphe Sulcatifrons* and *Hymenodora gracilis*, according to Judkins and 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 and 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 and 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). 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			
		North/ South Atlantic	Atlantic/ Global	North West Atlantic Sub-Arctic	Central North Atlantic	Tropical & West Equatorial	
Suborder Dendrobranchiata (branching gills)							
Benthesi-cymidae	<i>Altelatipes falkenhau-gae</i>	N		A			
	<i>Bentheogenennema in-termedia</i>	N	S	G			
	<i>Bentheogenennema</i> sp.	S		-			
	<i>Gennadas brevirostris</i>	S		G			
	<i>Gennadas capensis</i>	S	G			Y	
	<i>Gennadas elegans</i>	N		A			
	<i>Gennadas gilchristi</i>	S	A				
	<i>Gennadas parvus</i>	S	G				
	<i>Gennadas scutatus</i>	S	G			Y	
	<i>Gennadas talismani</i>	S	A			Y	
	<i>Gennadas tinayrei</i>	N	S	G		Y	
	<i>Gennadas valens</i>	N	S	A		Y	
Penaeidae	<i>Funchalia villosa</i>	N	S	G		Y	
	<i>Funchalia woodwardia</i>	N	S	G		Y	
Sergestidae	<i>Deosergestes corniculum</i>	N	S	A			
	<i>Deosergestes hensenii</i>	N	S	A			
	<i>Parasergestes armatus</i>	N	S	G			
	<i>Petalidium</i> sp.		S	-			
	<i>Sergestes arcticus</i>	N		G			
	<i>Sergestes atlanticus</i>	N	S	G		Y	
	<i>Sergestes pectinatus</i>	N		G			
	<i>Sergestes sargassi</i>	N		G			

Family	Species	Regional/Global distribution	North Atlantic Ecoregion preference			
		North/ South Atlantic	Atlantic/ Global	North West Atlantic Sub-Arctic	Central North Atlantic	Tropical & West Equatorial
	<i>Sergestes vigilax</i>	N	G			
	<i>Sergia creber</i>		S	G		
	<i>Sergia grandis</i>	N	S	A		
	<i>Sergia japonica</i>	N		G		
	<i>Sergia laminata</i>		S	A		Y
	<i>Sergia robusta</i>	N	S	A		
	<i>Sergia splendens</i>	N	S	G		
	<i>Sergia tenuiremis</i>	N	S	A		
Suborder Pleocyemata, Infraorder Caridea (true shrimps)						
Nematocar-	<i>Nematocarcinus ensifer</i>	N		G		
cinidae	<i>Nematocarcinus exilis</i>	N		A		
Acanthephy-	<i>Acanthephyra acanthi-</i>		S	A		Y
ridae	<i>telsonis</i>					
	<i>Acanthephyra brevi-</i>	N		G		
	<i>rostris</i>					
	<i>Acanthephyra curtiro-</i>	N	S	G		Y
	<i>stris</i>					
	<i>Acanthephyra gracili-</i>	N		A		
	<i>pes</i>					
	<i>Acanthephyra pelagica</i>	N	S	G		
	<i>Acanthephyra pur-</i>	N		A		Y
	<i>purea</i>					
	<i>Acanthephyra quadrispinosa</i>		S	A		
	<i>Acanthephyra stylo-</i>		S	G		
	<i>rostratis</i>					
	<i>Ephyrina benedicti</i>	N	S	G		
	<i>Ephyrina bifida</i>	N		A		
	<i>Ephyrina figureirai</i>	N		A		
	<i>Ephyrina ombango</i>	N		G		
	<i>Hymenodora gracilis</i>		S	G	Y	
	<i>Meningodora compsa</i>	N		A		
	<i>Meningodora miccylla</i>	N		G		
	<i>Meningodora mollis</i>	N		G		
	<i>Meningodora vesca</i>	N	S	G		
	<i>Notostomus elegans</i>	N	S	G		Y
	<i>Notostomus gibbosus</i>	N	S	G		

Family	Species	Regional/Global distribution		North Atlantic Ecoregion preference			
		North/ South Atlantic	Atlantic/ Global	North West Atlantic Sub-Arctic	Central North Atlantic	Tropical & West Equatorial	
	<i>Notostomus robustus</i>	N	S	A			
Oplophoridae	<i>Oplophorus novazelandiae</i>		S	G			
	<i>Oplophorus spinosus</i>	N	S	G		Y	
	<i>Systellaspis braueri</i>	N		A			
	<i>Systellaspis cristata</i>	N	S	G			
	<i>Systellaspis debilis</i>	N	S	G		Y	
	<i>Systellaspis pellucida</i>	N	S	G			
Pandalidae	<i>Stylopandalus richardi</i>	N	S	G		Y	
Pasiphaeidae	<i>Eupasiphae gilesi</i>	N		G			
	<i>Parapasiphae sulcifrons</i>	N	S	G	Y		
	<i>Pasiphaea ecarina</i>	N		A		y	
	<i>Pasiphaea hoplocera</i>	N		G			
	<i>Pasiphaea multidentata</i>	N		A			
	<i>Pasiphaea tarda</i>	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 chondrichthyan (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 1,000 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 MAR region in the equatorial Atlantic over the

Romanche transform fault and south-west of Cabo Verde. Juvenile habitats also occur west and north of the Azores.

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 south-central 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 International Union for Conservation of Nature (IUCN).

In 2012, the International Commission for the Conservation of Atlantic Tunas

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)

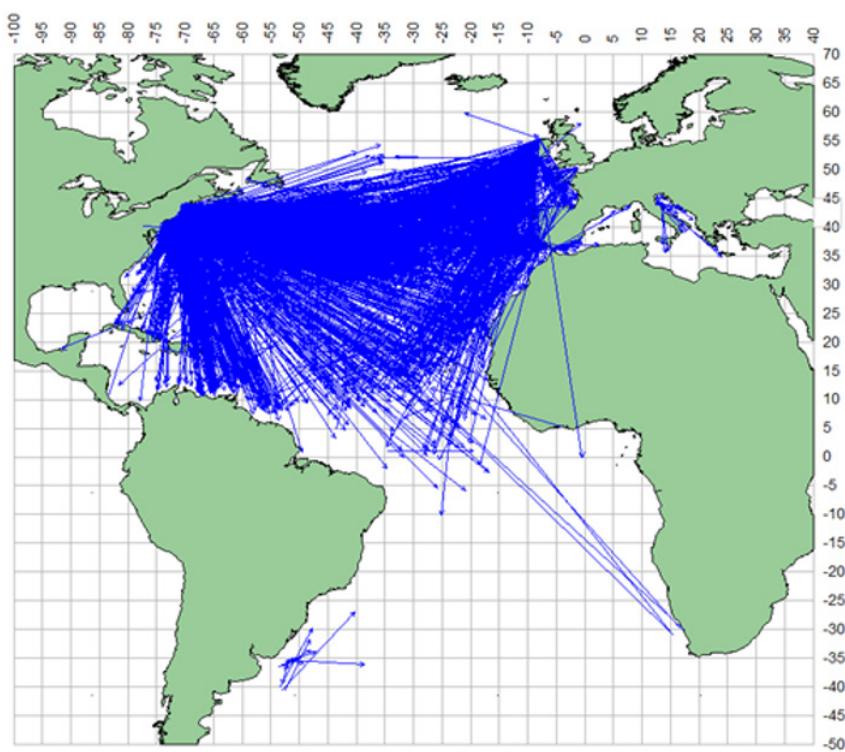
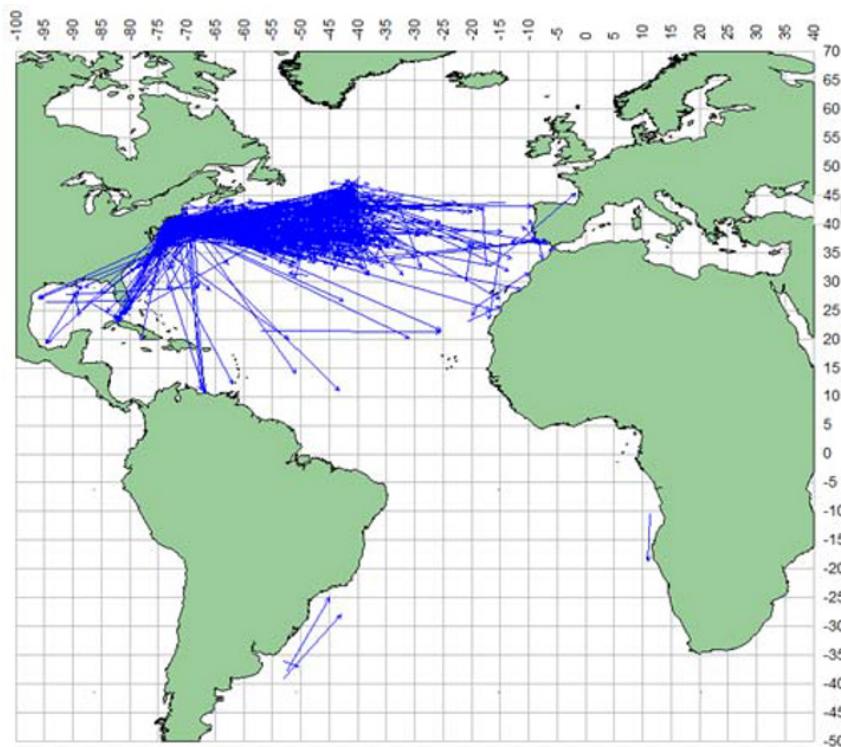


Figure 9.4 Tag and release distributions for *Isurus oxyrinchus* (Shortfin Mako) in the Atlantic Ocean. Lines describe straight displacement between release and recovery locations. (Reproduced from ICCAT, 2013)

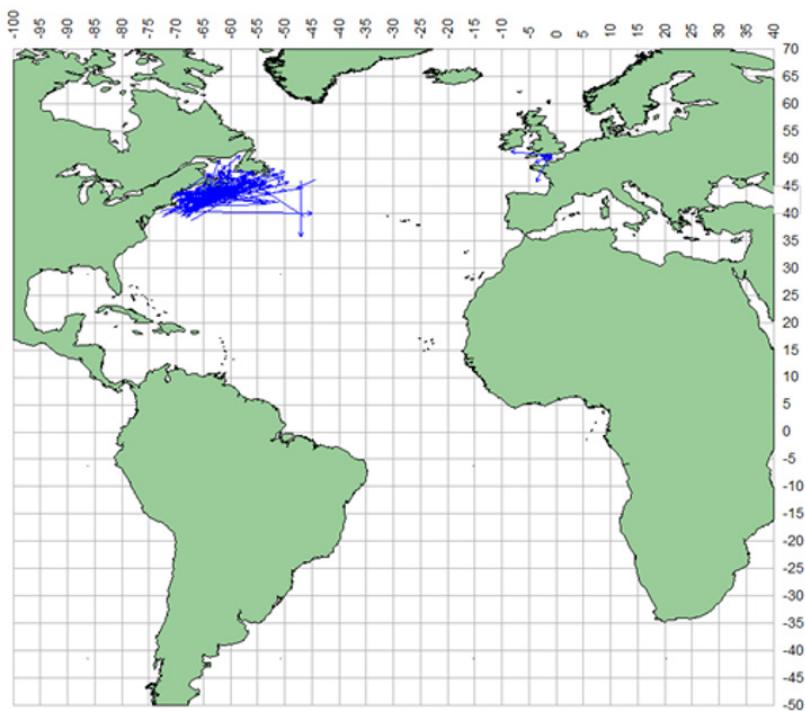


(ICCAT) collated 1203 tags recaptured since 1962 (largely from tags deployed off the northeast coast of the United States). The 2012 ICCAT report noted that most movement of *I. oxyrinchus* was between South and East within the Northwest Atlantic, with few individuals captured below 20°N and none captured South of 5°N. This is despite individuals being reported to travel considerable distances of up to 3,400 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 northeastern United States and Canada (Grand Banks) south into the Gulf Stream and Sargasso Sea to over-winter.

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 subpopulations (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

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



depths down to 1,600 m, they rarely occurred below 700 m.

9.1.3.1.4 *Carcharodon carcharias* (white shark)

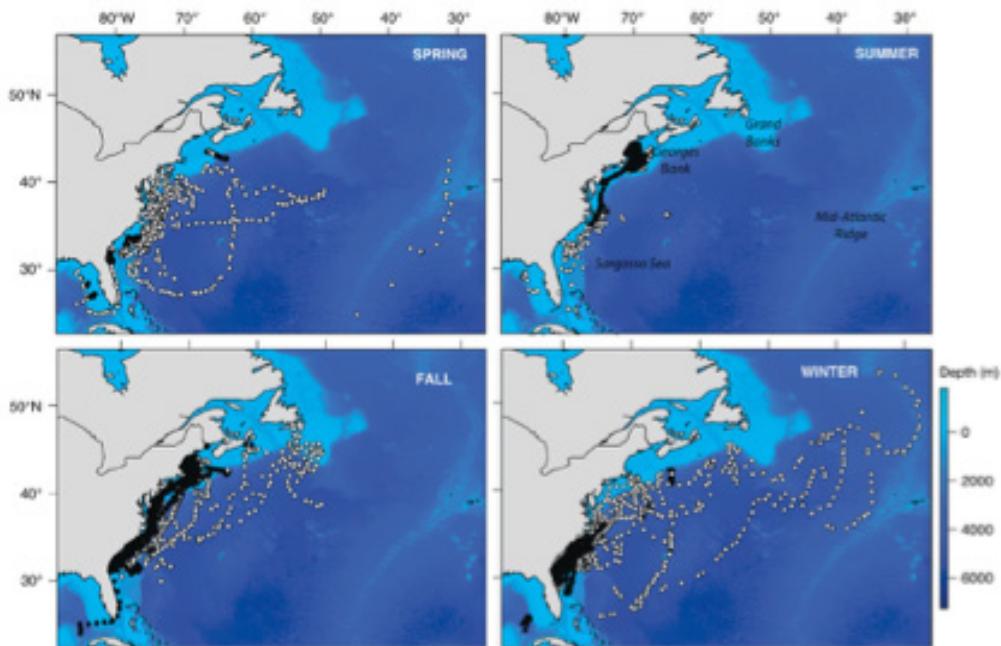
Despite being one of the better-known and more charismatic shark species, and despite numerous studies in the eastern Pacific Ocean, little is known about the distribution of *Carcharodon carcharias* (white shark) in the North Atlantic. Historically considered an epipelagic and neritic species with seasonal, 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 1,128 m and appeared to target specific mesopelagic depths to forage. *Carcharodon carcharias* are globally considered vulnerable by IUCN, though this listing has not been updated in a decade (IUCN, 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

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)



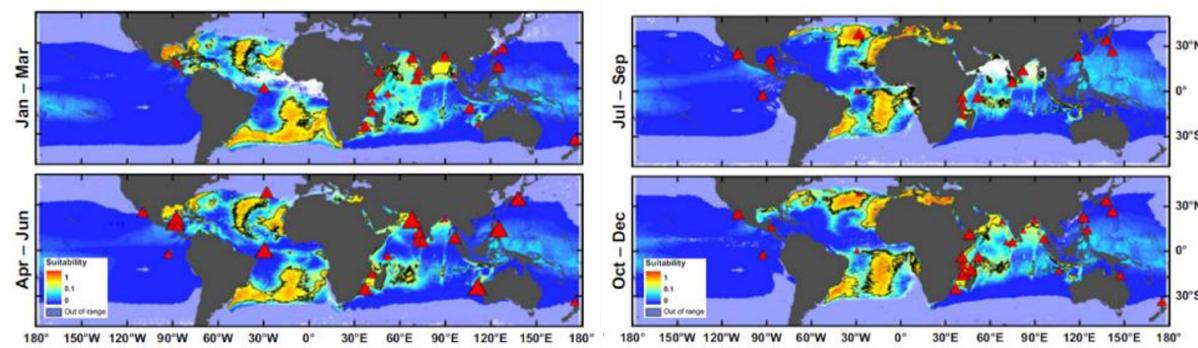
tagging site has not been demonstrated. During these horizontal travels, *R. typus* spend the majority of their time in the epipelagic zone, but have irregular deep dives to greater than 1,000 m.

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 and 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 and 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).

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, as observed by Doherty et al. (2017). These authors identified round-trip migrations to over-winter in these areas and then return to coastal United Kingdom and Irish waters during the spring and summer. Previously, *C. maximus* had been assumed to remain in temperate continental shelf areas, but new evidence over the last decade

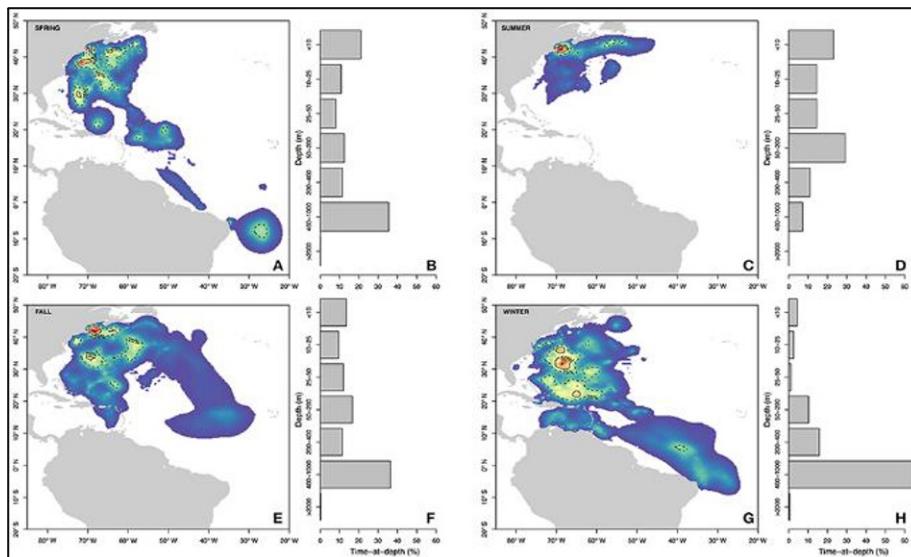
Figure 9.7 Global predictions of current seasonal habitat suitability for *Rhincodon typus* (whale sharks). Prediction maps generated from generalized linear mixed-effects models fit with the sightings and effort data collected by tuna purse-seine fisheries. Where environmental inputs fell outside the environmental space used for the original statistical fit, results are shown as “out of range” on 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 lines delineate areas where habitat suitability of greater than 0.1 was predicted. (Adapted from Sequeira et al., 2014)



indicates that 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 1,500 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 per cent 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

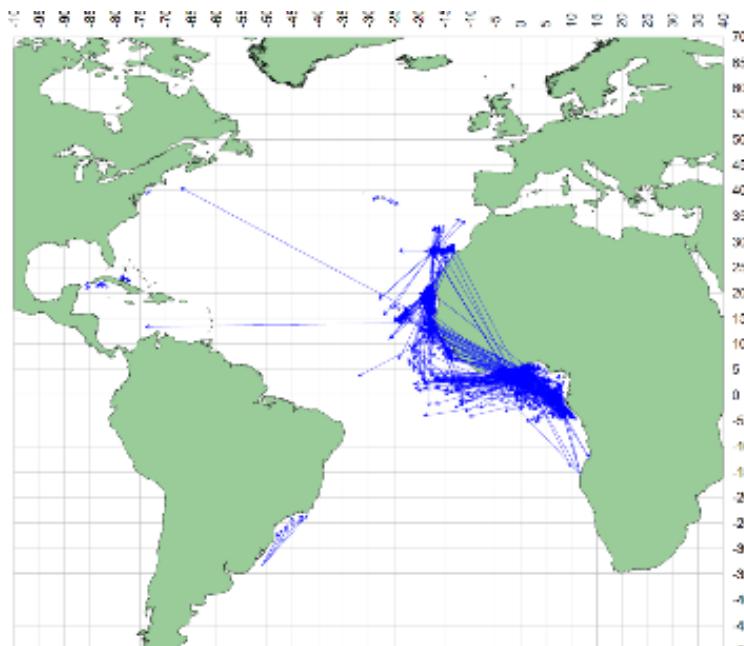
The pelagic environment of the northern MAR provides habitat for multiple commercially important tuna species: *Katsuwonus pelamis* (skipjack tuna), *Thunnus albacares* (yellowfin tuna), *Thunnus obesus* (bigeye tuna), *Thunnus alalunga* (albacore) and *Thunnus thynnus* (Atlantic bluefin tuna), alongside *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 into two stocks: 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 show quite limited horizontal movement (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 show that *K. pelamis* display 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. Lines describe straight displacement between release and recovery locations. (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 and Nauen, 1983). *Thunnus albacares* can attain a maximum size of more than 200 cm, with a life span of approximately 7 years (Diahia et al., 2016; Lessa and 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 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 and Soubrier, 1996). In general, juvenile fish move along the African coastal waters, perform transatlantic migration when pre-adults, and return to the eastern Atlantic at adult stage (Bard and Hervé, 1994; Fonteneau and 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).

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 and Nauen, 1983). *Thunnus obesus* is one of the largest tuna species,

Figure 9.10 Horizontal movements of 1,711 tagged and recaptured *Thunnus albacares* (yellowfin tuna). Lines describe straight displacement between release and recovery locations. (Reproduced from ICCAT, 2006)

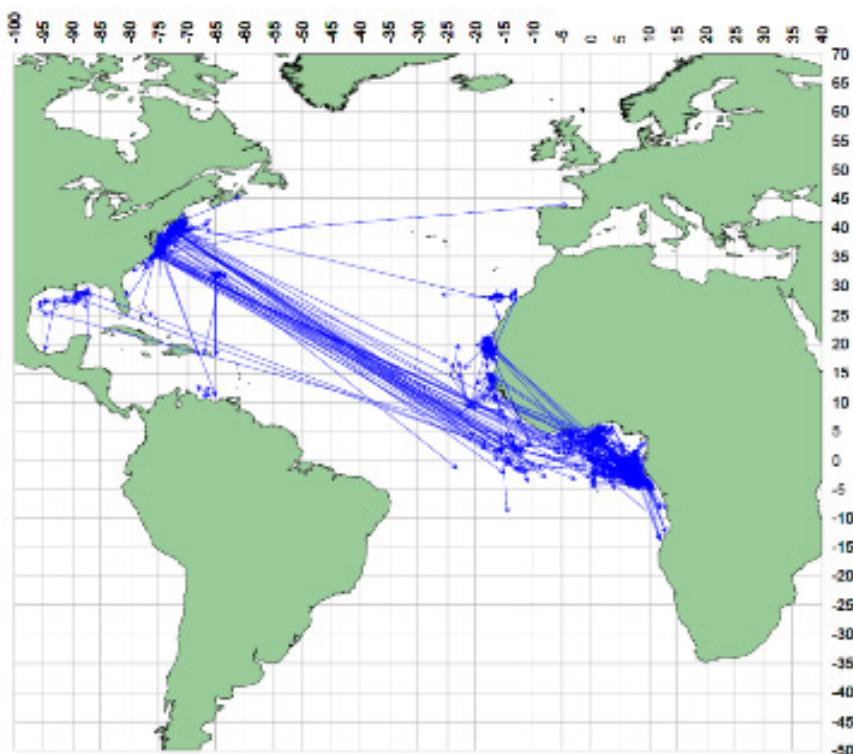
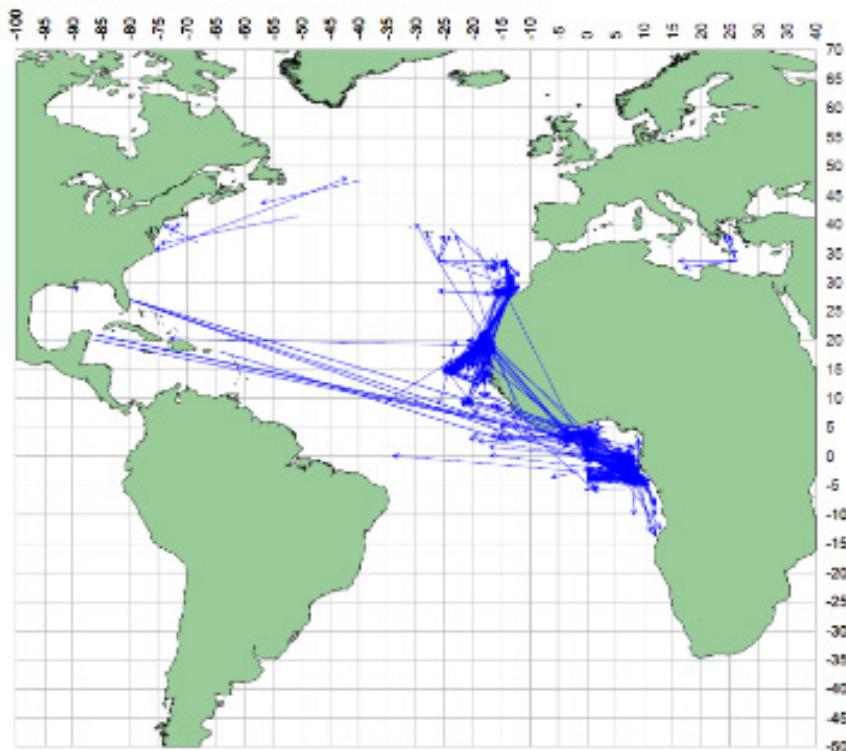


Figure 9.11 Horizontal movements of 3,021 tagged and recaptured *Thunnus obesus* (bigeye tuna). Direct trajectories between releases and recoveries. (Reproduced from ICCAT, 2006)



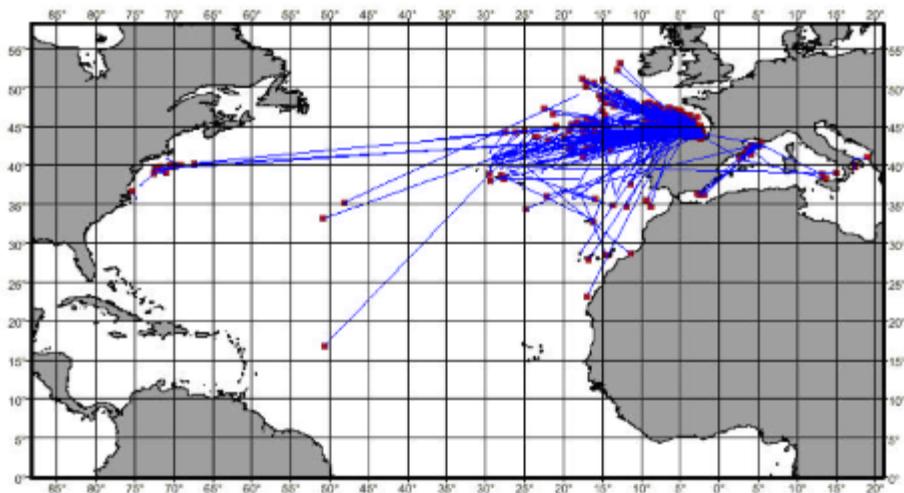
reaching a maximum size of approximately 250 cm, with a maximum longevity of 11 to 15 years (ICCAT, 2006). In the Atlantic Ocean, *T. obesus* may form a distinct stock, suggested by tagging studies which have shown transatlantic migrations from the Gulf of Guinea to the central and eastern Atlantic (Pereira, 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 continue to higher latitudes, such as the Azores (Bard et al., 1991; Bard and 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).

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*

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



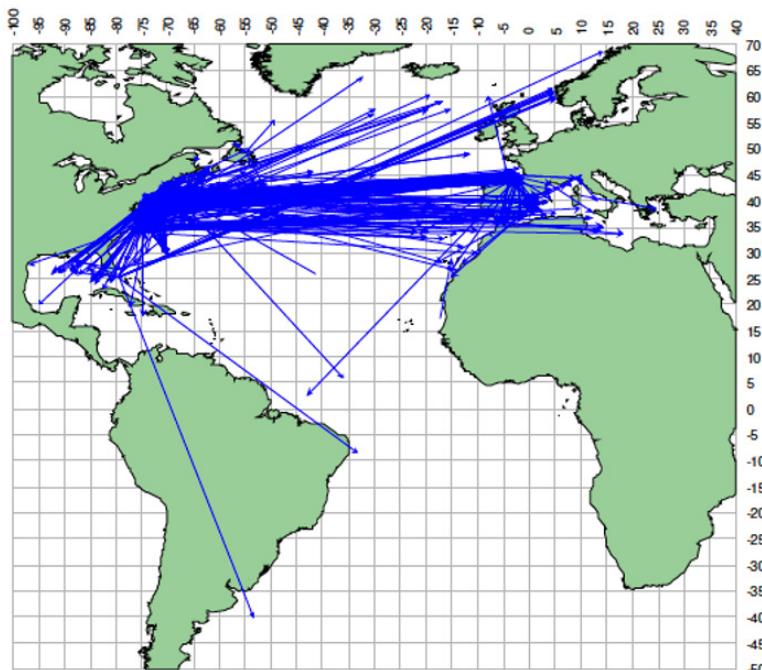
is the fourth most-caught tuna species in the Atlantic Ocean, with an average catch (2010–2017) of about 46,000 tonnes (ICCAT, 2019). Most of the catch is distributed in the northeast and southeast Atlantic, with only a small portion of *T. alalunga* being caught along the MAR close to and south of the 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).

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 warmer water (Brill et al., 2002). ICCAT currently manages *T. 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). *T. 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 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). Lines describe straight displacement between release and recovery locations. (Reproduced from ICCAT, 2006)



9.1.3.2.6 *Xiphias gladius* (swordfish)

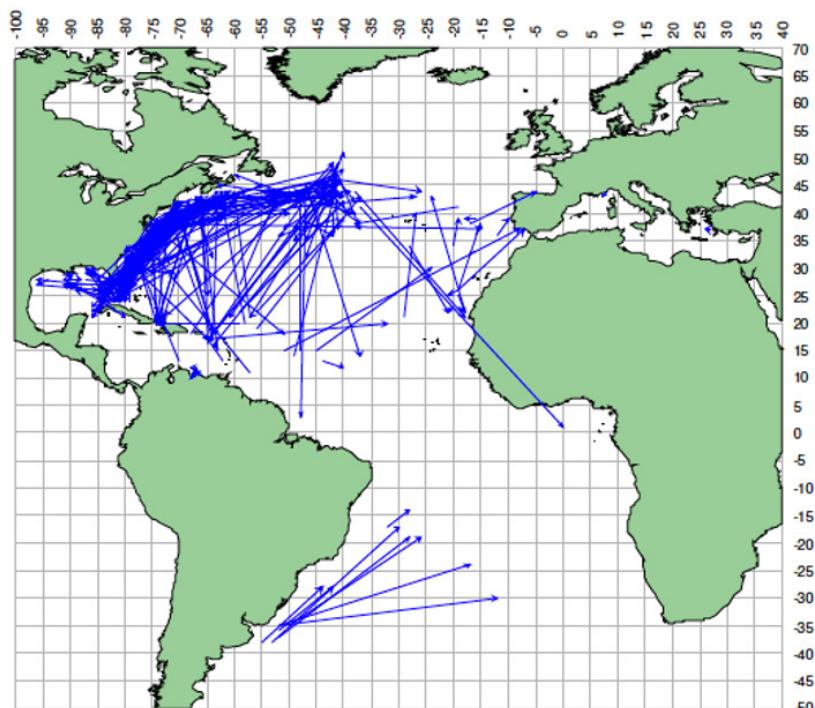
Xiphias gladius (swordfish) is a large epipelagic fish with a wide distribution across all the world's oceans and with a high tolerance to temperature ranges (Nakamura, 1985). *Xiphias gladius* can exceed 4 m total length and weigh more than 400 kg. ICCAT considers *X. gladius* to be divided into three 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).

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 restricted 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 "nekton", they are considered separately here to reflect their obligation to return to the surface

Figure 9.14 Horizontal movements of tagged and recaptured *Xiphias gladius* (swordfish). Lines describe straight displacement between release and recovery locations. (Reproduced from ICCAT, 2006)



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, but 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

of 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 (IUCN, 2017).

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 (IUCN, 2017).

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

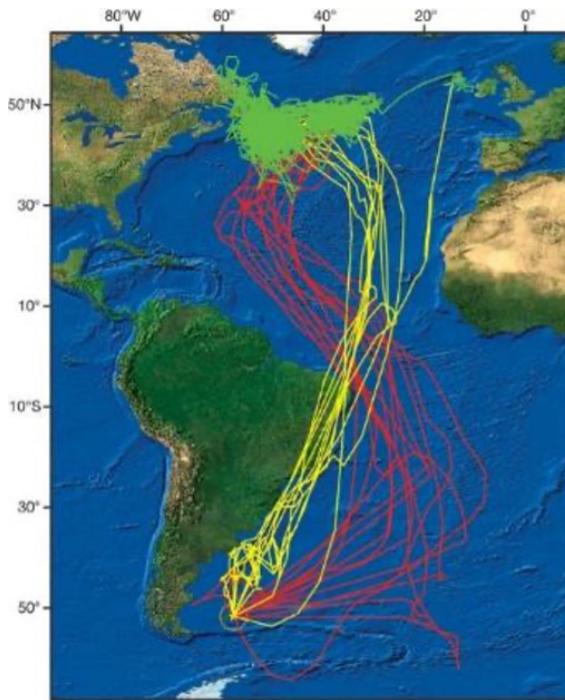
9.1.4.1.1 *Puffinus griseus* (sooty shearwater)

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 Banks and Newfoundland and Labrador shelves (Hedd et al., 2012; Figure 9.15). The migration pattern of *P. griseus* is similar to some *Sterna paradisaea* (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 future exploitation activities in the region could impact their navigational abilities. Globally, *P. griseus* is listed as near threatened with a declining population (IUCN, 2017).

9.1.4.1.2 *Fratercula arctica* (Atlantic puffin)

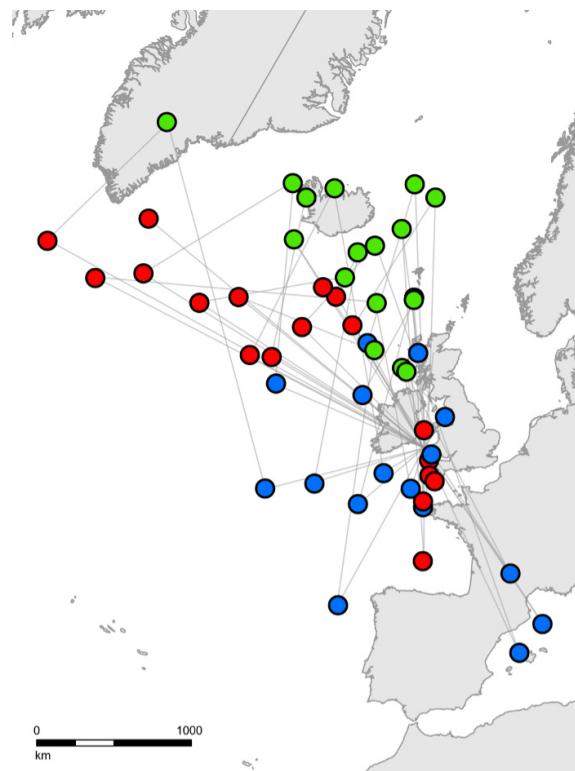
Fratercula arctica (Atlantic puffin) is one of the most common seabirds in the northern North Atlantic, with breeding colonies on both sides of the Atlantic and a species distribution which extends from around 45°N to polar regions. *Fratercula arctica* is entirely pelagic during the non-breeding period 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

Figure 9.15 Trans-equatorial migration and nonbreeding distribution of *Puffinus griseus* (sooty shearwater) 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)



Sea (Harris et al., 2010), individuals tracked from the west coast of Wales utilized the North Sea, coastal western Europe and the central North 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 nonbreeding 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 Puffin). 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 1,000 individuals, and it only breeds on Bugio Island (Madeira). The population of *P. deserta* is stable but listed as vulnerable (IUCN, 2017).

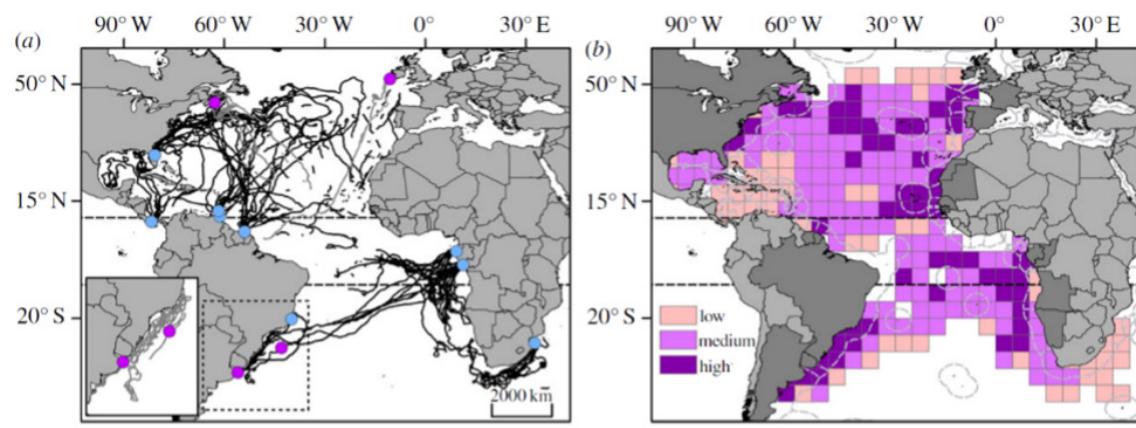
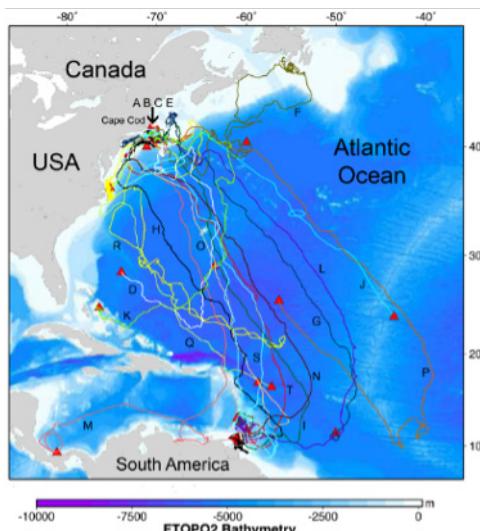
9.1.4.2 Sea turtles

Three sea turtle species were recorded by Jungblut et al. (2017) during four latitudinal transects of 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 of these species occur in both the North and South Atlantic Oceans, according to species ranges in the IUCN Red List of Threatened Species (IUCN, 2017). The regional distributions of *D. coriacea* and *C. caretta* are considered in more detail below.

9.1.4.2.1 *Dermochelys coriacea* (Leatherback sea turtles)

Dermochelys coriacea (Leatherback sea 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 1,300 m. The foraging behaviour of *D. coriacea* has been linked to the location of fronts, upwelling and downwelling zones, and mesoscale features.

Figure 9.17 Top: 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). Bottom left: Movements of 106 satellite-tracked *Dermochelys coriacea* (Leatherback sea turtles) during their migration in the Atlantic Ocean, between 1995 and 2010 tagged on nesting beaches (blue dots) or at sea (purple dots). Bottom 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. (Adapted from Fossette et al., 2014 (top) and Dodge et al., 2014 (bottom))



Dermochelys coriacea in the North Atlantic heavily utilize international waters, with more than 50 per cent 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 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).

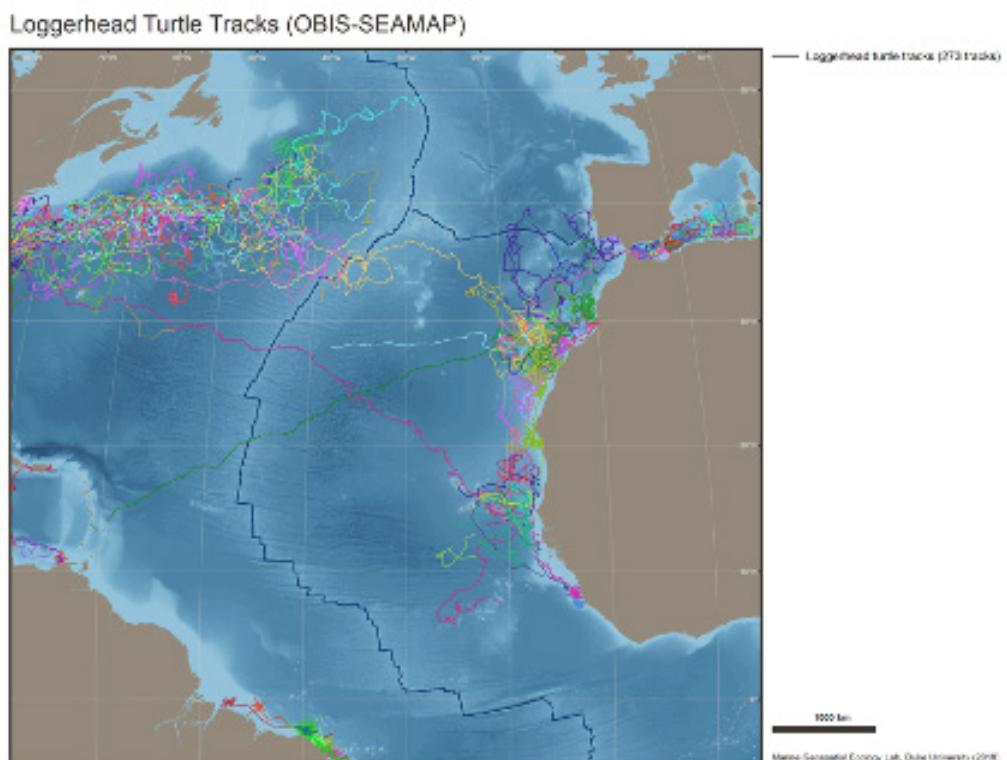
9.1.4.2.2 *Caretta caretta* (Loggerhead sea turtles)

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 and 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 and 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 at https://ran-s3.s3.amazonaws.com/isa.org.jm/s3fs-public/documents/datarport_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 of 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 in the IUCN Red List of Threatened Species (IUCN, 2017), 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.

9.1.4.3.1 Ziphidae (beaked whales)

Within the Odontoceti (toothed whales and dolphins), the Ziphidae (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.

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.

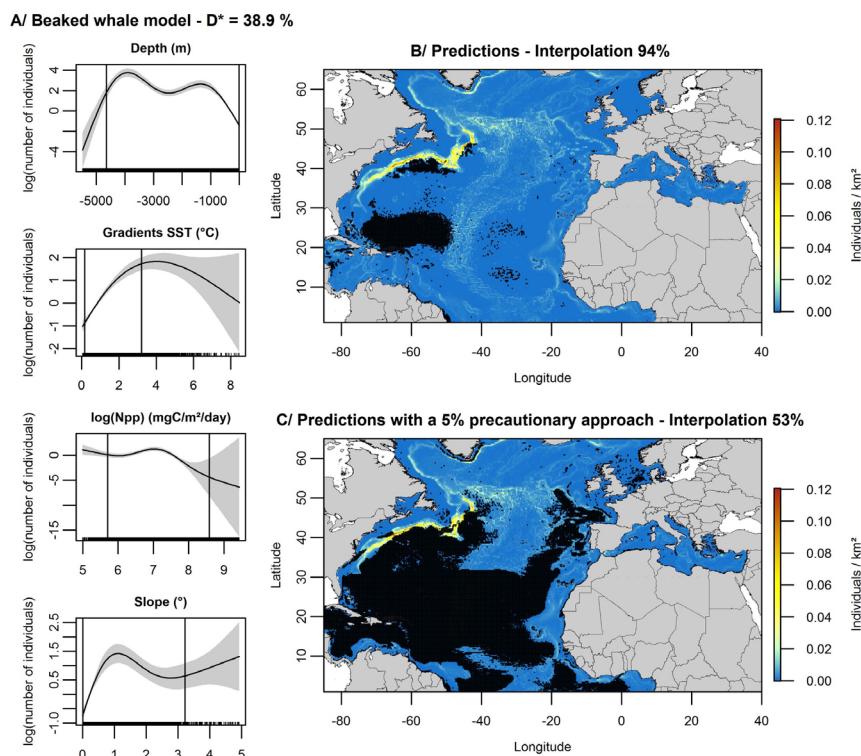
Odontoceti (toothed whales and dolphins)	Mysticeti (baleen whales)
<i>Lagenorhynchus albirostris</i> (White-beaked dolphin)*	<i>Megaptera novaeangliae</i> (Humpback whale)
<i>Physeter macrocephalus</i> (Sperm whale)	<i>Balaenoptera physalus</i> (Fin whale)
<i>Globicephala melas</i> (Long-finned pilot whale)	<i>Balaenoptera borealis</i> (Sei whale)
<i>Globicephala macrorhynchus</i> (Short-finned pilot whale)	<i>Balaenoptera acutorostrata</i> (Minke whale)
<i>Ziphius cavirostris</i> (Cuvier's beaked whale)	<i>Balaenoptera edeni</i> (Bryde's whale)
<i>Orcinus orca</i> (Killer whale)	
<i>Delphinus delphis</i> (Common dolphin)	
<i>Stenella frontalis</i> (Atlantic spotted dolphin)	
<i>Stenella coeruleoalba</i> (Striped dolphin)	
<i>Stenella clymene</i> (Clymene dolphin)	
<i>Tursiops truncatus</i> (Bottlenose dolphin)	
<i>Grampus griseus</i> (Risso's dolphin)	
<i>Steno bredanensis</i> (Rough-toothed dolphin)	
<i>Stenella longirostris</i> (Spinner dolphin)	
<i>Phocoena phocoena</i> (Harbour porpoise)	

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 1,500 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 CGFZ, 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 2,992 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 than they do during the day. This sort of deep-diving behaviour could bring *Z. cavirostris* into contact with mining activities at the

Figure 9.19 Functional relationships for the selected variable (A) and the predicted relative densities of individuals per km² 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 per cent 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 per cent precautionary approach) represent zones where predictions were not extrapolated. (Reproduced from Virgil, 2018)



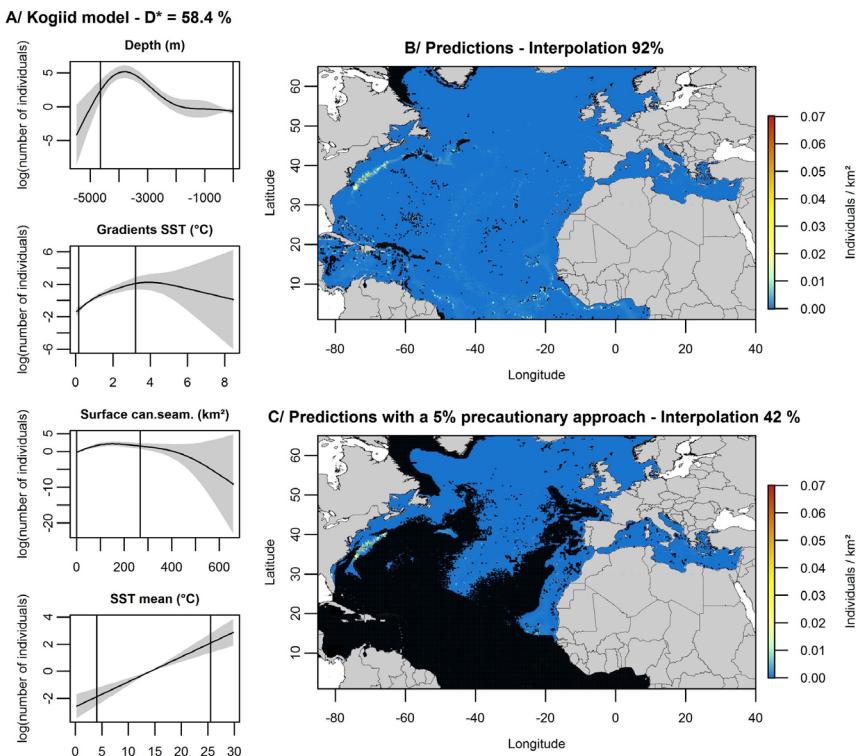
sea floor, whilst prolonged resting near the surface overnight may increase the likelihood of encounters with vessels.

A separate study addressing *H. ampullatus* in the northwest Atlantic during summer (June to August) also found that depth and sea surface temperature were the main drivers of whale distribution, with these environmental factors thought to 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*.

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 1,000 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

Figure 9.20 Functional relationships for the selected variable (A) and the predicted relative densities of individuals per km² 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)



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.

9.1.4.3.3 Other Odontoceti (toothed whales and dolphins)

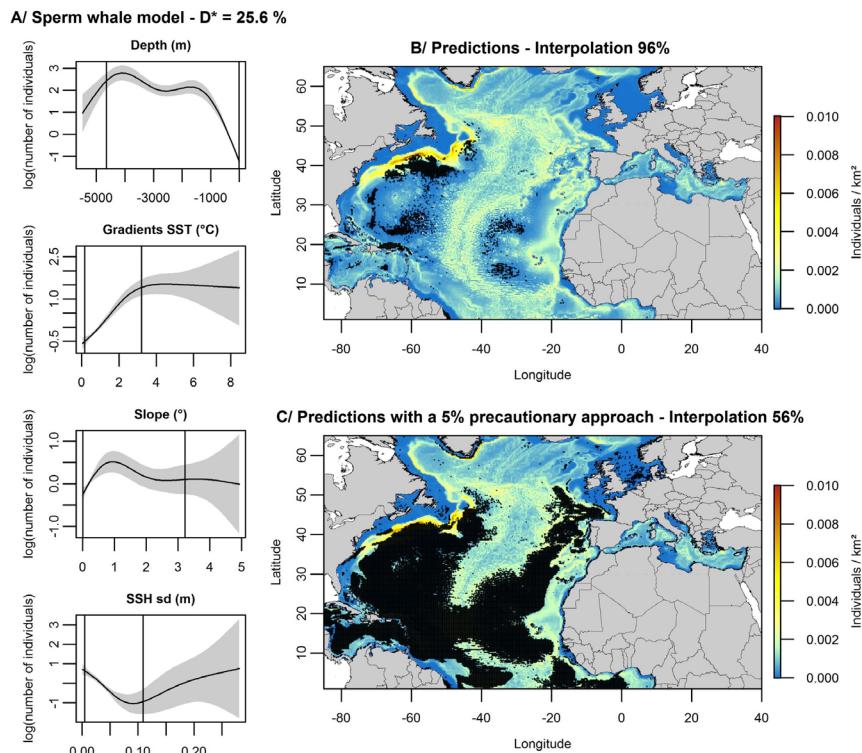
Heightened densities for the Odontoceti guilds Delphinidae and Globicephalinae have also been predicted along the MAR, in particular north and northwest of the Romanche Fracture Zone (Mannocci et al., 2015). The MAR axis south of 40°N was also predicted to be an area of increased density of *Physeter 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 (deeper than 2,000 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).

9.2 Temporal variability

Temporal variation in surface and mid-water fauna can occur on daily (e.g., diurnal migration and in 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 movements in

Figure 9.21 Functional relationships for the selected variable (A) and the predicted relative densities of individuals per km² 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)



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 mid-water nekton is the diel vertical migrations (DVM) displayed by many species (Pearcy and 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 2,000 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 200–1,000 m
- *Scopelogadus beanii* (Melamphaidae) – deep non-migrating mesopelagic <1,000 m
- *Serrivomer beanii* (sawtooth eel) – deep non-migrating mesopelagic <1,000 m
- *Cyclothona microdon* (bristlemouth) – non-migrator at 500–2,700 m
- *Bathylagus euryops* (deep-sea smelt) – weak migrator at 500–1,500 m
- *Maulisia microlepis* (tubeshoulder) – non-migrator at 700–2,000 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 (in the 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, DVM was less pronounced although acoustic backscatter and estimated biomass were higher.

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 MAR. (Based on data from Badcock and Merrett, 1976; Figure courtesy of Monty Priede)

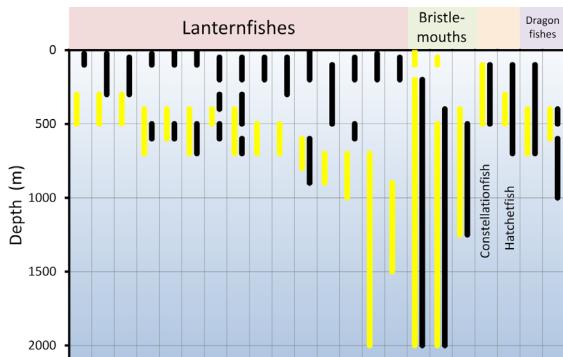
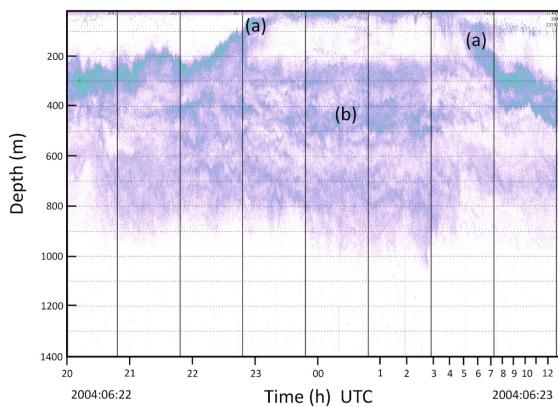
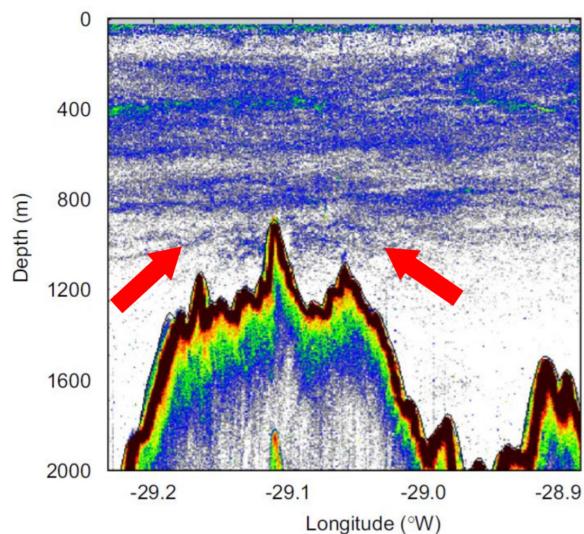


Figure 9.23 Daily Vertical Migration (DVM) of mid-water animals over the MAR. 18 kHz echogram taken between 2000h and 1300h by the RV GO Sars MAR-ECO voyage in 2004. Discrete deep-scattering layers move towards the surface at night (a), but important components do not move (b). (Courtesy of Odd Aksel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

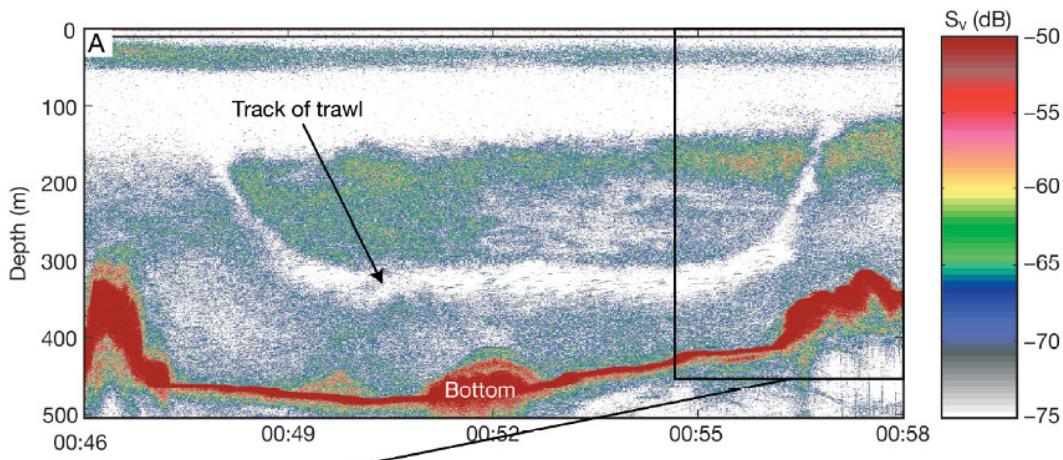
In schools of crustacea, the inter-individual distance is 5–60 cm, in fishes it is 5–120 cm, and for squid it is 5–260 cm. Schools can respond rapidly to presence of a predator. Squid schools respond by compression, reducing the average inter-individual spacing from approximately 110 to 50 cm, and are capable of a rapid “flash” compression within 4–5 seconds. Adjacent schools within the layer then expand to fill the available space. Thus, the structure of the mid-water layers is constantly changing and responding to disturbances on very short time scales of only seconds. When a net is towed through the DSL 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 of them are 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 imagery.

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 and Young, 1975), but sampling over the MAR is insufficient to provide definitive information on the species occurring there. The myctophid *Benthosema glaciale* in the northeast Atlantic begins spawning in late March, and larvae are found in the upper 75 m of the ocean from April to July. As the larvae grow, they move deeper, metamorphosing into juveniles at greater than 500 m depth from 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 and 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

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)



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 and thus ventilating the deep sea. The AMOC itself in turn has a periodicity imposed upon it by the 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 northeast Atlantic (Beaugard and Reid, 2003; Hátún et al., 2009).

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

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 sea floor.

In general, less is known about MAR mid-water trophic relationships than the regional distribution or temporal variations 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 at the trophic role of mid-water fishes in the global open ocean following publication of 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 per cent of the primary production in deep waters (Irigoién 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 kestiness 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 and nitrogen, Hoffman and 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 microneuston were at trophic level 3, while nearly half of the mesopelagic 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:

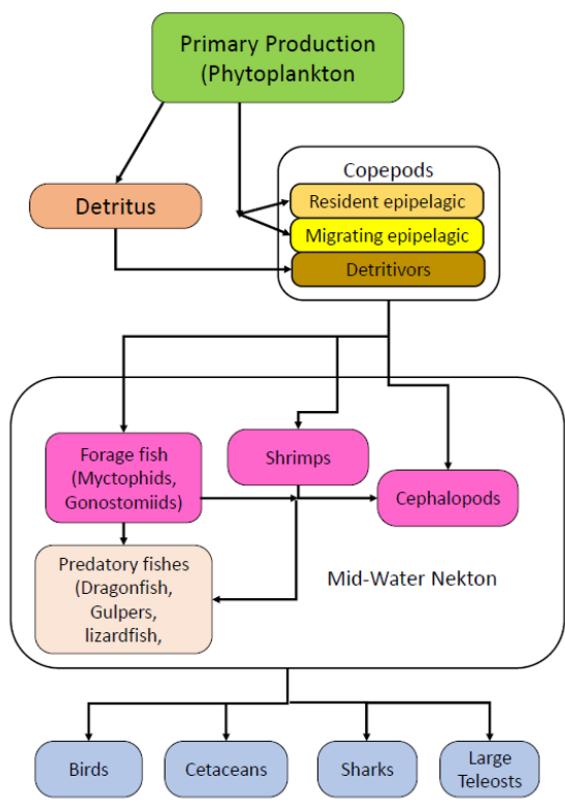
1. Resident epipelagic zooplankton – consumed near the surface by mesopelagic fish at night during daily vertical migration
2. Migrating epipelagic zooplankton – intercepted by mesopelagic fish waiting in the deep layers
3. Detritivore zooplankton – zooplankton feeding on sinking particulate organic 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, Sternopychidae 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 dragonfishes) 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 per cent of the standing stock of their fish prey per year (Clarke, 1982; Davison et al., 2013; Sutton and 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 the 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 and Godø, 2002).

Deep-sea cephalopods along the MAR have a variety of feeding strategies. The octopus *Japetella diaphana* feeds on euphausiids and copepods, and several species of squid are recorded as feeding on copepods including *Abraaliopsis* sp., *Histioteuthis corona* and *Pyrotheuthidae*. Many species feed on small crustacea such as euphausiids (krill and shrimps), and consumption of fish is important for the Gonatidae, Histioteuthidae, 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 for 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 and Gordon, 1991). Myctophid fishes alone along the MAR, through their diel vertical migrations, can transport up to 8 per cent 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, along 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 cetaceans 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 2,992 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 is 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 ROVs or other submersibles, will be required to develop our 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 subdividing 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 (200–1,000 m depth) occupies a large percentage of the global ocean volume and intercepts approximately 90 per cent

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 per cent of total ocean carbon dioxide production (Costello and Breyer, 2017; Robinson et al., 2010). An important feature of this in terms of global ecosystem function is the role of daily vertical migration with 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 of larger nekton remains to be determined.

Irigoién et al. (2014) suggest that mesopelagic fishes alone may be responsible for respiring 10 per cent 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 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 minuscule proportion of the global fish fauna. Gaither et al. (2016) updated this to

284 circumglobal species. Examining the species list of mid-water fishes occurring on the MAR in Table 9.1, 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 per cent 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 per cent) 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 the 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 and 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" above. 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 nMAR. (Based on data from Gaither et al., 2016 and Sutton et al., 2008)

Order	Family	Species
Anguilliformes	Derichthyidae (longneck eels)	<i>Derichthys serpentinus</i>
	Nemichthyidae (snipe eels)	<i>Nemichthys scolopaceus</i>
Saccopharyngiform	Eurypharyngidae (gulper eels)	<i>Eurypharynx pelecanoides</i>
Argentiniformes	Microstomatidae (pencil smelts)	<i>Melanolagus bericoides, Microstoma microstoma</i>
	Platyptroctidae (tubeshoulders)	<i>Maulisia mauli</i>
	Alepocephalidae (slickheads)	<i>Bajacalifornia megalops, Photostylus pycnopterus, Rouleina attrita</i>

Order	Family	Species
Stomiiformes	Gonostomatidae (bristle-mouths)	<i>Cyclothona microdon, Sigmops bathyphilum, Sigmops elongatus, Cyclothona braueri, Cyclothona pallida, Cyclothona pseudopallida</i>
	Sternopychidae (hatchetfish & pearlsides)	<i>Argyropelecus hemigymnus, Argyropelecus aculeatus, Argyropelecus olfersii, Sternopyx pseudobscura, Valenciennellus tripunctulatus</i> <i>Argyropelecus gigas</i>
	Phosichthyidae (lightfishes)	<i>Ichthyococcus ovatus</i>
	Stomiidae (barbeled dragon-fishes)	<i>Chauliodus sloani, Stomias boa ferox, Pachystomias microdon, Aristostomias tittmanni, Photonectes margarita</i>
Aulopiformes	Paralepididae (barracudinas)	<i>Arctozenus risso</i>
Myctophiformes	Myctophidae (lanternfishes)	<i>Benthosema suborbital, Ceratoscopelus warmingii, Diaphus effulgens, Diaphus mol-lis, Diogenichthys atlanticus, Electrona risso, Hygophum hygomii, Hygophum reinhardtii, Lampadена chavesi, Lampadena speculigera, Lampanyctus festivus, Lampanyctus pusillus, Lobianchia dofleini, Lobianchia gemellarii, Loweina interrupta, Notolychnus valdiviae, Taaningichthys bathyphilus</i>
Gadiformes	Moridae (deep-sea cods)	<i>Halargyreus johnsonii</i>
	Melanonidae (pelagic cods)	<i>Melanonus zugmayeri</i>
Lophiiformes (anglerfishes)	Melanocetidae (black sea devils)	<i>Melanocetus johnsonii</i>
	Oneirodidae (dreamers)	<i>Chaenophryne draco, Dolopichthys longicornis, Microlophichthys microlophus</i>
	Ceratiidae (seadevils)	<i>Ceratias holboelli, Cryptopsaras couesii</i>
	Gigantactinidae (whipnose anglers)	<i>Gigantactis vanhoefeni</i>
	Melamphaidae (bigscale fishes)	<i>Scopeloberyx opisthopterus</i>
Stephanoberyciformes	Rondeletiidae (redmouth whalefishes)	<i>Rondeletia loricata</i>
	Cetomimidae (flabby whalefishes)	<i>Cetostoma regani</i>
	Anoplogastridae (fangtooth)	<i>Anoplogaster cornuta</i>
Beryciformes	Diretmidae (spinyfins)	<i>Diretmus argenteus</i>
	Chiasmodontidae (swallowers)	<i>Pseudoscopelus altipinnis, Kali indica</i>
Perciformes	Gempylidae (snake mackerels)	<i>Diplospinus multistriatus</i>
	Tetragonuridae (squaretails)	<i>Tetragonurus cuvieri</i>

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 developing 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, while 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) System¹ (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

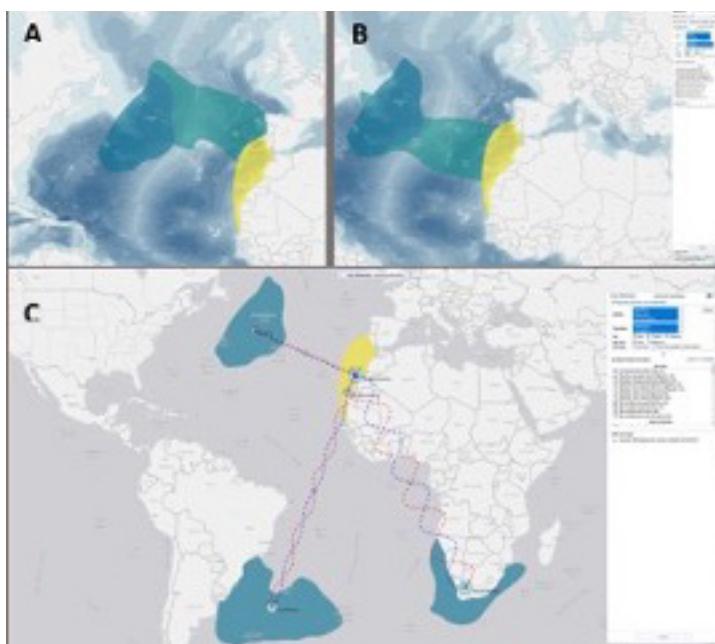
¹ MiCO System: <https://mico.eco/system>

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 and 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 thousands

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 MiCO 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, and 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 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.

Figure 9.28 Movement of 22 tracked *Megaptera novaeangliae* (Humpback whales). 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)

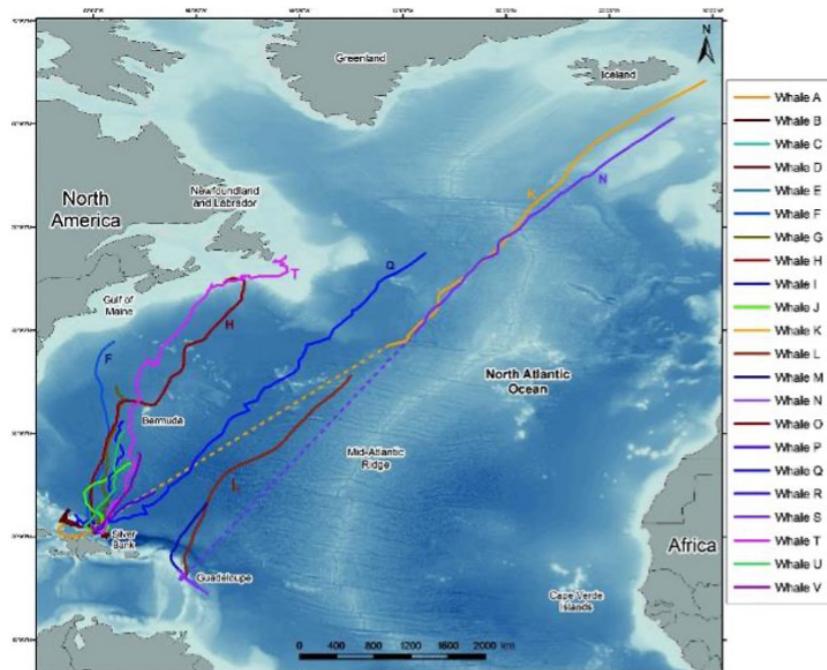
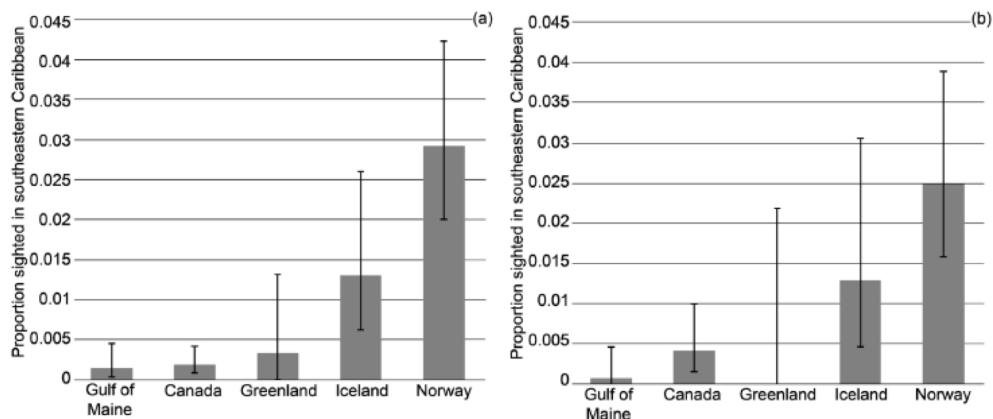


Figure 9.29 The proportion of *Megaptera novaeangliae* (Humpback whales) from each of the high-latitude feeding areas that also have been sighted in the southeastern Caribbean (with 95% Confidence Intervals). Left: all individuals identified in the high-latitude feeding areas; Right: only those records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



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 northeastern United States 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 Bank population.

Megaptera novaeangliae globally and in the 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.

9.6 Resilience and recovery

Resilience in marine ecosystems refers to the 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 future deep-sea mineral exploitation. To date, most studies on the resilience of marine organisms have focussed on static entities, such as coral reefs (Darling and 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 Niño 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

Table 9.8 Potential resilience of the MAR 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 nMAR have little anthropogenic disturbance.

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. Future deep-sea exploitation activities 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, "Cumulative impacts" above.

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 may still be high as a result of future deep-sea mineral exploitation activities. 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 and 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 or 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 or 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 ROVs, sampling equipment and 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 exploitation impacts is unknown. More information would be needed on the nature and extent of deep-sea exploitation 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 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 (greater than 95 per cent) 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 per cent 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 sea floor itself, the water column immediately above the sea floor (here, only to 50 m above the seabed is considered) provides important habitat for a range of organisms who are generally more mobile than the species found inhabiting the sea floor. Although not considered in detail within this document, buoyant and neutrally-buoyant hydrothermal plumes are also habitats 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 sea floor (benthopelagic). These broad habitat groups are not necessarily all-encompassing, but form the structure for this 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, and 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 related to future mining impacts.

The need to distinguish between hydrothermally active and inactive sulphide habitat is reflected in recommendations issued by the ISA LTC (ISBA/25/LTC/6/Rev.1), 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; and 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".² For the purposes of the regional environmental assessment (REA), 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/Rev.1, 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 and Gebruk, 2008; UK-led ECOMAR: Priede et al. 2013b).

² 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)."

Ongoing underwater surveys within the European Union Horizon 2020 ATLAS³ and SponGES⁴ 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. As this habitat connects the benthic and mid-water environments, it is likely that the benthopelagic biota will be a mix of taxa found in 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, while others may descend to the sediment surface to feed (Miller and 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; Billelt et al., 1985; Miller and Pawson, 1990; Rogacheva et al., 2012). In some locations of the northern MAR, deep-pelagic fish abundance peaks within the 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 (Billelt 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 sea floor and community composition. These combine to create site- and season-specific conditions for benthopelagic organisms (Craig et al., 2015).

The benthic environment section of the REA focusses on the seabed beyond national jurisdiction (the Area) from south of the Iceland ECS Submission to the Romanche Fracture Zone near the equator. However, the biota found in this area is 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

³ A transatlantic assessment and deep-water ecosystem-based spatial management plan for Europe (EU-ATLAS Project): <https://www.eu-atlas.org/>

⁴ Deep-sea sponge grounds ecosystems of the North Atlantic (SponGES): <http://www.deepseasponges.org/>

the ridge, or other occurrences within the region, to provide a regional context for the biota within the area of interest.

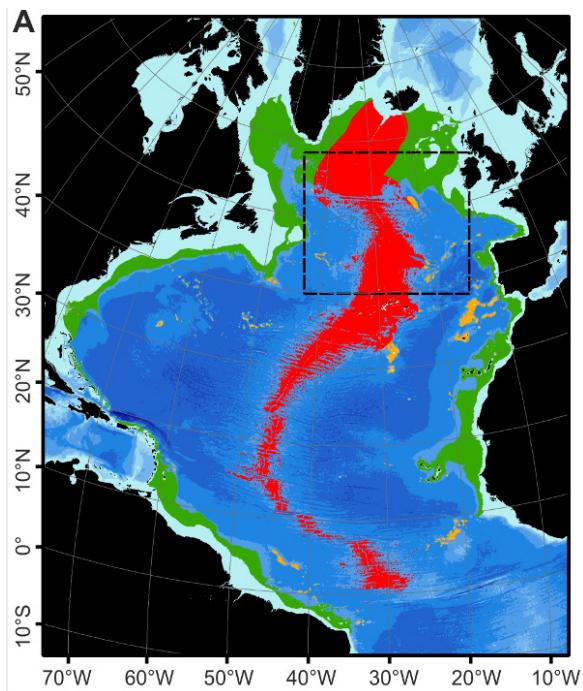
10.1 Regional distribution

Models of the regional distribution of benthic fauna along the MAR are intimately linked to the physical and chemical oceanography, and sea-floor 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 (800–3,500 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 GOODES 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 CGFZ 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 of 1,237–3,527 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 1,263–1,916 m depth and in samples from 2,350–3,512 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).

Figure 10.1 Bathymetry map of the North Atlantic Ocean, based on the GEBCO 30° grid, showing the extent of the lower bathyal (depth 800–3,500 m) area on the MAR (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)



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).

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. 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 3,500 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.

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

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



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 sampling 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 future data collections are more readily comparable.

The general pattern 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 less than 5 per cent 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 than 20 per cent non-hydrothermal hard substrata (stones and outcropping basaltic rock), indicating that these substrata can make 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's 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 non-hydrothermal hard substrata on the

MAR may need to be considered when developing 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 km², which is less than 0.00001 per cent 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”.⁵ These known inactive vent fields occur beyond national jurisdiction between the equator and 25°N.

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

Table 10.1 Inactive vent fields along the nMAR, from InterRidge Vents Database Ver.3.4

Vent field	Latitude (N)	Longitude (W)	Maximum depth (m)	Discovery references
Ashadze 4	12.97	-44.85	4,530	Fouquet et al. (2007)
Krasnov	16.64	-46.475	3,900	Bel'tenev et al. (2004); Fouquet et al. (2007)
Logatchev 4	14.7063	-44.9083	2,000	Kuhn et al. (2004)
Logatchev 5	14.75	-44.97	3,100	Fouquet et al. (2008)
MAR, 12 48'N	12.8	-44.7883	2,400	Rona et al. (1982)
MAR, 15 50'N	15.8667	-46.6667	3,000	Akimtsev et al. (1991)
MAR, 16 46'N	16.795	-46.38	3,300	Eberhart et al. (1988)
MAR, 22 30'N	22.5	-45.005	2,800	Rona et al. (1982)
MAR, 23 35'N	23.5833	-45	3,500	Delaney et al. 1987; Kelley and Delaney (1987)
MAR, 24 20'N	24.35	-46.2	3,200	Rona et al. (1980)
MAR, 24 30'N	24.5	-46.1533	3,900	Sudarikov et al. (1990); Krasnov et al. (1995)
MAR, 25 50'N	25.8083	-44.9833	3,000	Rona et al. (1982)
Vema Fracture Zone	10.85	-41.8	3,600	Bonatti et al. (1976); Rona et al. (1976)
Zenith-Victory	20.1292	-45.6225	2,390	Silantyev (2008)

⁵ InterRidge Vents Database Ver. 3.4, “About the Database”, https://vents-data.interridge.org/about_the_database. Accessed 18 September 2019.

along the MAR and globally, where hydrothermally-inactive sulphide habitat has been confirmed, 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 sea-floor survey imagery, however, there may be diverse microbial communities, which could provide a food source for other biota (Van Dover, 2019).

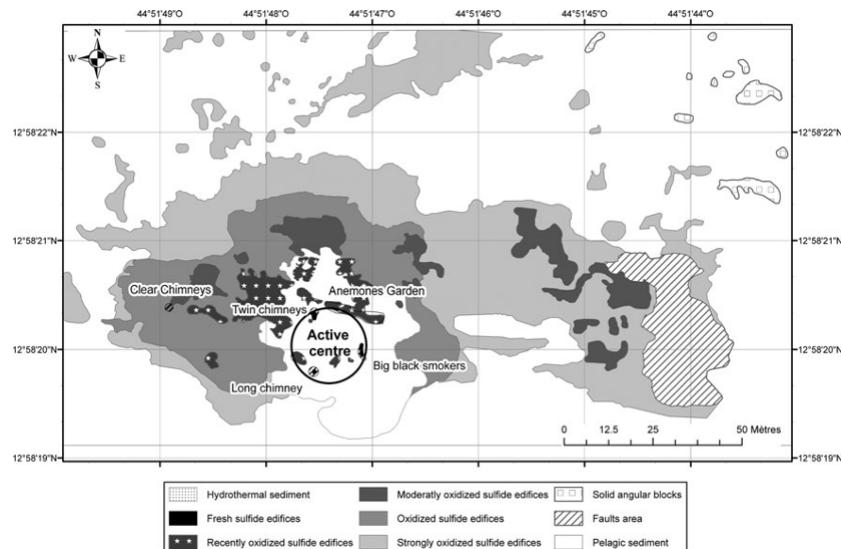
There are few occurrences of specific inactive sulphide habitat along the northern MAR, where the scientific literature has reported associated biological communities. Some of these occurrences are at a scale smaller than whole vent fields, and so may not be recorded in the InterRidge Database. Occurrences 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 zo-

nes 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 sea-floor surface can be either hydrothermally active or inactive, and tend to occur within a few hundred metres of active

Figure 10.3 Ashadze-1 substrata divided into nine classes. The active centre is located in the southwestern 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)

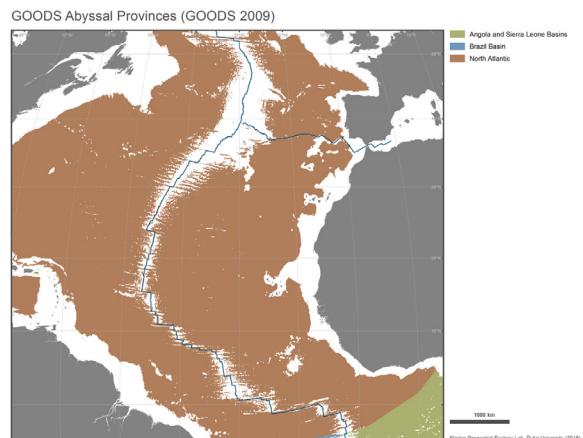


hydrothermal venting (Fabri et al., 2011). Little is known about the distribution of sub-surface hydrothermal sediments and any associated biological communities.

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 more than 95 per cent 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), although 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 (3,500–6,500 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 (greater than 6,500 m), such as the base of the trench occurring at the Romanche Fracture Zone.

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 (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 and Gebruk, 2006a), and later with the CML MAR-ECO project (Bergstad and Godø, 2003; Bergstad and

Figure 10.4 GOODS abyssal provinces, depth range 3,500–6,500 m. (Map reproduced with permission from Cleary et al., 2019. Data taken from Watling et al., 2013. Map available at: <https://ran-s3.s3.amazonaws.com/isa.org.jm/s3fs-public/files/documents/dataproject-19nov-lowres.pdf>)



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 sea floor, included within the ISA definition of the benthic environment, is largely equivalent to 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 sea-floor habitat type along the MAR. Some of these species (generally the best swimmers) are particularly widespread, while 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 have focussed on the fishes and cephalopods from north of the Azores to 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 CGFZ 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's 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 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 sea-floor 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)

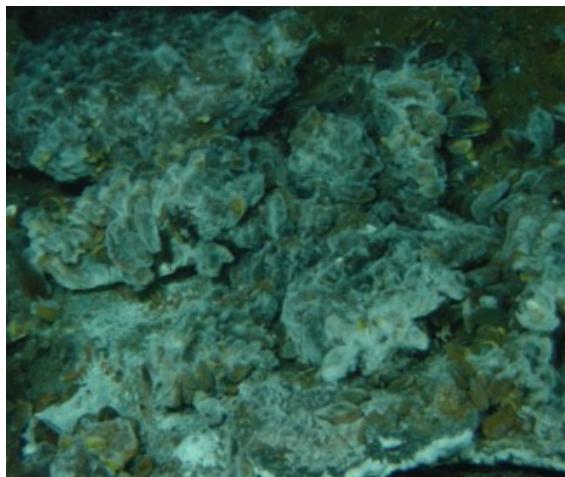
or within the structure of the sponge (endosymbionts). Microorganisms, such as Archaea, Bacteria and Fungi, can make up to 40 per cent of the sponge's volume (Osinga et al., 2001) and may play an important role in sponge metabolism and carbon fixing. They can also produce secondary metabolites, such 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 (meaning they 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 microorga-

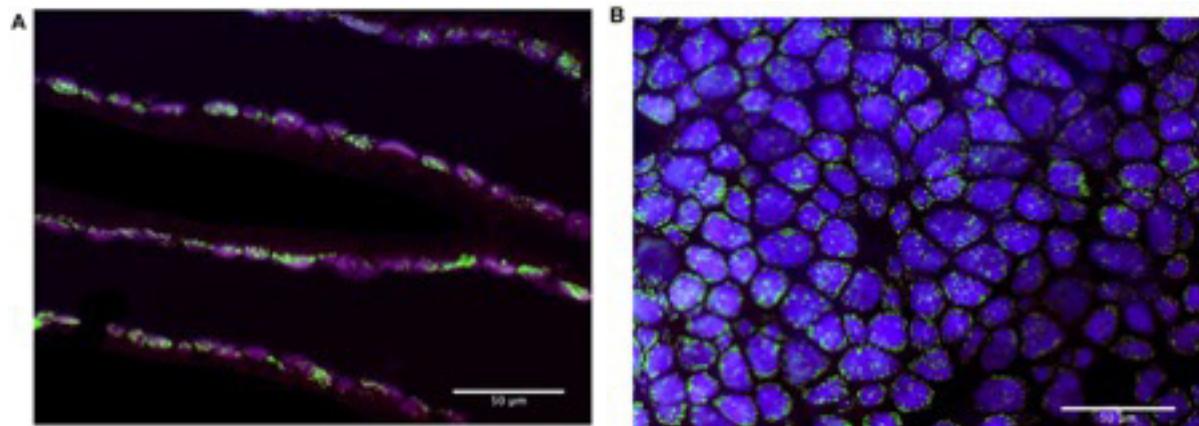
nisms will be restricted by the distribution of hydrothermally-active habitat (either basalt or ultra-maphic) along the MAR. Other microorganisms found at hydrothermally-active habitat are heterotrophic (metabolise organic carbon sources) and may occur in other deep-sea habitats along the MAR.

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 archaeal community was diverse and heterogeneously distributed between the hydrothermal sites and types of samples analysed (seawater, hydrothermal fluid, chimney and sediment) (Roussel et al.,

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)



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).

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

separated by only 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; Christakiss 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 the deep equatorial MAR sea floor, 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 than 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 and 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) species 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 so rare or undersampled, 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-ECHO 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 perspective, 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-Sánchez 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, although 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. As such, many are vulnerable marine ecosystem indicator taxa (ICES 2016, 2019b).

10.1.7.1.1.1 Anthozoa (corals and anemones)

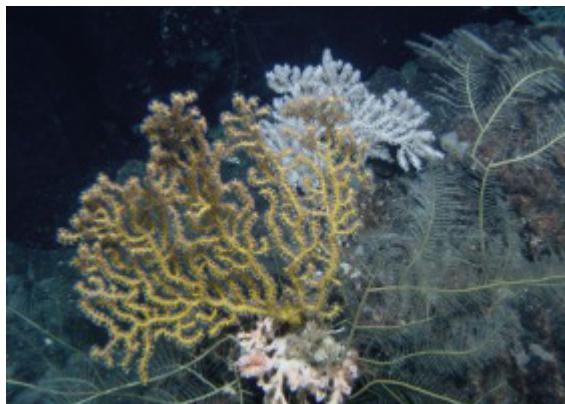
Many deep-sea Anthozoa species (including corals and anemones) are found on hard non-hydrothermal substrata along the northern MAR (Figure 10.7). During the ECO-MAR project, Anthozoa species from orders Actiniaria (anemones), Antipatharia (black corals), Scleractinia (hard corals), Alcyonacea (soft corals) and Pennatulacea (sea pens) were collected from the MAR. The collected anthozoan specimens were found to have high affinities with the Atlantic European continental slope (62.5 per cent), the northeast American continental slope (59.4 per cent) and the northwest continental slope of Africa (50.0

per cent). There are also a high percentage of species shared with Iceland and Greenland (53.1 per cent) and the Azores (46.9 per cent) (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, northeast America and northwest 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*, *Heteropolypus* 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 mariejoseae* (Molodtsova, 2013). Only one of the five species, *A. gyratus*, appeared to have a distribution limited to the MAR and Reykjanes Ridge, while 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 of 1,955–2,738 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 associations 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 nMAR, near Menez Gwen hydrothermal vent field Marine Protected Area. (Reproduced with permission: © SEAHMA - PDCTM/MAR/15281/1999)



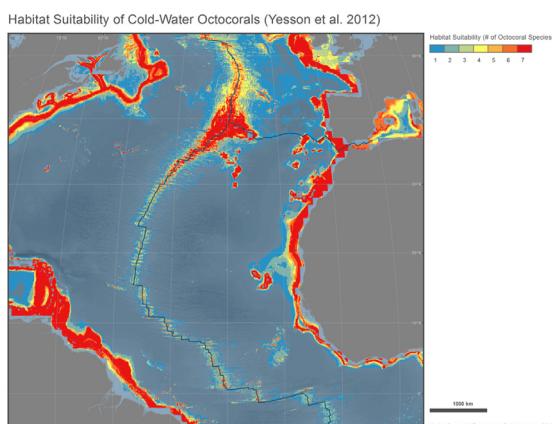
Video survey of Anthozoa along the MAR between the southern part of the Reykjanes Ridge and the Azores observed deep-water corals at all sites, across a depth range of 800–2,400 m, although most corals were observed at 1,400 m depth or shallower (Mortensen et al., 2008). A total of 40 taxa were observed 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 Species⁶, 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. *Lophelia 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

⁶ *Lophelia pertusa* (unaccepted) within the World Register of Marine Species: <http://www.marinespecies.org/aphia.php?p=taxdetails&id=135161>

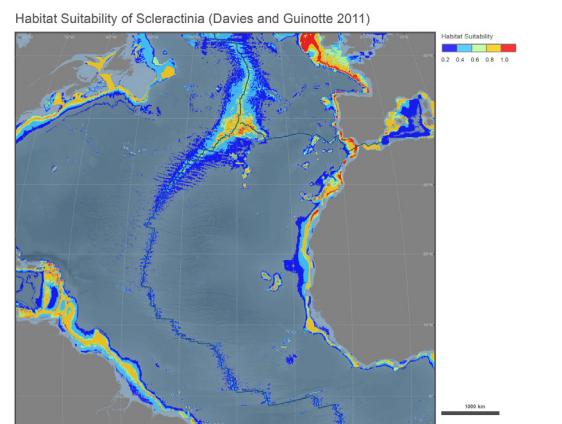
MAR offers suitable habitat for a range of octocorals, such as Alcyoniina, Holaxonia, Calcaxonia, Scleraxonia, Sessiliflorae, Stolonifera and Subsessiliflorae (Yesson et al., 2012; Figure 10.8). However, the predicted occurrence of suitable habitat does not guarantee that coral will colonise a given area. Also, if an area is predicted to have suitable habitat for a certain group of corals, different species from within that 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, northeast America and northwest 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.

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 at: <https://ran-s3.s3.amazonaws.com/isa.org.jm/s3fs-public/files/documents/dataproduct-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 and Guinotte, 2011; Figure 10.9). As observed for octocoral groups, the Azores have 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 suitability habitat along the MAR, with suitable habitat predicted to occur from south of Iceland all the way to the equator, and 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, northeast America, and northwest 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 and Guinotte, 2011. Map available at: <https://ran-s3.s3.amazonaws.com/isa.org.jm/s3fs-public/files/documents/dataproduct-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, while one specimen of Calcarea sponge was collected during MAR-ECO but has not yet been described (Cardenas and Tore Rapp, 2015). There are few studies on the distribution of either hexactinellid or demosponge sponges along the MAR.

Cardenas and Torre Rapp (2015) found the CGFZ 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 CGFZ, whilst four species only occur south of the northern part of the CGFZ. Eight of the demosponge species can be found both north and south of the CGFZ.

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 CGFZ acting as the barrier between the Northern Atlantic Boreal and North Atlantic provinces (Cardenas and Tore Rapp, 2015). There also appears to be a lower depth limit for bathyal demosponges of 3,000 m for most species (Cardenas and 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 and 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 CGFZ 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 and Collins, 2008), and some are new to science, such as *Sympagella cooki* and *Sympagella ecomari* (Tabachnick and Menshenina, 2013).

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 and Menshenina, 2013). Whilst some of

Figure 10.10 In-situ images of hexactinellids (glass sponges) from the nMAR in the vicinity of the CGFZ. 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)



these species (such as *F. herdendorfi*) appear to be widespread, 13 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 SponGES1 project,⁷ 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

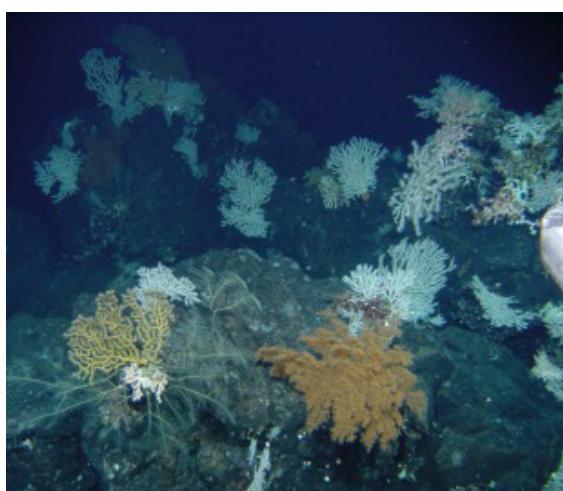
For Demospongiae, 22 species were collected from the northern MAR between the Azores and Iceland during the MAR-ECO project at 753–3,046 m depth. Fourteen of these demosponge species have an amphi-Atlantic distribution, being found on both the eastern and western sides of the Atlantic (Cardenas and Tore 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 *lotroata 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 northeast Atlantic and the MAR. According to distribution maps, 68 per cent 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 per cent of 80 species collected (Scleractinia, Cirripedia, Echinoidea, Asteroidea and Brachiopoda) were amphi-Atlantic (Mironov and 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 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 *Acesta excavata* and squat lobsters) to be 1.6 times higher where corals were present (Mortensen et al., 2018).

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,

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



⁷ SponGES: <http://www.deepseasponges.org/>

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 (1,067–1,477 m depth) south of the Azores hints at a diverse and relatively unknown Bryozoa fauna (Souto and Albuquerque, 2019). Some of the bryozoans collected were identified from other localities, but seven of the 15 bryozoans were described as new species. The work of Souto and Albuquerque (2019) is the first report of cheilostome bryozoans from 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, brittle stars and an arrow worm (Table 10.2). Together, these total 100 taxa, which at the time the records were published, represented nearly 20 per cent 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.

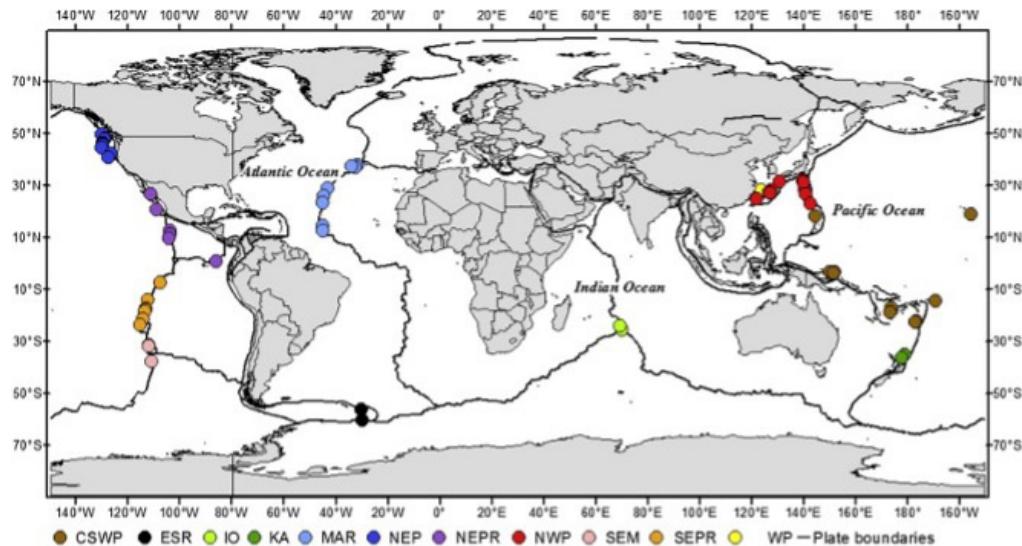
Global occurrence records for hydrothermal vent taxa have been used to conduct biogeographic analyses, to understand the relationship between vent fauna in different regions. Biogeographic

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

Phylum	Common name	Species name
Foraminifera	Foram	<i>Luffammina atlantica</i> *
Porifera	Sponge	<i>Asbestopluma</i> (<i>Asbestopluma</i>) <i>pennatula</i> ^G , <i>Cladorhiza abyssicola^G, <i>Euchelipluma pristina^G</i></i>
Cnidaria	Hydroid	<i>Candelabrum phrygium^G, <i>C. serpentarii</i>*, <i>Ectopleura larynx^G, <i>Eudendrium rameum^G, <i>Grammaria abietina^G, <i>Halisiphonia arctica</i>*, <i>Hydrallmania falcata^G, <i>Lafoea dumosa^G, <i>Polyplumaria flabellata^G, <i>Sertularella tenella^G, <i>Stegolaria geniculata^G, <i>Symplectoscyphus bathyalis^G, <i>Zygophylax echinata</i>*, <i>Z. leloupi</i>*</i></i></i></i></i></i></i></i></i></i>
Mollusca	Anemone	<i>Maractis rimicarivora</i> *
	Limpet	<i>Divia briandi</i> *, <i>Lepetodrilus atlanticus</i> *, <i>Paralepetopsis ferrugivora</i> *, <i>Pseudorimula midatlantica</i> *, <i>Sutilizona pterodon</i> *
	Sea snail	<i>Alvania stenolopha</i> *, <i>Laeviphitus desbruyeresi</i> *, <i>Lirapex costellatus</i> *, <i>Lurifax vitreus</i> *, <i>Neusas marshalli^G, <i>Peltospira smaragdina</i>*, <i>Phymorhynchus carinatus</i>*, <i>Ph. moskalevi</i>*, <i>Ph. ovatus</i>*, <i>Protolira thorvaldssoni</i>^{Ch}, <i>Pr. valvatoides</i>*, <i>Xylodiscula analoga</i>*</i>

Phylum	Common name	Species name
	Sea slug	<i>Dendronotus comteti</i> *
	Mussel	<i>Bathymodiolus azoricus</i> *, <i>B. puteoserpentis</i> *
	Octopus	<i>Cirrothauma magna</i> ^G
Nematoda	Nematode	<i>Moravecnelma segonzaci</i> *
Annelida	Scale worm	<i>Branchipolynoe seepensis</i> ^{Ch} , <i>Lepidonotopodium jouinae</i> *, <i>Levensteiniella iris</i> *
	Bristle worm	<i>Amphisamytha lutzi</i> *, <i>Glycera tesselata</i> ^G , <i>Laonice asaccata</i> *, <i>Prionospio unilamellata</i> *
	Tube worm	<i>Spiochaetopterus</i> sp.*
Arthropoda	Mite	<i>Halacarellus auzendei</i> *
	Sea spider	<i>Sericosura heteroscela</i> *, <i>Sericosura mitrata</i> ^G
	Benthic copepod	<i>Ambilimbus arcuscelestis</i> *, <i>Aphotopontius atlanteus</i> *, <i>Bathylaophonte azorica</i> *, <i>Heptnerina confusa</i> *, <i>Rimipontius mediospinifer</i> *, <i>Smacigastes micheli</i> *, <i>Stygiopontius cladarus</i> *, <i>St. latulus</i> *, <i>St. mirus</i> *, <i>St. pectinatus</i> *, <i>St. regius</i> *, <i>St. rimivagus</i> *, <i>St. serratus</i> *, <i>St. teres</i> *
	Cumacean	<i>Bathycuma brevirostre</i> ^G
	Tanaid	<i>Armaturanais atlanticus</i> *, <i>Leptognathiella fragilis</i> *, <i>Mesotanais styx</i> *, <i>Obesutanais sigridae</i> *, <i>Pseudotanais vulsellula</i> ^G , <i>Typhlotanais incognitus</i> *
	Isopod	<i>Heteromesus calcar</i> *, <i>H. ctenobasius</i> *
	Amphipod	<i>Gitanopsis alvina</i> *, <i>Autonoe longicornis</i> *, <i>Bouvierella curtirama</i> *, <i>Kyphometopa saldanhae</i> ^G , <i>Luckia strike</i> *, <i>Bonnierella compar</i> *, <i>Steleuthera ecoprophyea</i> *, <i>Stenothoe menezgweni</i> *
	Shrimp	<i>Alvinocaris markensis</i> *, <i>A. williamsi</i> *, <i>Mirorcaris fortunate</i> *, <i>Rimicaris chacei</i> *, <i>R. exoculata</i> *, <i>Thysanoessa parva</i> ^G
	Squat lobster/ Lobster	<i>Munidopsis acutispina</i> ^{Ch} , <i>G</i> , <i>Munidopsis exuta</i> *, <i>Thymopides laurentiae</i> *
	Crab	<i>Bathynectes maravigna</i> ^G , <i>Chaceon affinis</i> ^G , <i>Segonzacia mesatlantica</i> *
Echinodermata	Brisingid	<i>Brisinga endecacnemos</i> ^G
	Sea urchin	<i>Gracilechinus alexandri</i> ^G
	Brittle star	<i>Ophiactis tyleri</i> *, <i>Ophioctenella acies</i> ^{Ch}
Chaetognatha	Arrow worm	<i>Calispadella alata</i> *

Figure 10.12 Map of the global biogeography of hydrothermal vents communities, after Rogers et al. (2012). Abbreviations: 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)



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 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.

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 ($45^{\circ}28'N$, 2,095 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 and Galkin (2015), Menez Gwen ($37^{\circ}51'N$, 840–865 m) and Lucky Strike ($37^{\circ}17'N$, 1,620–1,730 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 ($36^{\circ}13'N$, 2,260–2350 m), Broken Spur ($29^{\circ}10'N$, 3,000 m), Snake Pit ($23^{\circ}23'N$, 3,480 m) and Logatchev ($14^{\circ}45'N$, 2,930–3,020 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 ($12^{\circ}58'N$, 4,080 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 nMAR. (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, but 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 and Doerries, 2005). Quantitative samples of the bathymodiolid vent mussels and associated macrofauna were compared from Logatchev (Van Dover and Doerries, 2005), Snake Pit (Turnipseed et al., 2004) and Lucky Strike (Van Dover and 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 and Doerries, 2005). Logatchev and Snake Pit mussel beds shared 55 per cent of associated macrofaunal benthic invertebrate species, whereas Logatchev and Snake Pit only shared 20–25 per cent 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 and 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, but 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 per cent of the sampled meiofauna individuals, and all seven species were new to science.

Copepods were the second most numerous, representing 35 per cent 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 two-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 had been 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 helena*, *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 per cent 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 northernmost 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 per cent of specimens; Tchesunov, 2015) and *H. vandoverae* for Snake Pit (75–91 per cent 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, while 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, while 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 and Defaye, 2004; Ivanenko et al., 2012; Cuvelier et al., 2014), *Bathylaphonte 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 publicly-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 bythograeid 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, although 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” while 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 more than 95 per cent 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 (deeper than 1000 m) determined that approximately 60 per cent 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 and 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 and 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 and Gebruk (2006b) shared 38 per cent of species sampled with the Pacific Ocean fauna. Only 1 per cent of the invertebrate

species sampled on the Reykjanes Ridge section of the MAR were endemic to the MAR (Mironov and 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 and 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. 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 italicica* (approximately 1 cm in 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 fracture 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 brittle stars *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 and Molodtsova, 2017). *Nanacalathis atlantica* is now known to occur in the Central Western Atlantic (off the Bahamas), at Great Meteor Seamount and in the tropical nMAR. Some *N. atlantica* specimens were attached to pteropod shells, which have also been found in high concentrations on the sea floor in some locations along the MAR, such as south of the CGFZ (Alt et al., 2019). Sea stars were only recorded from shallower stations, not deeper than 2,700 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 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 (lebenssspuren) created through the bioturbation of large epibenthic and infaunal organisms (Bell et al., 2013). Lebenssspuren at 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 lebenssspuren-forming megafaunal assemblages occurred both east and west of the MAR, and north and south of the CGFZ (Bell et al., 2013). Information on lebenssspuren distribution on sediments at 4,200–4,500 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 per cent 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 ROV

survey (Gebruk and 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 new species: *Benthodytes gosarsi*, *Penilpida midatlantica*, *Peniagone marecoi* and *Peniagone longipapillata* (Gebruk, 2008). Thirty-two species of holothurians were also collected from the CGFZ region by ECOMAR, including a further three new species, *Laetmogone billetti*, *Ellipinion alani* and *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 m²) of small (10–15 mm length) *Kolga nana* holothurians discovered in the CGFZ region (Gebruk and Krylova, 2013). Aggregations of *K. nana* have also been observed at the Porcupine Abyssal Plain (aggregations with a mean density of 50 individuals per m²), where *K. nana* were

Figure 10.14 In-situ images of holothurians (sea cucumbers) from the nMAR in the vicinity of the CGFZ. 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)



thought to aggregate in response to periodical fluxes of organic matter to the sea floor (Billett and Hansen, 1982).

10.1.7.4.2.2 Ophiuroidea (brittle stars)

Ophiuroids (brittle stars) were also observed on the soft sediments of the MAR (Gebruk and 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 and 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 per cent of species shared between the Reykjanes Ridge and the MAR between the CGFZ and the Azores. Fifty-two per cent of species occurred along the MAR and on both the East and West sides of the North Atlantic, with 35 per cent of species occurring along the MAR and in either the east or the west. Only 13 per cent (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 from the CGFZ during MAR-ECO. *Ophioplithus 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 and 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 3,509 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 CGFZ 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 from 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 northeast, northwest, 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), 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 and 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).

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 *Allapalus isidis* (Priede et al., 2012). Enteropneusts are thought to be able to float in the water column to passively move from one benthic foraging

Figure 10.15 In-situ images of echinoids (sea urchins) from the nMAR in the vicinity of the CGFZ. 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)



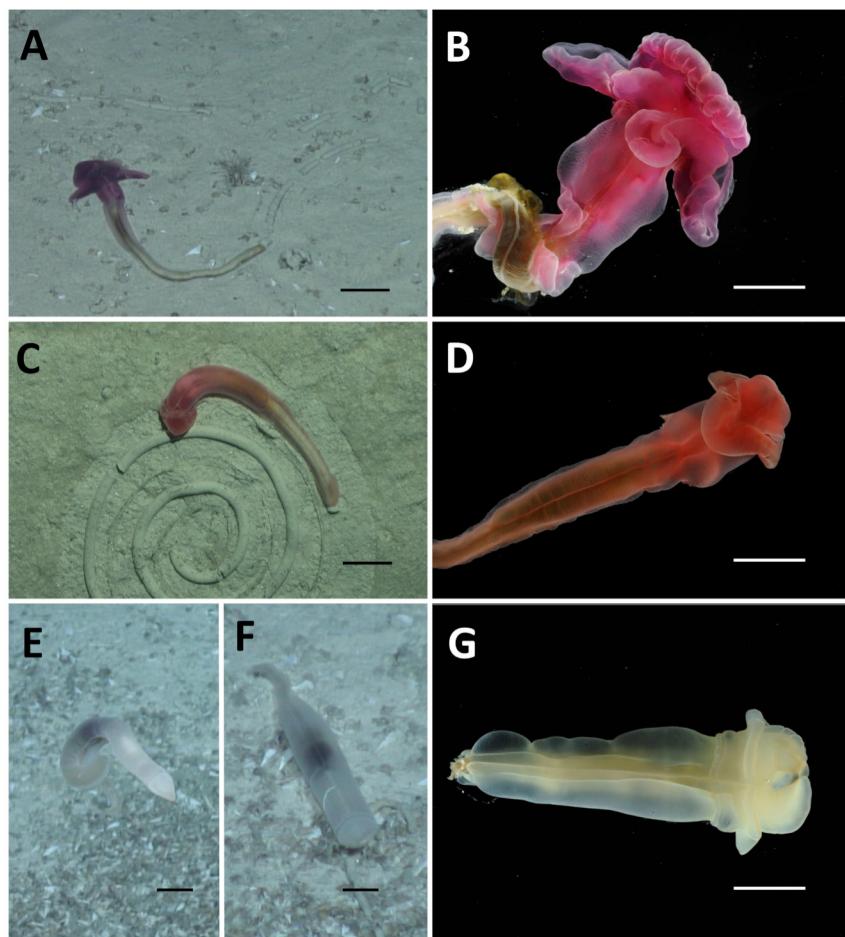
site to the next, in a similar fashion to benthopelagic holothurians, and produce distinctive feeding patterns on the sea floor (Priede et al., 2012). Very little is known about enteropneusts in general, and there is insufficient information available to describe their regional distribution along the 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).

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 be too small to sample by trawl, and in part 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.

Figure 10.16 Three new species of enteropneusts (free-living acorn worms) discovered on the MAR (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. *Allapalus 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 2,500 m depth. (Courtesy of Monty Priede and David Shale)



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 and 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 and Blanco-Perez, 2013). Comparisons between samples collected from the northeast, northwest, southeast and southwest 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 neither the CGFZ nor the MAR presented a physical barrier to the distribution of bathyal polychaetes (Shields and 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 from 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 are comprised of three known species or subspecies: *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 northeast America and west Greenland (Brandt and Andres, 2008). A subsequent expedition along the Vema Fracture Zone (occurring at approximately 11°N) suggested that certain macrostyliid isopods have ranges extending more than 2,000 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.

10.1.8 Benthic and demersal zooplankton

The benthic and demersal zooplankton, whilst not 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 sea floor but in the

water column immediately above (the benthopelagic). As a result, this section is not subdivided into sea-floor habitat types. Where benthopelagic zooplankton are predominantly found either on or immediately above a particular sea-floor 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 and Baker, 1982; Roe, 1988). At a depth of 5,000 m the biomass is 0.1 per cent of that of zooplankton in surface waters (Wishner, 1980a). Zooplankton biomass may rise slightly close to the seabed within the BBL (Wishner, 1980a; Angel and 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

Figure 10.17 Left: High-definition image of *Paleodictyon nodosum* trace at the MAR, 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)



octopods, swimming holothurians and appendicularians (Barnes et al. 1976; Billett et al., 1985; Wishner, 1980b; Pawson and Foel, 1986; Miller and Pawson, 1990; Larson et al., 1992; Christiansen et al., 1999; Bühring and Christiansen, 2001; Vinogradov, 2005; Collins and 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 northeast Atlantic, Christiansen et al. (2010) sampled at 1, 15, 50 and 100 m above the seabed. They found that while zooplankton communities (excluding gelatinous forms) in the upper three layers were similar and were dominated by copepods (around 75 per cent), the community close to the seabed (1 m 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 Oceans found that the dominant benthopelagic family was composed mainly of detritivores (Renz and 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 sea floor but in the water column immediately above (the benthopelagic). As a result, this section is not subdivided into sea-floor habitat types. Where benthic and demersal nekton are predominantly found either on or immediately above a particular sea-floor 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, while 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 sea-floor types and are present in both hard substrata and soft sediment communities along the MAR (Duffy et al., 2013; Horton et al., 2013; Horton and 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 per cent 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 (more than 90 per cent of the specimens in some samples) was *Abyssorchromene 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). *Abyssorchromene 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 CGFZ 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 and Merrett's (1988) "rise" fauna, found along continental slopes at depths less than 4,500 m, whilst the few forms seen on deeper dives were those more typically associated with the abyssal plain (depths greater than 4,500 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 sea-floor types (Felley et al., 2008).

Bottom trawling of soft sediment areas around 2,500 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 per cent 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

Figure 10.18 Images of scavenging fishes observed attracted to bait deployed at around 2,500 m depth on the MAR. (Reproduced from Cousins et al., 2013a)



of the 19 species observed at all baited camera locations (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 CGFZ, 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 sea floor. The fish *Bathysaurus mollis* was observed motionless on the bottom, whilst *Antimora rostrata* was seen swimming either close to or several meters above the sea floor. Two ophidiid fish individuals and one synaphobranchid eel were also observed swimming 1–2 m above the sea floor.

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, while other trawl types predominantly sample 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 per cent of individuals collected by benthic trawls (74 individuals), followed by the squid *Gonatus stenstrupi* (47 individuals), and octopod *Stauroteuthis syrtensis* (25 individuals). The other 13 species collected in both benthic and pelagic trawls occurred in very low abundance (fewer than 10 individuals), with nine of these species only being sampled once across all benthic trawls.

The squid *G. stenstrupi* 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. stenstrupi* were most abundant in the surface samples, and particularly so in the CGFZ area. Only large *G. stenstrupi* were observed at the sea floor 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. stenstrupi* 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 concentration 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 sea floor (Roper and 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 sea floor (Vecchione et al., 2010a). It is thought that this species may aggregate near the sea floor 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 MAR, although 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 fewer 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 sea floor or swim and drift just above it (Vecchione and Roper, 1991; Vecchione and 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 and Brundage, 1972; Vecchione and Young, 1997), they have a benthopelagic distribution (Villanueva et al., 1997; Collins and 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.

The biological communities of inactive sulphide substrata have been very sparsely 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 exhibit distribution patterns not only 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 hydrothermal vent communities, with multiple scales of both temporal and spatial scale potentially interacting to influence overall productivity of the 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.

Different MAR benthic habitats experience variability on different time scales, and

Table 10.3 Fish species recorded from hydrothermal vents along the MAR. 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	<i>Cataetyx laticeps</i> ^G	Bythtid fish
Chimaeridae	<i>Hydrolagus affinis</i> ^G	Small-eyed rabbit fish
	<i>Hydrolagus pallidus</i> ^G	Pallid ghost shark
Lotidae	<i>Gaidropsarus</i> sp.*	Gadoid fish
Macrouridae	<i>Coryphaenoides armatus</i> ^G	Armed grenadier
Moridae	<i>Lepidion schmidti</i> ^G	Schmidt's cod
Sebastidae	<i>Trachyscorpia echinata</i> ^G	Spiny scorpion fish
Synaphobranchidae	<i>Ilyophis saldanhai</i> *	Arrow-tooth eel
Zoarcidae	<i>Pachycara saldanhai</i> *	Eel pout
	<i>Pachycara thermophilum</i> *	Eel pout

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

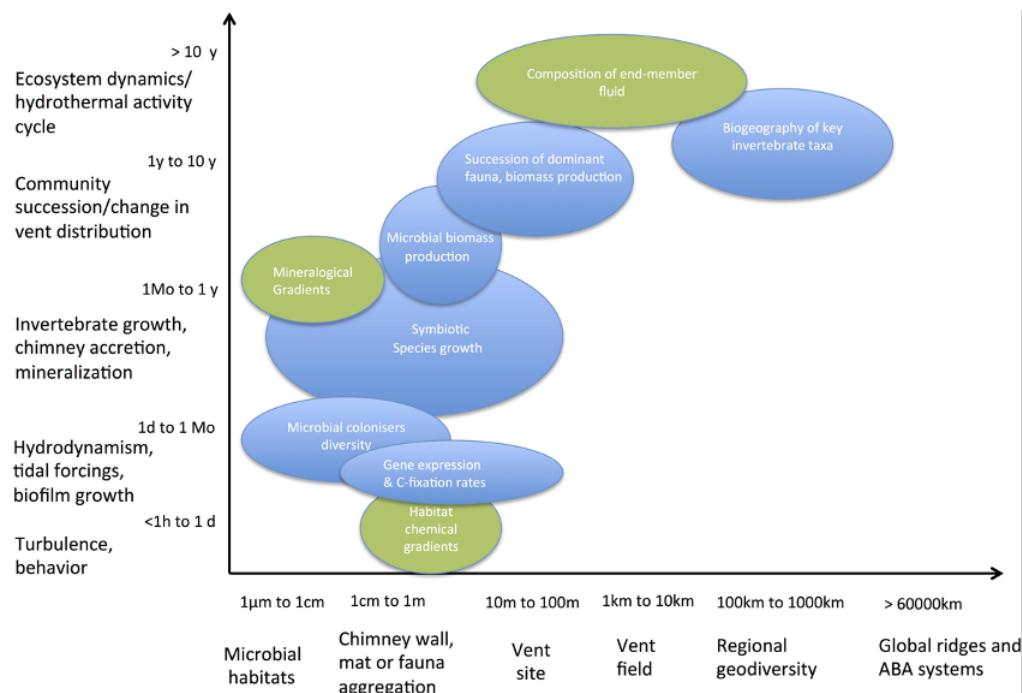
the benthic invertebrate fauna, whilst hydrothermally-active communities are the best studied to date.

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

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)



MAR. Whilst there are no published studies on the temporal variability of microbial communities at inactive sulphide habitat along the MAR, 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) than those at high-temperature habitat (Perner et al., 2009). This was attributed to short-term hydrothermal fluid variability resulting from dynamic sub-sea-floor 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 long timescale, studies at Lost City hydrothermal vents discovered shifts in archaea and bacteria communities over 1,000-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 1,000-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 (ventcap) 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 (from 70 to 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 sea floor 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, Nautiales and 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 shifts 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 and 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 northeast Atlantic populations (Waller and 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 northeast Atlantic was thought to be in response to seasonal phytoplankton blooms, which lead to an increased input of organic matter to the sea floor around July, acting as the cue for *L. pertusa* to initiate gametogenesis (Waller and 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 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 in Chapter 7, "Cumulative impacts" above.

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 sea floor multidisciplinary observatory at 37N (Lucky Strike vent field), which was established in 2010.⁸ Annual cruises to the EMSO-Azores observatory coordinated by Ifremer through the international Monitoring the Mid-Atlantic Ridge (MoMAR)⁹ project 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 demonstrate 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 per cent 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

⁸ EMSO-Azores non-cabled seafloor observatory: <http://www.emso-fr.org/EMSO-Azores>

⁹ MoMARSAT: <https://campagnes.flotteoceanographique.fr/series/130/>

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 (Vrijenhoek, 2010).

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 *Phymorhynchus* 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 sea floor, 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 sea floor, 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 sea-floor depressions, which supported increased numbers of giant Syringamminidae forams, polychaete tubes and anemones (Gebruk and Krylova, 2013). These organisms all have limited mobility, suggesting a longer-term enrichment of the sea floor, perhaps associated with the retention of phytodetrital material in sea-floor hollows. Seasonal phytodetritus enrichment of the sea floor can also lead to high abundances of opportunistic mobile benthic invertebrates, such as the aggregations (23–76 individuals per m²) of small (10–15 mm length) *Kolga nana* swimming holothurians discovered in the CGFZ region (Gebruk and 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 sea floor (Billett and 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 sea floor 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°N 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 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 sea floor 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 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 subdivided into sea-floor 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), but 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 subdivided into sea-floor 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 migration, to link the seabed environment with higher levels within the water column (Billett et al., 1985; Angel, 1990; Roe et al., 1990), and 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 and 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 localised increases in population in response to whale falls. The periodicity of whale falls to the MAR sea floor 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 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 sea floor. 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. (2012), 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 and 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. Sea-floor depressions and sea-floor 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, this "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 a 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 sea floor. 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 ^{13}C and ^{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, and 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 feed on either bacteria or detritus trapped within the byssus net. The crab *Segonzacia mesatlantica* predaes 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; and 2) 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 addition 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 $\delta^{13}\text{C}$ values for these species from Ashadze-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 $\delta^{15}\text{N}$ values for these four species at Ashadze-1 suggests that their nitrogen source does not stem directly from a 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 $\delta^{34}\text{S}$ 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, detritivore/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 ^{13}C and ^{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 per cent of the total meiobenthos at the site, followed by parasitic copepods and mites. All the nematodes and the majority of copepod individuals (80 per cent of Dirivultidae) were primary consumers, with parasites only making up 20 per cent 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 detritore/scavengers or bacterivore/archivores, depending on the assemblage they occurred within. The deposit-feeding *Oncholaimus dyvae* nematodes were either detritore/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, it 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 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 (10–15 mm length) *Kolga* sp. holothurians (later identified as *Kolga nana*: Rogacheva, 2012) on soft sediment habitat at approximately 4,500 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 sea floor (Billett and Hansen, 1982). Also, within the deep central part of the CGFZ, Gebruk and 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 and Blanco-Perez (2013) determined that surface deposit feeders represented more than 70 per cent of polychaete abundance at each soft sediment site visited. Carnivore or scavenging species accounted for much less, being approximately 15 per cent 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 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*, *Parapaspheaea sulcatifrons* and *Sergia japonicus*) collected from 2,000 m water depth along the MAR were consistent with unmodified photosynthetic food sources, 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 MAR. Bergstad et al. (2010) determined that the diet of *Coryphaenoides rupestris* was 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. They 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 and biological habitat formation. Others could be classified as supporting services, such as nutrient cycling, circulation, chemosynthetic and secondary production, and biodiversity. Still 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- and 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 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 sea-floor 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 sea-floor-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, 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. Hugler 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°-phosphosulphate pathway and fix carbon dioxide via the Calvin-Benson-Bassham cycle. Hugler 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°-phosphosulphate pathway (Hugler 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 sea-floor subsurface, where higher temperatures are reached, and are carried to the sea floor within the vent fluids (Hugler 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, 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 thought to have the metabolic potential for nitrogen (nitrogen fixation, ammonia oxidation and 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 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 sea floor (Beazley et al., 2013; Henry and 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 and Folke, 1999).

Sponges, with their filter-feeding capacity, can filter more than 90 per cent of bacteria and organic matter from seawater, thus 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 nutrient 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 and 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

The 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 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 exploitation. 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, population genetic studies of MAR symbionts have not yet been performed. A study from the 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

There are still considerable knowledge gaps hampering the use of connectivity data and information in the development of environmental management measures. 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 microsatellite markers have 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), attach to the substratum, and develop into juvenile sponges.

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; DeBiase 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 and 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 (850–2,251 m) northern localities, and *B. puteoserpentis* occurs at the deeper (3,080–3,650 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 less than 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 MAR 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, 4,090 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 CGFZ. 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 or 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 a 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 removal of larger areas of habitat is not known and is particularly important as the global extent of known active hydrothermal vent ecosystems is not known and is particularly important, as the global extent of active hydrothermal vent ecosystems is estimated to cover only 50 km², less than 0.00001 per cent 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 future 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 and 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

Abascal, F. J., Mejuto, J., Quintans, M., García-Cortés, B. and Ramos-Cartelle, A. (2015). Tracking of the broadbill swordfish, *Xiphias gladius*, in the central and eastern North Atlantic. *Fisheries Research* 162, 20-28.

Abell, R. E., Brand, T., Dale, A. C., Tilstone, G. H. and Beveridge, C. (2013). Variability of particle flux over the Mid-Atlantic Ridge. *Deep-Sea Research II* 98, 257-268.

Afonso, P., McGinty, N., Graça, G., Fontes, J., Inácio, M., Totland, A. and Menezes, G. (2014a). Vertical migrations of a deep-sea fish and its prey. *PLoS ONE* 9(5), e97884.

Afonso, P., McGinty, N. and Machete, M. (2014b). Dynamics of whale shark occurrence at their fringe oceanic habitat. *PLoS ONE* 9(7), e102060.

Akimtsev et al. (1991). *Transactions (Doklady) of the U.S.S.R. Academy of Science: Earth Science Section* 312, 32-37.

Alt, C. H. S., Rogacheva, A., Boorman, B., Hughes, J. A., Billett, D. S. M., Gooday, A. J. and Jones, D. O. B. (2013). Trawled megafaunal invertebrate assemblages from bathyal depth of the Mid-Atlantic Ridge (48°–54°). *Deep Sea Research Part II* 98(B), 326-340.

Alt, C. H. S., Kremenetskaia (Rogacheva), A., Gebruk, A. V., Gooday, A. J., Jones, D. O. B. (2019). Bathyal benthic megafauna from the Mid Atlantic Ridge in the region of the Charlie Gibbs fracture zone based on remotely operated vehicle operations. *Deep-Sea Research I* 145, 1-12.

Anderson, T. R., Martin, A. P., Lampitt, R. S., Trueman, C. N., Henson, S. A. and Mayor, D. J. (2019). Quantifying carbon fluxes from primary production to mesopelagic fish using a simple food web model. *ICES Journal of Marine Science* 76, 690-701.

Angel, M. V. (1990). Life in the Benthic Boundary Layer: connections to the mid-water and the seafloor. *Philosophical Transactions of the Royal Society of London, Series A* 331, 15-28.

Angel, M. V. and Baker, A. D. C. (1982). Vertical distribution of the standing crop of plankton and micronekton at three

- stations in the northeast Atlantic. *Biological Oceanography* 2, 1-30.
- Aksnes, D. L., Røstad, A., Kaartvedt, S., Martinez, U., Duarte, C. M. and Irigoien, X. (2017) Light penetration structures the deep acoustic scattering layers in the global ocean. *Scientific Advances* 3, e1602468.
- Arregui, I., Galuardi, B., Goni, N., Lam, C. H., Fraile, I., Santiago, J., Lutavage, M. and Arrizabalaga, H. (2018). Movements and geographic distribution of juvenile bluefin tuna in the Northeast Atlantic, described through internal and satellite archival tags. *ICES Journal of Marine Science* 75(5), 1560-1572.
- Arrizabalaga, H., López-Rodas, V., Ortiz de Zárate, V., Costas, E. and González-Garcés, A. (2002). Study on the migrations and stock structure of albacore (*Thunnus alalunga*) from the Atlantic Ocean and the Mediterranean Sea based on conventional tag release-recapture experiences. *Collective Volume of Scientific Papers ICCAT* 54(4), 1479-1494.
- Ashford, O. S., Kenny, A. J., Frojan, C. R. S. B., Downie, A.-L., Horton, T., Rogers, A. D. (2019). On the influence of vulnerable marine ecosystem habitats on peracarid crustacean assemblages in the Northwest Atlantic Fisheries Organisation regulatory area. *Frontiers in Marine Science* 6, 401.
- Bachraty, C., Legendre, P. and Desbruyeres, D. (2009). Biogeographic relationships among deep-sea hydrothermal vent faunas at a global scale. *Deep-Sea Research I* 56(8), 1371-1378.
- Badcock, J. and Merrett, N. R. (1976). Midwater fishes in the eastern North Atlantic—I. Vertical distribution and associated biology in 30°N, 23°W, with developmental notes on certain myctophids. *Progress in Oceanography* 7, 3-58.
- Baker, P., Minzlaff, U., Schoenle, A., Schwabe, E., Hohlfeld, M., Jeuck, A., Brenke, N., Prausse, D., Rothenbeck, M., Brix, S., Frutos, I., Jorger, K. M., Neusser, T. P., Koppelman, R., Devey, C., Brandt, A. and Arndt, H. (2018). Potential contribution of surface-dwelling *Sargassum* algae to deep-sea ecosystems in the southern North Atlantic. *Deep-Sea Research II* 48, 21-34.
- Barnes, A. T., Quetin, L. B., Childress, J. I., Pawson, D. L. (1976). Deep-Sea macroplanktonic sea cucumbers: Suspended sediment feeders captured from deep submergence vehicle. *Science* 194, 1083-1085.
- Bard, F. X. and Amon Kothias, J. B. (1986). Résultats des campagnes e marquage de thonidés tropicaux menées par la Côte d'Ivoire (1983-1984). *Collective Volume of Scientific Papers ICCAT* 25(1), 30-36.
- Bard, F. X., Cayré, P. and Diouf, T. (1991). Migraciones. In: Fonteneau A & Marcille J (Eds.) Recursos, pesca y biología de los túnidos tropicales del Atlántico centro-oriental. *Collective Volume of Scientific Papers ICCAT* 37(1), 120-168.
- Bard, F. X. and Hervé, A. (1994). Structure de stock de l'albacore (*Thunnus albacares*) Atlantique d'après les marquages comparés aux lieux de ponte. *Collective Volume of Scientific Papers ICCAT* 42(1), 204-208.
- Beaugard, G. and Reid, P. (2003). Long-term changes in phytoplankton, zooplankton and salmon related to Climate. *Global Change Biology* 9, 801-817.
- Beaulieu, S. E., Baker, E. T. and German, C. R. (2015). Where are the undiscovered hydrothermal vents on oceanic spreading ridges? *Deep-Sea Research II* 121, 202-212 & Supplementary information.

- Beazley, L. I., Kenchington, E. L., Murillo, F. J. and Sacau, M. M. (2013). Deep-sea sponge grounds enhance diversity and abundance of epibenthic megafauna in the Northwest Atlantic. *ICES Journal of Marine Science* 70(7), 1471-1490.
- Belkin, I. M., Cornillon, P. C. and Sherman, K. (2009). Fronts in large marine ecosystems. *Progress in Oceanography* 81(1-4), 223-236.
- Bell, J. B., Jones, D. O. B. and Alt, C. H. S. (2013). Lebenssspuren of the Bathyal Mid-Atlantic Ridge. *Deep-Sea Research II* 98, 341-351.
- Bellec, L., Cambon Bonavita, M. A., Cueff-Gauchard, V., Durand, L., Gayet, N. and Zeppilli, D. (2018). A nematode of the mid-Atlantic ridge hydrothermal vents harbors a possible symbiotic relationship. *Frontiers in Microbiology* 9, 2246.
- Bel'tenev, V. E., Lazareva, L. I., Cherkashev, G. A., Ivanov, V. I., Rozhdestvenskaya, I. I., Kuznetsov, V. A., Laiba, A. A. and Narkevskiy, E. V. (2017). New hydrothermal sulphide fields of the Mid-Atlantic Ridge: Yubileinoe ($20^{\circ}09'N$) and Surprise ($20^{\circ}45.4'N$). *Doklady Earth Sciences* 476(1), 1010-1015.
- Bel'tenev, V., Shagin, A., Markov, V., Rozhdestvenskaya, I., Stepanova, T., Cherkashev, G., Fedorov, I., Rumyantsev, A. and Poroshina, I. (2004). A new hydrothermal field at $16^{\circ}38.4'N$, $46^{\circ}28.5'W$ on the Mid Atlantic Ridge. *InterRidge News* 13, 5-6.
- Benoit-Bird, K. J., Moline, M. A. and Southall, B. L. (2017). Prey in oceanic sound scattering layers organize to get a little help from their friends. *Limnology and Oceanography* 62, 2788-2798.
- Bergstad, O. A., Clark, L., Hansen, H. O., Cousins, N. (2012). Distribution, population biology, and trophic ecology of the deepwater demersal fish *Halosauropsis macrochir* (Pisces: Halosauridae) on the Mid-Atlantic Ridge. *PLoS ONE* 7(2), e131493.
- Bergstad, O. A., Falkenhaug, T., Astthorsson, O. S., Byrkjedal, I., Gebruk, A. V., Piatkowski, U., Priede, I. G., Santos, R. S., Vecchione, M., Lorance, P. and Gordon, J. D. M. (2008). Towards improved understanding of the diversity and abundance patterns of the mid-ocean ridge macro- and megafauna. *Deep-Sea Research II* 55, 1-5.
- Bergstad, O. A. and Gebruk, A. V. (2008). Approach and methods for sampling of benthic fauna on the 2004 MAR-ECO expedition to the Mid-Atlantic Ridge. *Marine Biology Research* 4(1-2), 160-163.
- Bergstad, O. A., Gjelsvik, G., Schander, C. and Hoines, A. S. (2010). Feeding ecology of *Coryphaenoides rupestris* from the Mid-Atlantic Ridge. *PLoS one* 5(5), e10453.
- Bergstad, O. A. and Godø, O. R. (2003). The pilot project "Patterns and processes of the ecosystems of the northern Mid-Atlantic": aims, strategy and status. *Oceanologica Acta* 25, 219-226.
- Bergstad, O. A., Menzes, G. and Hoines, A. S. (2008). Demersal fish on a mid-ocean ridge: Distribution patterns and structuring factors. *Deep-Sea Research II* 55(1-2), 185-202.
- Bergstad, O. A., Menezes, G. M. M., Hoines, A. S., Gordon, J. D. M. and Galbraith, J. K. (2012). Patterns of distribution of deepwater demersal fishes of the North Atlantic mid-ocean ridge, continental slopes, islands and seamounts. *Deep-Sea Research I* 61, 74-83.
- Bernard, A. M., Finnegan, K. A. and Shivji, M. S. (2019). Genetic connectivity dynamics of the giant barrel sponge, *Xestospongia muta*, across the Florida Reef Tract and Gulf of Mexico. *Bulletin of Marine Science* 95(2), 161-175.

- Biais, G., Coupeau, Y., Séret, B., Calmettes, B., Lopez, R., Hetherington, S. and Righton, D. (2017). Return migration patterns of porbeagle shark (*Lamna nasus*) in the Northeast Atlantic: implications for stock range and structure. *ICES Journal of Marine Science* 74, 1268-1276.
- Billet, D. S. M. (1991). Deep-sea holothurians. *Oceanography and Marine Biology: An Annual Review* 29, 259-317.
- Billett, D. S. M. and Hansen, B. (1982). Abyssal aggregations of *Kolga hyalina* Danielssen & Koren (Echinodermata, Holothuroidea) in the northeast Atlantic Ocean, a preliminary report. *Deep-Sea Research* 29, 799-818.
- Billett, D. S. M., Hansen, B., Huggett, Q. J. (1985). Pelagic Holothuroidea (Echinodermata) of the northeast Atlantic. In: Keegan, B. F. and O'Connor, B. D. S. (Eds.), *Echinodermata: Proceedings of the 5th International Echinoderms Conference, Galway*, 399-411.
- Billings, A., Kaiser, C., Young, C. M., Hiebert, L. S., Cole, E., Wagner, J. K. S. and Van Dover, C. L. (2017). SyPRID sampler: A large-volume, high-resolution, autonomous, deep-ocean precision plankton sampling system. *Deep-Sea Research II* 137, 297-306.
- Bitner, M. A. and Molodtsova, T. N. (2017). Redescription of *Nanacalathis atlantica* Zezina, 1991 (Brachiopoda: Chlidonophoridae) from the North Atlantic. *Marine Biodiversity*, 1-5.
- Block, B. A., Dewar, H., Blackwell, S. B., Williams, T. D., Prince, E. D., Farwell, C. J., Boustany, A., Teo, S. L. H., Seitz, A., Walli, A. and Fudge, D. (2001). Migratory movements, depth preferences, and thermal biology of Atlantic bluefin tuna. *Science* 293(5533), 1310-1314.
- Block, B. A., Teo, S. L., Walli, A., Boustany, A., Stokesbury, M. J., Farwell, C. J., Weng, K. C., Dewar, H. and Williams, T. D. (2005). Electronic tagging and population structure of Atlantic bluefin tuna. *Nature* 434(7037), 1121-1127.
- Bober, S., Brix, S., Riehl, T., Schwentner, M. and Brandt, A. (2018). Does the Mid-Atlantic Ridge affect the distribution of abyssal benthic crustaceans across the Atlantic Ocean? *Deep-Sea Research II* 148, 91-104.
- Bonatti, E., Guerstein-Honnerez, B.-M. and Honnerez, J. (1976). Copper-Iron sulphide mineralizations from the equatorial Mid-Atlantic Ridge. *Economic Geology* 71, 1515-1525.
- Boschen, R. E., Rowden, A. A., Clark, M. R., Gardner, J. P. A. (2013). Mining of deep-sea seafloor massive sulphides: A review of the deposits, their benthic communities, impacts from mining, regulatory frameworks and management strategies. *Ocean and Coastal Management* 84, 54-67.
- Boschen, R. E., Rowden, A. A., Clark, M. R., Pallentin, A., Gardner, J. P. A. (2015). Seafloor massive sulfide deposits support unique megafaunal assemblages: Implications for seabed mining and conservation. *Marine Environmental Research* 115, 78-88.
- Boschen, R. E., Collins, P. C., Tunnicliffe, V., Carlsson, J., Gardner, J. P. A., Lowe, J., McCrone, A., Metaxas, A., Sinniger, F. and Swaddling, A. (2016). A primer for use of genetic tools in selecting and testing the suitability of set-aside sites protected from deep-sea seafloor massive sulfide mining activities. *Ocean and Coastal Management* 122, 37-48.
- Bower, A. S., Le Cann, B., Rossby, T., Zenk, W., Gould, J., Speer, K., Richardson, P. L., Prater, M. D. and Zhang, H.-M. (2002b). Directly measured mid-depth circulation in the northeastern North Atlantic Ocean. *Nature* 419(6907), 603.

- Bower, A. S., Serra, N. and Ambar, I. (2002a). Structure of the Mediterranean Undercurrent and Mediterranean Water spreading around the southwestern Iberian Peninsula. *Journal of Geophysical Research: Oceans* 107(C10), 25-1.
- Bower, A. S. and von Appen, W. J. (2008). Interannual variability in the pathways of the North Atlantic Current over the Mid-Atlantic Ridge and the impact of topography. *Journal of Physical Oceanography* 38(1), 104-120.
- Braga-Henriques, A., Porteiro, F. M., Ribeiro, P. A., de Matos, V., Sampaio, I., Ocana, O. and Santos, R. S. (2013). Diversity, distribution and spatial structure of the cold-water coral fauna of the Azores (NE Atlantic). *Biogeosciences* 10, 4009-4036.
- Brandt, A. and Andres, H. G. (2008). Description of *Aega sarsae* sp. nov. and redescription of *Syscenus atlanticus* Kononenko, 1988 (Crustacea, Isopoda, Aegidae) from the Mid-Atlantic Ridge. *Marine Biology Research* 4(1-2), 61-75.
- Braun, C. D., Skomal, G. B. and Thorrold, S. R. (2018). Integrating archival tag data and a high-resolution oceanographic model to estimate basking shark (*Cetorhinus maximus*) movements in the Western Atlantic. *Frontiers in Marine Science* 5, 25.
- Brazelton, W. J., Ludwig, K. A., Sogin, M. L., Andreishcheva, E. N., Kelley, D. S., Shen, C.-C., Edwards, R. L. and Baross, J. A. (2009). Archaea and bacteria with surprising microdiversity show shifts in dominance over 1,000-year time scales in hydrothermal chimneys. *PNAS* 107(4), 1612-1617.
- Breusing, C., Biastoch, A., Drews, A., Metaxas, A., Jollivet, D., Vrijenhoek, C., Bayer, T., Melzner, F., Sayavedra, L., Petersen, J. M., Dubilier, N., Schilhabel, M. B., Rosenstiel, P. and Reusch, B. H. (2016). Biophysical and population genetic models predict the presence of "phantom" stepping stones connecting Mid-Atlantic Ridge vent ecosystems. *Current Biology* 26, 2257-2267.
- Breusing, C., Vrijenhoek, R. C. and Reusch, T. B. H. (2017). Widespread introgression in deep-sea hydrothermal vent mussels. *BMC Evolutionary Biology* 17, 13.
- Briggs, J. C. (1960). Fishes of worldwide (circumtropical) distribution. *Copeia*, 171-180.
- Brill, R. W., Lutcavage, M. E., Metzger, G., Bushnell, P. G., Arendt, M., Lucy, J., Watson, C. and Foley, D. (2002). Horizontal and vertical movements of juvenile bluefin tuna (*Thunnus thynnus*) in relation to oceanographic conditions of the western North Atlantic, determined with ultrasonic telemetry. *Fishery Bulletin* 100(2), 155-167.
- Brix, S., Bober, S., Tschesche, C., Kihara, T. C., Driskell, A. and Jennings, R. M. (2018). Molecular species delimitation and its implications for species descriptions using desmosomatid and nannoniscid isopods from the VEMA fracture zone as example taxa. *Deep-Sea Research II* 148, 180-207.
- Brongersma, L. D. (1972). European Atlantic Turtles. *Zoologische Verhandelingen* 121, 318.
- Brown, C. A. (1995). Preliminary examination of size and location data for US tagged and recaptured swordfish. *Collective Volume of Scientific Papers ICCAT* 44(3), 217-224.
- Bühring, S. I. and Christiansen, B. (2001). Lipids in selected abyssal benthopelagic animals: links to the epipelagic zone. *Progress in Oceanography* 50, 369-382.
- Cairns, S. (2007). Deep-water corals: An overview with special reference to diversity and distribution of deep-water scleractinian corals. *Bulletin of Marine Science* 81(3), 311-322.
- Cameron, L. W. J., Roche, W., Green, P., Houghton, J. D. R. and Mensink, P. J. (2018).

Transatlantic movement in porbeagle sharks, *Lamna nasus*. *Fisheries Research* 207, 25-27.

Campana, S. E., Dorey, A., Fowler, M., Joyce, W., Wang, Z., Wright, D. and Yashayaev, I. (2011). Migration pathways, behavioural thermoregulation and overwintering grounds of blue sharks in the Northwest Atlantic. *PLoS One* 6, e16854.

Catry, P., Dias, M. P., Phillips, R. A. and Granadeiro, J. P. (2013). Carry-over effects from breeding modulate the annual cycle of a long-distance migrant: an experimental demonstration. *Ecology* 94, 1230-1235.

Cardenas, P. and Tore Rapp, H. (2015). Demospanges from the Northern Mid-Atlantic Ridge shed more light on the diversity and biogeography of North Atlantic deep-sea sponges. *Journal of the Marine Biological Association of the United Kingdom*, 1-42.

Cardoso, I. A., Falkenhaug, T. and Fernandes, L. F. L. (2014). Comparison between the shrimp species richness (Caridea and Dendrobranchiata, Decapoda, Crustacea) of the South and North Mid-Atlantic Ridge. *Brazilian Journal of Oceanography* 62(1), 47-56.

Carlsson, J., McDowell, J. R., Carlsson, J. E., Olafsdóttir, D. and Graves, J. E. (2006). Genetic heterogeneity of Atlantic bluefin tuna caught in the eastern North Atlantic Ocean south of Iceland. *ICES Journal of Marine Science* 63(6), 1111-1117.

Carlsson, J., McDowell, J. R., Díaz-Jaimes, P., Carlsson, J. E., Boles, S. B., Gold, J. R. and Graves, J. E. (2004). Microsatellite and mitochondrial DNA analyses of Atlantic bluefin tuna (*Thunnus thynnus*) population structure in the Mediterranean Sea. *Molecular Ecology* 13(11), 3345-3356.

Carney, R. S. (2005). Zonation of deep biota on continental margins. *Oceanography*

and *Marine Biology: An Annual Review* 43, 211-278.

Carreiro-Silva, M., Andrews, A. H., Braga-Henriques, A., Porteiro, F. M., Matos, V. and Santos, R. S. (2013). Variability in growth rates of long-lived black coral *Leiopathes* sp. from the Azores (NE Atlantic). *Marine Ecology Progress Series* 473, 189-199.

Carreiro-Silva, M., Braga-Henriques, A., Sampaio, I., Matos, V., Porteiro, F. and Ocaña, O. (2011). *Isozoanthus primnoides*, a new zoanthid species (Anthozoa: Hexacorallia) associated with the gorgonian *Callogorgia verticillata* (Anthozoa: Octocorallia) in the Azores. *ICES Journal of Marine Science* 68, 408-415.

Carreiro-Silva, M., Ocaña, O. V., Stanković, D., Sampaio, I., Porteiro, F., Fabri, M.-C. and Stefanni, S. (2017). Zoanthids associated with cold-water corals in the Azores Region: hidden diversity in the deep-sea. *Frontiers in Marine Science* 4, 88.

Cerqueria, T., Pinho, D., Egas, C., Froufe, H., Altermark, B., Candeias, C., Santos, R. S. and Bettencourt, R. (2015). Microbial diversity in deep-sea sediments from the Menez Gwen hydrothermal vent system of the Mid-Atlantic Ridge. *Marine Genomics* 24(3), 343-355.

Chapman, A. S., Beaulieu, S. E., Colaço, A., Gebruk, A. V., Hilario, A., Kihara, T. C., Ramirez-Llodra, E., Sarrazin, J., Tunnicliffe, V., Amon, D. J., Baker, M. C., Boschen-Rose, R. E., Chen, C., Cooper, I. J., Copley, J. T., Corbari, L., Cordes, E. E., Cuvelier, D., Duperron, S., Du Preez, C., Gollner, S., Horton, T., Hourdez, S., Krylova, E. M., Linse, K., LokaBharathi, P. A., Marsh, L., Matabos, M., Mills, S. W., Mullineaux, L. S., Tore Rapp, H., Reid, W. D. K., Rybakova (Goroslavskaya), E., Thomas, T. R. A., Southgate, S. J., Stöhr, S., Turner, P. J., Watanabe, H. K., Yasuhara, M. and Bates, A. E. (2019). sFDvent: A global trait database for deep-sea hydrothermal vent fauna. *Global Ecology and Biogeography* 28, 1538-1551.

- Chevreux, E. (1903). Note préliminaire sur les amphipodes de la famille des Lysianassidae recueillis par la *Princess-Alice* dans les eaux profondes de l'Atlantique et de la Méditerranée. *Bulletin de la Société Zoologique de France* 28, 81-97.
- Chow, S., Okamoto, H., Miyabe, N., Hiramatsu, K. and Barut, N. (2000). Genetic divergence between Atlantic and Indo-Pacific stocks of bigeye tuna (*Thunnus obesus*) and a mixture around South Africa. *Molecular Ecology* 9(2), 221-227.
- Choy, C. A., Haddock, S. H. D. and Robison, B. H. (2017). Deep pelagic food web structure as revealed by *in situ* feeding observations. *Proceedings of the Royal Society Biological Sciences* 284, 20172116.
- Christakis, C. A., Polymenakou, P. N., Mandalakis, M., Nomikou, P., Kristoffersen, J. B., Lampridou, D., Kotoulas, G. and Magoulas, A. (2018). Microbial community differentiation between active and inactive sulphide chimneys of the Kolumbo submarine volcano, Hellenic Volcanic Arc. *Extremophiles* 22(1), 13-27.
- Christiansen, B. (2016). Deep-Sea Zooplankton Sampling. In: Clark MR, Consalvey M & Rowden AA (Eds.), *Biological Sampling in the deep sea*. 103-125.
- Christiansen, B., Bühring, S. I., Pfannkuche, O. and Weikert, H. (2010). The near-bottom plankton community at the Porcupine Abyssal Plain, NE-Atlantic: Structure and vertical distribution. *Marine Biology Research* 6, 113-120.
- Christiansen, B., Drüke, B., Koppelman, R. and Weikert, H. (1999). The near-bottom zooplankton at the abyssal BIOTRANS site, northeast Atlantic: composition, abundance and variability. *Journal of Plankton Research* 21, 1847-1863.
- Clarke, M. R., Martins, H. R. and Pascoe, P. (1993). The diet of sperm whales (*Physeter macrocephalus* Linnaeus 1758) off the Azores. *Philosophical Transactions: Biological Sciences* 339, 67-82.
- Clarke, T. A. (1982). Feeding habits of stomiatoid fishes from Hawaiian waters. *Fishery Bulletin* 80, 287-304.
- Cleary, J. S., DeLand, E., Mennini, S., McCrory, K., Ismail, P. N. and Halpin, P. N. (2019). *Data Report: Workshop on the Regional Environmental Management Plan for the Area of the Northern Mid-Atlantic Ridge*, 151 pp. Atlantic REMP Project.
- Clingham, E., Brown, J., Henry, L., Beard, A, and Dove, A. D. (2014). Evidence that St. Helena island is an important multi-use habitat for whale sharks, *Rhincodon typus*, with the first description of putative mating in this species. *PeerJ Preprints* 4, e1885v1.
- Coelho, R., Mejuto, J., Domingo, A., Yokawa, K., Romanov, E. V., Cortés, K. L. E., Hazin, F., Arocha, F., Masawbi, A., Pascal, M., Ortiz, V., William, D. Z., Pedro, R., Ana, B. G., Forselledo, M. R. R., Mas, F., Ohshima, S., Courtney, D., Sabarros, P. S., Perez, B., Wogerbauer, C., Felipe, W. T. and Santos, M. N. (2018). Distribution patterns and population structure of the blue shark (*Prionace glauca*) in the Atlantic and Indian Oceans. *Fish and Fisheries* 19(1), 90-106.
- Colaço, A., Dehairs, F. and Desbruyeres, D. (2002). Nutritional relations of deep-sea hydrothermal fields at the Mid-Atlantic Ridge: a stable isotope approach. *Deep-Sea Research I* 49(2), 395-412.
- Colaço, A., Desbruyeres, D., Guezennec, J. (2007). Polar lipid fatty acids as indicators of trophic associations in a deep-sea vent system community. *Marine Ecology* 28(1), 15-24.
- Colaço, A., Giacomello, E., Porteiro, F. and Menezes, G. M. (2013). Trophodynamic studies on the Condor seamount (Azores, Portugal, North Atlantic). *Deep-Sea Research II* 98(A), 178-189.

- Collette, B. B. and Nauen, C. E. (1983). FAO species catalogue. Vol. 2: Scombrids of the world: an annotated and illustrated catalogue of tunas, mackerels, bonitos, and related species known to date. FAO Fisheries Synopsis, 125. FAO: Rome. 137 p.
- Collins, M. A. and Henriques, C. (2000). A revision of the family Stauroteuthidae (Octopoda: Cirrata) with redescriptions of *Stauroteuthis syrtensis* and *S. gilchristi*. *Journal of the Marine Biological Association of the United Kingdom* 80, 685-697.
- Collins, M. A. and Villanueva, R. (2006). Taxonomy, ecology and behaviour of the cirrate octopods. *Oceanography and Marine Biology - An Annual Review* 44, 277-322.
- Collins, P. C., Kennedy, R., Van Dover, C. L. (2012). A biological survey method applied to seafloor massive sulphides (SMS) with contagiously distributed hydrothermal-vent fauna. *Marine Ecology Progress Series* 452, 89-107.
- Copley, J. T. P., Jorgensen, P. B. K. and Sohn, R. A. (2007). Assessment of decadal-scale ecological change at a deep Mid-Atlantic hydrothermal vent and reproductive time-series in the shrimp *Rimicaris exoculata*. *Journal of the Marine Biological Association of the UK* 87, 859-867.
- Copley, J. T. P., Tyler, P. A., Murton, B. J. and Van Dover, C. L. (1997). Spatial and interannual variation in the faunal distribution at Broken Spur vent field (29N, Mid-Atlantic Ridge). *Marine Biology* 129, 723-733.
- Cosgrove, R., Arregui, I., Arrizabalaga, H., Goni, N. and Sheridan, M. (2014). New insights to behaviour of North Atlantic albacore tuna (*Thunnus alalunga*) observed with pop-up satellite archival tags. *Fisheries research* 150, 89-99.
- Costello, M. J. and Breyer, S. (2017). Ocean depths: The mesopelagic and implications for global warming. *Current Biology* 27(1), R36-R38.
- Costello, M. J., Emblow, C. S. and White, R. (Eds.) (2001). European Register of Marine Species. A check-list of the marine species in Europe and a bibliography of guides to their identification. *Patrimoines naturels* 50, 463.
- Cousins, N. J., Linley, T. D., Jamieson, A. J., Bagley, P. M., Blades, H., Box, T., Chambers, R., Ford, A., Shields, M. A. and Priede, I. G. (2013a). Bathyal demersal fishes of Charlie-Gibbs Fracture Zone regions (49 - 54N) of the Mid-Atlantic Ridge: II. Baited camera lander observations. *Deep-Sea Research II* 98, 397-406.
- Cousins, N. J., Shields, M. A., Crockard, D. and Priede, I. G. (2013b). Bathyal demersal fishes of Charlie Gibbs Fracture Zone region (49 - 54N) of the Mid-Atlantic Ridge, I: Results from trawl surveys. *Deep-Sea Research II* 98, 388-396.
- Coykendall, D. K., Johnson, S. B., Karl, S. A., Lutz, R. A. and Vrijenhoek, R. C. (2011). Genetic diversity and demographic instability in *Riftia pachyptila* tubeworms from eastern Pacific hydrothermal vents. *BMC Evolutionary Biology* 11, 96.
- Craig, J., Youngbluth, M., Jamieson, A.J., and Priede, I. G. (2015). Near-floor bioluminescence, macrozooplankton and macroparticles at the Mid-Atlantic Ridge. *Deep-Sea Research I* 98, 62-75.
- Crepeau, V., Bonavita, M.-A. C., Lesongeur, F., Randrianalivello, H., Sarradin, P.-M., Sarrazin, J. and Godfroy, A. (2011). Diversity and function in microbial mats from the Lucky Strike hydrothermal vent field. *Federation of European Microbiological Societies Microbiology Ecology* 76, 524-540.
- Curtis, T. H., McCandless, C. T., Carlson, J. K., Skomal, G. B., Kohler, N. E., Natanson, L. J., Burgess, G. H., Hoey, J. J. and Pratt,

- H. L. Jr. (2014). Seasonal distribution and historic trends in abundance of white sharks, *Carcharodon carcharias*, in the Western North Atlantic Ocean. *PLoS ONE* 9(6), e99240.
- Cuvelier, D., Beesau, J., Ivanenko, V. N., Zeppilli, D., Sarradin, P.-M. and Sarrazin, J. (2014). First insights into macro- and meiofaunal colonisation patterns on paired wood/slate substrata at Atlantic deep-sea hydrothermal vents. *Deep-Sea Research I* 87, 70-81.
- Cuvelier, D., de Busserolles, F., Lavaud, R., Floc'h, E., Fabri, M. C., Sarradin, P. M. and Sarrazin, J. (2012). Biological data extraction from imagery - How far can we go? A case study from the Mid-Atlantic Ridge. *Marine Environmental Research* 82, 15-27.
- Cuvelier, D., Legendre, P., Laes-Huon, A., Sarradin, P. M. and Sarrazin, J. (2017). Biological and environmental rhythms in (dark) deep-sea hydrothermal ecosystems. *Biogeosciences* 14, 2955-2977.
- Cuvelier, D., Sarrazin, J., Colaco, A., Copley, J. T., Desbruyeres, D., Glover, A. G., Tyler, P. A. and Serrao Santos, R. (2009). Distribution and spatial variation of hydrothermal faunal assemblages at Lucky Strike (Mid-Atlantic Ridge) revealed by high-resolution video image analysis. *Deep-Sea Research I* 56, 2026-2040.
- Cuvelier, D., Sarrazin, J., Colaco, A., Copley, J. T., Glover, A. G., Tyler, P. A., Serrao Santos, R. and Desbruyeres, D. (2011). Community dynamics over 14 years at the Eiffel Tower hydrothermal edifice on the Mid-Atlantic Ridge. *Limnology and Oceanography* 56(5), 1624-1640.
- Dagorn, L., Bach, P. and Josse, E. (2000). Movement patterns of large bigeye tuna (*Thunnus obesus*) in the open ocean, determined using ultrasonic telemetry. *Marine Biology* 136(2), 361-371.
- Dahlgren, T. G., Wiklund, H., Kallstrom, B., Lundalv, T., Smith, C. R. and Glover, A. G. (2006). A shallow-water whale-fall experiment in the north Atlantic. *Cahiers de Biologie Marine* 47, 385-389.
- Danovaro, R. (2012). Extending the approaches of biodiversity and ecosystem functioning to the deep ocean. In: Solan, M., Aspden, R. J. and Paterson, D. M. (Eds.), *Marine biodiversity and ecosystem functioning: Frameworks, methodologies, and integration*. Oxford: Oxford University Press, 115-126.
- Davies, A. J. and Guinotte, J. M. (2011). Global habitat suitability for framework-forming cold-water corals. *PLoS one* 6(4), e18483.
- Davison, P. C., Checkley Jr., D. M., Koslow, J. A. and Barlow, J. (2013). Carbon export mediated by mesopelagic fishes in the northeast Pacific Ocean. *Progress in Oceanography* 116, 14-30.
- De Biasse, M., Richards, V. P. and Shivji, M. S. (2010). Genetic assessment of connectivity in the common reef sponge, *Callyspongia vaginalis* (Demospongidae: Haplosclerida) reveals high population structure along the Florida reef tract. *Coral Reefs* 29(1), 47-55.
- De Busserolles, F., Sarrazin, J., Gauthier, O., Gelinas, Y., Fabri, M. C., Sarradin, P. M. and Desbruyeres, D. (2009). Are spatial variations in the diets of hydrothermal fauna linked to local environmental conditions? *Deep-Sea Research II* 56(1-2), 1649-1664.
- De Groot, R. S., Wilson, M. A. and Bourmans, R. M. J. (2002). A typology for the classification, description and valuation of ecosystem functions, goods and services. *Ecological Economics* 41(3), 393-408.
- Delaney, J. R., Mogk, D. and Mottl, M. (1987). Quartz-cemented breccias from

the Mid-Atlantic Ridge: Samples of a high-salinity hydrothermal upflow zone. *Journal of Geophysical Research: Solid Earth* 92(B9), 9175-9192.

De Matos, V., Braga-Henriques, A., Santos, R. S. and Ribeiro, P. A. (2014). New species of Heteropathes (Anthozoa: Antipatharia) expands genus distribution to the NE Atlantic. *Zootaxa* 3827, 293-300.

Demopoulos, A. W. J., Ross, S. W., Kellogg, C. A., Morrison, C. L., Nizinski, M., Prouty, N. G., Bourque, J. R., Galkiewicz, J. P., Gray, M. A., Springmann, M. J., Coykendall, D. K., Miller, A., Rhode, M., Quattrini, A., Ames, C. L., Brooke, S., McClain-Counts, J., Roark, E. B., Buster, N. A., Philips, R. M. and Frometa, J. (2017). Deepwater Program: *Lophelia II*, continuing ecological research on deep-sea corals and deep-reef habitats in the Gulf of Mexico. U.S. Geological Survey Open-File Report 2017 - 1139, 269 p.

Desbruyeres, D., Biscoito, M., Caprais, J.-C., Colaco, A., Comtet, T., Crassous, P., Fouquet, Y., Khripounoff, A., Le Bris, N., Olu, K., Riso, R., Sarradin, P.-M., Segonzac, M. and Vangriesheim, A. (2001). Variations in deep-sea hydrothermal vent communities on the Mid-Atlantic Ridge near the Azores plateau. *Deep Sea Research I* 48(5), 1325-1346.

Desbruyeres, D., Almeida, A., Biscoito, M., Comtet, T., Khripounoff, A., Le Bris, N., Sarradin, P. M. and Segonzac, M. (2000). A review of the distribution of hydrothermal vent communities along the northern Mid-Atlantic Ridge: dispersal vs. environmental controls. *Hydrobiologia* 440, 201-216.

Desbruyeres, D., Segonzac, M., Bright, M. (2006). *Handbook of deep-sea hydrothermal vent fauna*. Denisia: 18, Linz-Dornach, 544 p.

Diahia, N. C., Zudaire, I., Chassot, E., Barrigah, B. D., Irié, Y. D., Gbeazere, D. A., Kouadio, D., Pecoraro, C., Romeo, M. U.,

Mura, H., Amande, M. J., Dewals, P. and Bodin, N. (2016). Annual monitoring of reproductive traits of female yellowfin tuna (*Thunnus albacares*) in the eastern Atlantic Ocean. *Collective Volume of Scientific Papers ICCAT* 72(2), 534-548.

Dias, M. P., Granadeiro, J. P. and Catry, P. (2013). Individual variability in the migratory path and stopovers of a long-distance pelagic migrant. *Animal Behaviour* 86, 359-364.

Dias, M. P., Granadeiro, J. P., Phillips, R. A., Alonso, H. and Catry, P. (2011). Breaking the routine: individual Cory's shearwaters shift winter destinations between hemispheres and across ocean basins. *Proceedings of the Royal Society Biological Sciences* 278, 1786-1793.

Dick, G. J. (2019). The microbiomes of deep-sea hydrothermal vents: distributed globally, shaped locally. *Nature Reviews Microbiology* 17, 271-283.

Dilman, A. B. (2006). Asteroid fauna of the Reykjanes Ridge. In: Mironov, A. N., Gebruk, A. V. and Southward, A. J. (Eds.), *Biogeography of the North Atlantic Seamounts*. Moscow: KMK Scientific Press Ltd., 177-192.

Dilman, A. B. (2008). Asteroid fauna of the northern Mid-Atlantic Ridge with description of a new species *Hymenasterides mironovi* sp. nov. *Marine Biology Research* 4, 131-151.

Dilman, A. B. (2013). Asteroid fauna of the northern Mid-Atlantic Ridge: additional records. *Marine Biology Research* 9(5-6), 563-586.

Ding, J., Zhang, Y., Wang, H., Jian, H., Leng, H. and Xiao, X. (2017). Microbial community structure of deep-sea hydrothermal vents on the ultraslow spreading Southwest Indian Ridge. *Frontiers in Microbiology* 8, 1012.

- Dixon, D. R. and Dixon, L. R. J. (1996). Results of DNA analyses conducted on vent shrimp post larvae collected above the Broken Spur vent field during the CD95 cruise, August 1995. *BRIDGE Newsletter* 11, 9-15. BRIDGE Office, Department of Earth Sciences, University of Leeds, Leeds, UK.
- Dixon, D. R., Lowe, D. M., Miller, P. I., Villemin, G. R., Colaco, A., Serrao-Santos, R. and Dixon, L. R. J. (2006). Evidence of seasonal reproduction in the Atlantic vent mussel *Bathymodiolus azoricus*, and an apparent link with the timing of photosynthetic primary production. *Journal of the Marine Biological Association of the UK* 86, 1363-1371.
- Dodge, K. L., Galuardi, B., Miller, T. J. and Lutcavage, M. E. (2014). Leatherback turtle movements, dive behavior, and habitat characteristics in ecoregions of the Northwest Atlantic Ocean. *PLoS ONE* 9(3), e91726.
- Doherty, P. D., Baxter, J. M., Gell, F. R., Godley, B. J., Graham, R. T., Hall, G., Hall, J., Hawkes, L. A., Henderson, S. M., Johnson, L., Speedie, C. and Witt, M. J. (2017). Long-term satellite tracking reveals variable seasonal migration strategies of basking sharks in the north-east Atlantic. *Scientific Reports* 7, 42837.
- Doney, S. C., Fabry, V. J., Feely, R. A. and Kleypas, J. A. (2009). Ocean acidification: The other CO₂ problem. *Annual Review of Marine Science* 1, 169-192.
- Druon, J. N., Chassot, E., Murua, H. and Soto, M. (2016). Preferred feeding habitat of skipjack tuna in the eastern central Atlantic and western Indian Oceans: relations with carrying capacity and vulnerability to purse seine fishing. *IOTC Proceedings*, IOTC-2016-WPTT18-31.
- Duffy, G. A., Horton, T., Shearer, M. and Thurston, M. H. (2013). Population structure of *Abyssorchromene abyssorum* (Stebbing, 1888) (Amphipoda: Lysianassoidea), a scavenging amphipod from the Mid-Atlantic Ridge in the vicinity of the Charlie Gibbs Fracture Zone. *Deep-Sea Research II* 98(B), 360-369.
- Dunn, D. C., Harrison, A.-L., Curtice, C., Appeltans, W., Bailey, H., Ballance, L., Block, B., Boustany, A., Brenner, J., Corkeron, P., Costa, D. P., Crespo, G. O., Davies, T., DeLand, S., Dias, M., Donnelly, B., Douvere, F., Ferretti, F., Freestone, D., Frisch-Nwakanma, H., Froján, C. B., Fujioka, E., Gjerde, K. M., Glowka, L., Godley, B. J., Gunn, V., Hays, G. C., Hazien, C., Heywood, E., Jimenez, J., Johnson, D. E., Kot, C. Y., Maxwell, S., di Sciara, G. N., Palacios, D. M., Pauly, A., Salazar, E. R., Secor, D., Sequiera, A., Spalding, M., Spina, F., Van Parijs, S., Wallace, B., Virtue, M., Weimerskirch, H., Woodward, B., Alberini, A., Blondin, H., Poulin, S., Cleary, J. and Halpin, P. N. (2019). The importance of migratory connectivity to global ocean policy. *Proceedings of the Royal Society Biological Sciences* 286, 20191472.
- Duperron, S., Bergin, C., Zielinski, F., Blazejak, A., Pernthaler, A., McKinney, Z. P., DeChaine, E., Cavanaugh, C. M. and Dubilier, N. (2006). A dual symbiosis shared by two mussel species, *Bathymodiolus azoricus* and *Bathymodiolus puteoserpentis* (Bivalvia: Mytilidae), from hydrothermal vents along the northern Mid-Atlantic Ridge. *Environmental Microbiology* 8(8), 1441-1447.
- Duperron, S., Quiles, A., Szafranski, K. M., Leger, N. and Shilito, B. (2016). Estimating symbiont abundances and gill surface areas in specimens of the hydrothermal vent mussel *Bathymodiolus puteoserpentis* maintained in pressure vessels. *Frontiers in Marine Science* 3, 16.
- Durden, J. M., Simon-Lledo, E., Gooday, A. J. and Jones, D. O. B. (2017). Abundance and morphology of *Paleodictyon nodosum*, observed at the Clarion-Clipperton Zone. *Marine Biodiversity* 47(2), 265-269.

- Eberhart, G. L., Rona, P. and Honnorez, J. (1988). Geologic controls of hydrothermal activity in the Mid-Atlantic Ridge rift valley: Tectonics and volcanics. *Marine Geophysical Researches* 10, 233-259.
- Eckert, S. A., Moore, J. E., Dunn, D. C., van Buiten, R. S., Eckert, K. L. and Halpin, P. N. (2008). Modeling loggerhead turtle movement in the Mediterranean: Importance of body size and oceanography. *Ecological Applications* 18, 290-308.
- Edwards, K. J., McCollom, T. M., Konishi, H. and Buseck, P. R. (2003). Seafloor bioalteration of sulphide minerals: results from *in situ* incubation studies. *Geochimica et Cosmochimica Acta* 67(15), 2843-2856.
- Edwards, K. J., Bach, W. and McCollom, T. M. (2005). Geomicrobiology in oceanography: microbe-mineral interactions at and below the seafloor. *Trends in Microbiology* 13, 449-456.
- Egevang, C., Stenhouse, I. J., Phillips, R. A., Petersen, A., Fox, J. W. and Silk, J. R. D. (2010). Tracking of Arctic terns *Sterna paradisaea* reveals longest animal migration. *PNAS* 107, 2078-2081.
- Erickson, K. L., Macko, S. A. and Van Dover, C. L. (2009). Evidence for a chemoautotrophically based food web at inactive hydrothermal vents (Manus Basin). *Deep-Sea Research II* 56, 1577-1585.
- Fabri, M.-C., Bargain, A., Briand, P., Gebruk, A., Fouquet, Y., Morineaux, M. and Desbruyeres, D. (2011). The hydrothermal vent community of a new deep-sea field, Ashadze-1, 12°58'N on the Mid-Atlantic Ridge. *Journal of the Marine Biological Association of the United Kingdom* 91(1), 1-13.
- Fallon, E. K., Petersen, S., Brooker, R. A. and Scott, T. B. (2017). Oxidative dissolution of hydrothermal mixed-sulphide ore: an assessment of current knowledge in relation to seafloor massive sulphide mining. *Ore Geology Reviews* 86, 309-337.
- Falkowski, P. G., Zieman, D., Kolber, Z., and Bienfang, P. K. (1991). Role of eddy pumping in enhancing primary production in the ocean. *Nature* 352(6330), 55.
- Faure, B., Jollivet, D., Tanguy, A., Bonhomme, F. and Bierne, N. (2009). Speciation in the deep sea: Multi-locus analysis of divergence and gene flow between two hybridizing species of hydrothermal vent mussels. *PLoS ONE* 4(8), e6485.
- Fell, P. E. (1974). Diapause in the gemmules of the marine sponge *Haliclona loosanoffi* with a note on the gemmules of *Haliclona oculata*. *Biological Bulletin* 147, 333-351.
- Felley, J. D., Vecchione, M. and Wilson, R. R. (2008). Small-scale distribution of deep-sea demersal nekton and other megafauna in the Charlie-Gibbs Fracture Zone of the Mid-Atlantic Ridge. *Deep-Sea Research II* 55(1-2), 153-160.
- Flores, G. E., Campbell, J. H., Kirshstein, J. D., Meneghin, J., Podar, M., Steinberg, J. I., Seewald, J. S., Tivey, M. K., Viytek, M. A., Yang, Z. K. and Reysenbach, A.-L. (2011). Microbial community structure of hydrothermal deposits from geochemically different vent fields along the Mid-Atlantic Ridge. *Environmental Microbiology* 13(8), 2158-2171.
- Fonteneau, A. (1994). Structure de la population d'albacore de l'Atlantique: quelques considérations sur les migrations et la modélisation. *Rec. Doc. Sci. ICAAT* 42(2), SCRS/93/43, 215-218.
- Fonteneau, A. (2015). On the movement patterns and stock structure of skipjack (*Katsuwonus pelamis*) in the Atlantic: how many Skipjack stocks in the Atlantic Ocean? *Collective Volumes of Scientific Papers ICCAT* 71(1), 205-220.
- Fonteneau, A. and Soubrier, P. (1996). Interactions between tuna fisheries: a global review with specific examples from the Atlantic Ocean. *FAO Fisheries Technical Paper*, 84-123.

- Fortunato, C. S., Larson, B., Butterfield, A. B. and Huber, J. A. (2018). Spatially distinct, temporally stable microbial populations mediate biogeochemical cycling at and below the seafloor in hydrothermal vent fluids. *Environmental Microbiology* 20(2), 769-784.
- Fossette, S., Witt, M. J., Miller, P., Nalovic, M. A., Albareda, D., Almeida, A. P., Broderick, A. C., Chacón-Chaverri, D., Coyne, M. S., Domingo, A., Eckert, S., Evans, D., Fallabrino, A., Ferraroli, S., Formia, A., Giffoni, B., Hays, G. C., Hughes, G., Kelle, L., Leslie, A., López-Mendilaharsu, M., Luschi, P., Prosdocimi, L., Rodriguez-Heredia, S., Turny, A., Verhage, S. and Godley, B. J. (2014). Pan-Atlantic analysis of the overlap of a highly migratory species, the leatherback turtle, with pelagic longline fisheries. *Proceedings of the Royal Society Biological Sciences* 281, 20133065.
- Fouquet, Y., Cherkashov G., Charlou, J. L., Ondreas, H., Birot, D., Cannat, M., Bortnikov, N., Silantyev, S., Sudarikov, S., Cambon-Bonavita, M. A., Desbruyeres, D., Fabri, M. C., Querellou, J., Hourdez, S., Gebruk, A., Sokolova, T., Hoise, E., Mercier, E., Kohn, C., Donval, J. P., Etoubleau, J., Normand, A., Stephan, M., Briand, P., Crozan, J., Fernagu, P., Buffier, E. (2008). Serpentine cruise - ultramafic hosted hydrothermal deposits on the Mid-Atlantic Ridge: First submersible studies on Ashadze 1 and 2, Logatchev 2 and Krasnov vent fields. *InterRidge News* 17 online supplement, 16-21.
- Fouquet, Y., Cherkashov G., Charlou, J. L., Ondreas, H., Cannat, M., Bortnikov, N., Silantyev, S., Etoubleau, J., Scientific Party of the Serpentine Cruise (2007). Diversity of ultramafic hosted hydrothermal deposits on the Mid-Atlantic Ridge: First submersible studies on Ashadze, Logatchev 2 and Krasnov vent fields during the Serpentine Cruise. *American Geophysical Union, Fall Meeting 2007*. Abstract ID: T51F-03.
- Freitas, C., Caldeira, R. and Dellinger, T. (2019). Surface behavior of pelagic juvenile loggerhead sea turtles in the eastern North Atlantic. *Journal of Experimental Marine Biology and Ecology* 510, 73-80.
- Gablina, I. F., Dobretsova, I. G., Bel'tenev, V. E., Lyutkevich, A. D., Narkenskii, E. V. and Gustaitis, A. N. (2012). Peculiarities of present-day sulfide mineralization at 19°15'N - 20°08'N, Mid-Atlantic Ridge. *Doklady Earth Sciences* 442(2), 163-167.
- Gaither, M. R., Bowen, B. W., Rocha, L. A. and Briggs, J. C. (2016). Fishes that rule the world: circumtropical distributions revisited. *Fish and Fisheries* 17, 664-679.
- Galkin, S. V. (1997). Megafauna associated with hydrothermal vents in the Manus Back-arc Basin (Bismarck Sea). *Marine Geology* 142, 197-206.
- Galkin, S. V., Molodtsova, T. N., Minin, K. V. and Kobyliansky, S. G. (2019). Ecological studies of the Russian Exploration Area on the Mid-Atlantic Ridge on the 39th cruise of RV Professor Logachev. *Oceanology* 59(4), 616-617.
- Gao, X., Gao, W., Cui, Z., Han, B., Yang, P., Sun, C. and Zheng, L. (2015). Biodiversity and degradation potential of oil-degrading bacteria isolated from deep-sea sediments of South Mid-Atlantic Ridge. *Marine Pollution Bulletin* 97, 373-380.
- García-Cortés, B., Mejuto, J. and Quintans, M. (2003). Summary of swordfish (*Xiphias gladius*) recaptures carried out by the Spanish surface longline fleet in the Atlantic Ocean: 1984-2002. *Collective Volume of Scientific Papers ICCAT* 55(4), 1476-1484.
- Gebruk, A. V. (2008). Holothurians (Holothuroidea, Echinodermata) of the northern Mid-Atlantic Ridge collected by the G.O. Sars MAR-ECO expedition with descriptions of four new species. *Marine Biology Research* 4(1-2), 48-60.
- Gebruk, A. V., Budaeva, N. E. and King, N. J. (2010). Bathyal benthic fauna of the

Mid-Atlantic Ridge between the Azores and the Reykjanes Ridge. *Journal of the Marine Biological Association of the United Kingdom* 90(1), 1-14.

Gebruk, A. V., Fabri, M.-C., Briand, P. and Desbruyeres, D. (2010). Community dynamics over a decadal scale at Logatchev, 1445'N, Mid-Atlantic Ridge. *Cahiers de Marine Biologie* 51, 383-388.

Gebruk, A. V. and Kryolova, E. M. (2013). Megafauna of the Charlie-Gibbs Fracture Zone (northern Mid-Atlantic Ridge) based on video observations. *Journal of the Marine Biological Association of the United Kingdom* 93(5), 1143-1150.

German, C. R., Parson, L. M., Bougalt, H., Coller, D., Critchley, M., Dapoigny, A., Day, C., Eardley, D., Fearn, A., Flewellen, C., Kirk, R., Klinkhammer, G., Landure, J.-Y., Ludford, E., Miranda, M., Needham, H. D., Patching, J., Pearce, R., Pelle, H., Radford-Knoery, J., Rouse, I., Scott, J., Stoffregen, P., Taylor, P., Teare, D. and Wynar, J. (1996). Hydrothermal exploration near the Azores Triple Junction: tectonic control of venting at slow-spreading ridges? *Earth and Planetary Science Letters* 138(1-4), 93-104.

Gollner, S., Fontaneto, D. and Martinez-Arbizu, P. (2011). Molecular taxonomy confirms morphological classification of deep-sea hydrothermal vent copepods (Dirivultidae) and suggests broad physiological tolerance of species and frequent dispersal along ridges. *Marine Biology* 158, 221-31.

Gollner, S., Ivanenko, V. N., Martinez-Arbizu, P. and Bright, M. (2010a). Advances in taxonomy, ecology, and biogeography of Dirivultidae (Copepoda) associated with chemosynthetic environments in the deep sea. *PLoS one* 5(8), e9801.

Gollner, S., Reimer, B., Martinez-Arbizu, P., Le Bris, N. and Bright, M. (2010b). Diversity of meiofauna from the 950'N East Pacific

Rise across a gradient of hydrothermal fluid emissions. *PLoS one* 5(8), e12321.

Gollner, S., Stuckas, H., Kihara, T. C., Laurent, S., Kodami, S. and Arbizu, P. M. (2016). Mitochondrial DNA analyses indicate high diversity, expansive population growth and high genetic connectivity of vent copepods (Dirivultidae) across different oceans. *PLoS ONE* 11(10), e0163776.

Gomes-Pereira, J. N., Carmo, V., Catarino, D., Jakobsen, J., Alvarez, H., Aguilar, R., Hart, J., Giacomello, E., Menezes, G., Stefanni, S., Colaço, A., Morato, T., Santos, R. S., Tempera, F. and Porteiro, F. (2017). Cold-water corals and large hydrozoans provide essential fish habitat for *Lappanella fasciata* and *Benthocometes robustus*. *Deep-Sea Research II* 145, 33-48.

Gomez, C., Lawson, J., Kouwenberg, A. L., Moors-Murphy, H., Buren, A., Fuentes-Yaco, C., Marotte, E., Wiersma, Y. F. and Wimmer, T. (2017). Predicted distribution of whales at risk: Identifying priority areas to enhance cetacean monitoring in the Northwest Atlantic Ocean. *Endangered Species Research* 32, 437-458.

Gooday, A. J., Alt, C. H. S., Jones, D. O. B., Shale, D., Marsden, K. and Brasier, M. D. (2013). The ecology and biogeography of *Discospirina tenuissima* (Foraminifera) in the Atlantic and Indian Oceans. *Deep-Sea Research II* 98, 301-314.

Gore, M. A., Rowat, D. and Hall, J. (2008). Transatlantic migration and deep mid-ocean diving by basking shark. *Biology Letters* 4(4), 395-398.

Grice, G. D. (1972). The existence of a bottom-living calanoid copepod fauna in deep water with descriptions of five new species. *Crustaceana* 23, 219-242.

Guilford, T., Freeman, R., Boyle, D., Dean, B., Kirk, H., Phillips, R. and Perrins, C. (2011). A dispersive migration in the Atlantic Puffin and its implications for

- migratory navigation. *PLoS ONE* 6(7), e21336.
- Haedrich, R. L. and Merrett, N. R. (1988). Summary atlas of deep-living demersal fishes in the North Atlantic Basin. *Journal of Natural History* 22, 1325–1362.
- Halpern, B. S., Walbridge, S., Selkoe, K. A., Kappel, C. V., Micheli, F., D'Agrosa, C., Bruno, J. F., Casey, K. S., Ebert, C., Fox, H. E., Fujita, R., Heinemann, D., Lenihan, H. S., Madin, E. M. P., Perry, M. T., Selig, E. R., Spalding, M., Steneck, R. and Watson, R. (2008). A global map of human impact on marine ecosystems. *Science* 319(5865), 948–952.
- Han, Y., Gonnella, G., Adam, N., Schippers, A., Burkhardt, L., Kurtz, S., Schwarzschafer, U., Franke, H. and Perner, M. (2018). Hydrothermal chimneys host habitat-specific microbial communities: analogues for studying the possible impact of mining seafloor massive sulfide deposits. *Scientific Reports* 8, 10386.
- Hannington, M., Jamieson, J., Monecke, T., Petersen, S. and Beaulieu, S. (2011). The abundance of seafloor massive sulfide deposits. *Geology* 39(12), 1155–1158.
- Harris, M. P., Daunt, F., Newell, M., Phillips, R. A. and Wanless, S. (2010). Wintering areas of adult Atlantic puffins *Fratercula arctica* from a North Sea colony as revealed by geolocation technology. *Marine Biology* 157(4), 827–836.
- Harris, P. T., Macmillan-Lawler, M., Rupp, J. and Baker, E. K. (2014). Geomorphology of the oceans. *Marine Geology* 352, 4–24.
- Hátún, H., Payne, M. R., Beaugrand, G., Reid, P. C., Sandø, A. B., Drange, H., Hansen, B., Jacobsen, J. A. and Bloch, D. (2009). Large bio-geographical shifts in the north-eastern Atlantic Ocean: From the subpolar gyre, via plankton, to blue whiting and pilot whales. *Progress in Oceanography* 80, 149–162.
- Hedd, A., Monteverdi, W. A., Otley, H., Phillips, R. A. and Fifield, D. A. (2012). Trans-equatorial migration and habitat use by sooty shearwaters *Puffinus griseus* from the South Atlantic during the nonbreeding season. *Marine Ecology Progress Series* 449, 277–290.
- Heger, A., Ieno, E. N., King, N. J., Morris, K. J., Bagley, P. M. and Priede, I. G. (2008). Deep-sea pelagic bioluminescence over the Mid-Atlantic Ridge. *Deep Sea Research Part II* 55, 126–136.
- Heino, M. and Godø, O. R. (2002). Blue whiting – a key species in the mid-water ecosystems of the north-eastern Atlantic. ICES CM 2002/L:28. Theme Session L: Census of Marine Life: Turning Concept into Reality.
- Henrich, R., Freiwald, A., Shipboard Party (1997). *Lophelia reef on Sula Ridge, mid-Norwegian shelf*. Cruise Report No. 228/97, IFM-GEOMAR, Kiel.
- Hentschel, U., Hopke, J., Horn, M., Friedrich, A. B., Wagner, M., Hacker, J. and Moore, B. S. (2002). Molecular evidence for a uniform microbial community in sponges from different oceans. *Applied and Environmental Microbiology* 68(9), 4431–4440.
- Herrera, S., Shank, T. M. and Sanchez, J. (2012). Spatial and temporal patterns of genetic variation in the widespread antitropical deep-sea coral *Paragorgia arborea*. *Molecular Ecology* 21(24), 6053–6067.
- Ho, P. T., Park, E., Hong, S. G., Kim, E. H., Kim, K., Jang, S. J., Vrijenhoek, R. C. and Won, Y. J. (2017). Geographical structure of endosymbiotic bacteria hosted by *Bathymodiolus* mussels at eastern Pacific hydrothermal vents. *BMC Evolutionary Biology* 17, 121.
- Hoffman, J. and Sutton, T. T. (2010). Bathypelagic food web structure of the

Northern Atlantic Mid-Atlantic Ridge based on stable isotope analysis. Presented at 2010 Ocean Sciences Meeting, Portland, OR, February 22-26, 2010.

Horton, T. and Thurston, M. H. (2013). *Hirondellea namarensis* (Crustacea: Amphipoda: Lysianassoidea: Hirondelleidae), a new deep-water scavenger species from the Mid-Atlantic Ridge. *Marine Biology Research* 9(5-6), 554-562.

Horton, T. and Thurston, M. H. (2015). A revision of the genus *Paracallisoma* Chevreux, 1903 (Crustacea: Amphipoda: Scopelocheridae: Paracallismominae) with a redescription of the type species of the genus *Paracallisoma* and the description of two new genera and two new species from the Atlantic Ocean. *Zootaxa* 3995(1), 91-132.

Horton, T., Thurston, M. H. and Duffy, G. A. (2013). Community composition of scavenging amphipods at bathyal depths on the Mid-Atlantic Ridge. *Deep Sea Research Part II* 98(B), 352-359.

Hoving, H.-J. T., Perez, J. A. A., Bolstad, K. S. R., Braid, H. E., Evans, A. B., Fuchs, D., Judkins, H., Kelly, J., Marian, J. E. A. R., Nakajima, R., Piatkowski, U., Reid, A., Vecchione, M. and Xavier, J. C. C. (2014). Chapter Three - The Study of Deep-Sea Cephalopods. *Advances in Marine Biology* 67, 235-359.

Howell, K. L., Billett, D. S. M., Tyler, P. A. (2002). Depth-related distribution and abundance of seastars (Echinodermata: Asteroidea) in the Porcupine Seabight and Porcupine Abyssal Plain, N.E. Atlantic. *Deep Sea Research I* 49, 1901-1920.

Howell, K. L., Davies, J. S., Allcock, A. L., Braga-Henriques, A., Buhl-Mortensen, P., Carreiro-Silva, M., Dominguez-Carrio, C., Durden, J. M., Foster, N. L., Game, C. A., Hitchin, B., Horton, T., Hosking, B., Jones, D. O. B., Mah, C., Laguionie Marchais, C., Menot, L., Morato, T., Pearman, T. R.

R., Piechaud, N., Ross, R. E., Ruhl, H. A., Saeedi, H., Stefanoudis, P. V., Taranto, G. H., Thompson, M. B., Taylor, J. R., Tyler, P. A., Vad, J., Victorero, L., Vieira, R. P., Woodall, L. C., Xavier, J. R. and Wagner, D. (2019). A framework for the development of a global standardised marine taxon reference image database (SMarTaR-ID) to support image-based analysis. *PLoS ONE* 14(12), e0218904.

Hudson, J. M., Steinberg, D. K., Sutton, T. T., Graves, J. E. and Latour, R. J. (2014). Myctophid feeding ecology and carbon transport along the northern Mid-Atlantic Ridge. *Deep-Sea Research I* 93, 104-116.

Hughes, G. M. and Adeney, R. J. (1977). Variations in the pattern of coughing in rainbow trout. *Journal of Experimental Biology* 68, 109-133.

Hügler, M., Gärtner, A. and Imhoff, J. F. (2010). Functional genes as markers for sulfur cycling and CO₂ fixation in microbial communities of hydrothermal vents of the Logatchev field. *FEMS Microbial Ecology* 73(3), 526-537.

ICCAT (2001). Report of the ICCAT SCRS albacore stock assessment session, 9-15 October 2000, Madrid, Spain. *Collective Volume of Scientific Papers ICCAT* 52, 1283-1390.

ICCAT (2002). ICCAT Workshop on Bluefin Tuna mixing. *Collective Volume of Scientific Papers ICCAT* 54, 261-352.

ICCAT (2006). *ICCAT Statistical Bulletin*. Volume 35. Madrid, Spain. 16 pp.

ICCAT (2013). 2012 Shortfin mako stock assessment and ecological risk assessment. *Collective Volume of Scientific Papers ICCAT* 69, 1427-1570.

ICCAT (2015). *Report of the Standing Committee on Research and Statistics (SCRS)*. 2014-15 report states: International Commission for the Conservation of Atlantic Tunas. 515 pp.

ICCAT (2017). *Report of the 2017 ICCAT Shortfin Mako assessment meeting, 12-16 June 2017, Madrid, Spain.* 64 pp.

ICCAT (2019) *ICCAT Report for biennial period, 2018-19 Part I (2018) - Vol.2.* Madrid, Spain. 443 pp.

ICES (2016). *Report of the workshop on Vulnerable Marine Ecosystem database (WVME), 10-11 December 2015, Peterborough, UK.* ICES CM 2015/ACOM:62. 42 pp.

ICES (2017). *Report of the Working Group on Elasmobranchs (2017), 31 May - 7 June 2017, Lisbon, Portugal.* ICES CM 2017/ACOM:16. 10118 pp.

ICES (2019a). *Working Group on Marine Mammal Ecology (WGMME).* ICES Scientific Reports. 1: 22. 131 pp.

ICES (2019b). *ICES/NAFO Joint Working Group on Deep-water Ecology (WGDEC).* ICES Scientific Reports. 1: 56. 119 pp.

International Seabed Authority (2019). *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.

International Seabed Authority (2019). *Draft regulations on exploitation of mineral resources in the Area.* ISBA/25/C/WP.1.

Irigoién, X., Klevjer, T. A., Røstad, A., Martínez, U., Boyra, G., Acuña, J. L., Bode, A., Echevarría, F., González-Gordillo, J. L., Hernández-León, S., Agustí, S., Aksnes, D. L., Duarte, M., and Kaartvedt, S. (2014). Large mesopelagic fishes biomass and trophic efficiency in the open ocean. *Nature Communications* 5, 3271.

IUCN (2017). *The IUCN Red List of Threatened Species.* Version 2017-3. Cambridge, UK: IUCN.

IUCN, Ivanenko, V. N., Corgosinho, P. H. C., Ferrari, F., Sarradin, P.-M. and Sarrazin, J. (2012). Microhabitat distribution of *Smacigastes micheli* (Copepoda: harpacticoida: Tegastidae) from deep-sea hydrothermal vents at the Mid-Atlantic Ridge, 37N (Lucky Strike), with a morphological description of its Nauplius. *Marine Ecology*, 1-11.

Ivanenko, V. N. and Defaye, D. (2004). A new and primitive genus and species of deep-sea Tegastidae (Crustacea, Copepoda, Harpacticoida) from the Mid-Atlantic Ridge, 37N (Azores Triple Junction, Lucky Strike). *Cahiers de Biologie Marine* 45, 255-268.

Jan, C., Petersen, J. M., Werner, J., Teeling, H., Huang, S., Golyshina, O. V., Dubilier, N., Golyshin, P. N., Jebbar, M. and Cambon-Bonavita, M. A. (2014). The gill chamber epibiosis of deep-sea shrimp *Rimicaris exoculata*: an in-depth metagenomic investigation and discovery of Zetaproteobacteria. *Environmental Microbiology* 16(9), 2723-2738.

Jessopp, M. J., Cronin, M., Doyle, T. K., Newton, S. and Phillips, R. A. (2013). Transatlantic migration by post-breeding puffins: a strategy to exploit a temporarily abundant food resource? *Marine Biology* 160(10), 2755-2762.

Judkins, D. C. and Haedrich, R. L. (2018). The deep scattering layer micronektonic fish faunas of the Atlantic mesopelagic ecoregions with comparison of the corresponding decapod shrimp faunas. *Deep Sea Research I* 136, 1-30.

Jungblut, S., Nachtsheim, D. A., Boos, K. and Joiris, C. R. (2017). Biogeography of top predators - seabirds and cetaceans - along four latitudinal transects in the Atlantic Ocean. *Deep Sea Research II* 141, 59-73.

Kaartvedt, S., Langbehn, T. J. and Aksnes, D. L. (2019). Enlightening the ocean's twilight zone. *ICES Journal of Marine Science* 76, 803-812.

- Kaartvedt, S., Røstad, A. and Aksnes, D. L. (2017). Changing weather causes behavioral responses in the lower mesopelagic. *Marine Ecology Progress Series* 574, 259-263.
- Kaartvedt, S., Staby, A. and Aksnes, D. L. (2012). Efficient trawl avoidance by mesopelagic fishes causes large underestimation of their biomass. *Marine Ecology Progress Series* 456, 1-6.
- Kato, S., Shibuya, T., Takaki, Y., Hirai, M., Nunoura, T. and Suzuki, K. (2018). Genome-enabled metabolic reconstruction of dominant chemosynthetic colonizers in deep-sea massive sulfide deposits. *Environmental Microbiology* 20, 862-877.
- Kato, S., Takano, Y., Kakegawa, T., Oba, H., Inoue, K., Kobayashi, C., Utsumi, M., Marumo, K., Kobayashi, K., Ito, Y., Ishibashi, J. and Yamagishi, A. (2010). Biogeography and biodiversity in sulphide structure of active and inactive vents at deep-sea hydrothermal fields of the southern Mariana Trough. *Applied and Environmental Microbiology* 76(9), 2968-2979.
- Kato, S. and Yamagishi, A. (2015). Prokaryotes in metal deposits on the deep seafloor. In: Wilson N. (Ed.), *Deep Sea: Biodiversity, Human Dimension and Ecological Significance*. Nova Science Publishers. 103-134.
- Kelley, D. S. and Delaney, J. R. (1987). Two-phase separation and fracturing in mid-ocean ridge gabbros at temperatures greater than 700C. *Earth and Planetary Science Letters* 83(1-4), 53-66.
- Keller, G. H., Anderson, S. H. and Lavelle, J. W. (1975). Near-bottom currents in the Mid-Atlantic Ridge rift valley. *Canadian Journal of Earth Sciences* 12(4), 703-710.
- Kelly, T. B., Davison, P. C., Goericke, R., Landry, M. R., Ohman, M. D. and Stukel, M. R. (2019). The importance of mesozooplankton diel vertical migration for sustaining a mesopelagic food web. *Frontiers in Marine Science* 6, 508.
- Kennedy, A. S., Zerbini, A. N., Vasquez, O. V., Gandilhon, N., Clapham, P. J. and Adam, O. (2014). Local and migratory movements of humpback whales (*Megaptera novaeangliae*) satellite-tracked in the North Atlantic Ocean. *Canadian Journal of Zoology* 92(1), 9-18.
- Kobyliansky, S. G., Orlov, A. M. and Gordeeva, N. V. (2010). Composition of deep-sea pelagic ichthyocenes of the Southern Atlantic, from waters of the area of the Mid-Atlantic and Walvis Ridges. *Journal of Ichthyology* 50(10), 932-949.
- Kohler, N. E., Turner, P. A., Hoey, J. J., Natanson, L. J. and Briggs, R. (2002). Tag and recapture data for three pelagic shark species: blue shark (*Prionace glauca*), shortfin mako (*Isurus oxyrinchus*), and porbeagle (*Lamna nasus*) in the North Atlantic Ocean. SCRS/2001/064. *Collective Volumes of Scientific Papers ICCAT* 54, 1231-1260.
- Krasnov, S. G., Cherkashev, G. A., Stepanova, T. V., Batuyev, B. N., Krotov, A. G., Malin, B. V., Malsov, M. N., Markov, V. F., Poroshina, I. M., Samovarov, M. S., Ashadze, A. M., Lazareva, L. I. and Ermolayev, I. K. (1995). Detailed geological studies of hydrothermal fields in the North Atlantic. In: Parson, L. M., Walker, C. L. and Dixon, D. R. (Eds.), *Hydrothermal vents and processes. Geological Society Special Publication* 87, 43-64.
- Krylova, E. M., Sahling, H. and Janssen, R. (2010). Abyssogena: A new genus of the family Vesicomyidae (Bivalvia) from deep-water vents and seeps. *Journal of Molluscan Studies* 76, 107-132.
- Kuhn, T., Alexander, B., Augustin, N., Birgel, D., Borowski, C., de Carvalho, L. M., Engemann, G., Ertl, S., Franz, L., Grech, C., Herzig, P. M., Hekinian, R., Imhoff, J. F., Jellinek, T., Klar, S., Koschinsky, A., Kuever,

- J., Kulescha, F., Lackschewitz, K., Petersen, S., Ratmeyer, V., Renken, J., Ruhland, G., Scholten, J., Schreiber, K., Seifert, R., Suling, J., Turkay, M., Westernstroer, U. and Zielinski, F. (2004), The Logatchev hydrothermal field - revisited: Preliminary results of the R/V Meteor Cruise HYDROMAR I (M60/3). *InterRidge News* 13, 1-4.
- Kawaguchi, K. and Mauchline, J. (1982). Biology of Myctophid fishes (Family Myctophidae) in the Rockall Trough, Northeastern Atlantic Ocean. *Biological Oceanography* 1(4), 337-373.
- LaBella, A. L., Van Dover, C. L., Jollivet, D. and Cunningham, C. W. (2017). Gene flow between Atlantic and Pacific Ocean basins in three lineages of deep-sea clams (Bivalvia: Vesicomyidae: Pliocardiinae) and subsequent limited gene flow within the Atlantic. *Deep-Sea Research II* 137, 307-317.
- Lalou, C., Reyss, J. L. and Brichet, E. (1998). Age of sub-bottom sulphide samples at the TAG active mound. *Proceedings of the Ocean Drilling Program, scientific results* 158, 111-117.
- Langbehn, T. J., Aksnes, D. L., Kaartvedt, S., Fiksen, Ø. and Jørgensen, C. (2019). Light comfort zone in a mesopelagic fish emerges from adaptive behaviour along a latitudinal gradient. *Marine Ecology Progress Series* 623, 161-174.
- Larson, R. J., Matsumoto, G. I., Madin, L. P. and Lewis, L. M. (1992). Deep-sea benthic and benthopelagic medusa: Recent observations from submersibles and a Remotely Operated Vehicle. *Bulletin of Marine Science* 51, 277-286.
- Lavery, T.J., Roudnew, B., Gill, P., Seymour, J., Seuront, L., Johnson, G., Mitchell, J. G. and Smetacek, V. (2010). Iron defecation by sperm whales stimulates carbon export in the Southern Ocean. *Proceedings of the Royal Society Biological Sciences* 277(1699), 3527-3531.
- Le Bris, N., Yucel, M., Das, A., Sievert, S. M., LokaBharathi, P.-P. and Girguis, P. R. (2019). Hydrothermal energy transfer and organic production at the deep seafloor. *Frontiers in Marine Science* 18.
- Lelievre, Y., Legendre, P., Matabos, M., Mihaly, S., Lee, R. W., Sarradin, P.-M., Arango, C. P. and Sarrazin, J. (2016). Astronomical and atmospheric impacts on deep-sea hydrothermal vent invertebrates. *Proceedings of the Royal Society: Biology* 284, 20162123.
- Lessa, R. and Duarte-Neto, P. (2004). Age and growth of yellowfin tuna (*Thunnus albacares*) in the western equatorial Atlantic, using dorsal fin spines. *Fisheries Research* 69(2), 157-170.
- Li, J., Cui, J., Yang, Q., Cui, G., Wei, B., Wu, Z., Wang, Y. and Zhou, H. (2017). Oxidative weathering and microbial diversity of an inactive seafloor hydrothermal sulphide chimney. *Frontiers in Microbiology* 8, 1378.
- Lilley, M. D., Feely, R. A. and Trefry, J. H. (1995). Chemical and biochemical transformations in hydrothermal plumes. In: Humphris, S. E., Zierenberg, R. A., Mullineaux, L. S. and Thomson, R. E. (Eds.), *Seafloor Hydrothermal Systems: Physical, Chemical, Biological, and Geological Interactions*. American Geophysical Union, pp 369-391.
- Lima, A. O. D. S., Cabral, A., Andreote, F. D., Cavalett, A., Pessatti, M. L., Dini-Andreote, F. and da Silva, M. A. C. (2013). Draft genome sequence of *Bacillus stratosphericus* LAMA 585, isolated from the Atlantic deep sea. *Genome Announcements* 1(3), e00204-13.
- Lindegren, M., Checkley, D. M. Jr., Ohman, M. D., Koslow, J. A. and Goericke, R. (2016). Resilience and stability of a pelagic marine ecosystem. *Proceedings of the Royal Society Biological Sciences* 283, 20151931.
- Linley, T. D., Alt, C. H. S., Jones, D. O. B. and Priede, I. G. (2013). Bathyal demersal fishes

- of the Charlie-Gibbs Fracture Zone region (49 - 54N) of the Mid-Atlantic Ridge: III. Results from remotely operated vehicle (ROV) video transects. *Deep-Sea Research II* 98, 407-411.
- Logan, J. M., Toppin, R., Smith, S., Galuardi, B., Porter, J. and Lutcavage, M. (2013). Contribution of cephalopod prey to the diet of large pelagic fish predators in the central North Atlantic Ocean. *Deep-Sea Research II* 95, 15, 74-82.
- Lohmann, K. J. and Lohmann, C. M. F. (1996). Detection of magnetic field intensity by sea turtles. *Nature* 380, 59-61.
- Longhurst, A. (1998). *Ecological Geography of the Sea*. New York: Academic Press.
- Lopes, D. A. and Tabachnick, K. R. (2013). New data on glass sponges (Porifera, Hexactinellida) of the northern Mid-Atlantic Ridge. Part 1. Farreidae. *Marine Biology Research* 9(5-6), 462-468.
- Lopez-Garcia, P., Philippe, H., Gail, F. and Moreira, D. (2003). Autochthonous eukaryotic diversity in hydrothermal sediment and experimental microcolonizers at the Mid-Atlantic Ridge. *Proceedings of the National Academy of Sciences of the United States of America* 100(2), 697-702.
- Lunden, J. J., McNicholl, C. G., Sears, C. R., Morrison, C. L. and Cordes, E. E. (2014). Acute survivorship of the deep-sea coral *Lophelia pertusa* from the Gulf of Mexico under acidification, warming, and deoxygenation. *Frontiers in Marine Science* 1(78).
- Lutcavage, M., Brill, R. W., Skomal, G. B., Chase, B. C. and Howey, P. W. (1999). Results of pop-up satellite tagging of spawning size class fish in the Gulf of Maine: do North Atlantic bluefin tuna spawn in the mid-Atlantic? *Canadian Journal of Fisheries and Aquatic Science* 56, 173-177.
- Maas, P. A. Y., O'Mullan, G. D., Lutz, R. A. and Vrijenhoek, R. C. (1999). Genetic and morphometric characterization of mussels (Bivalvia: Mytilidae) from Mid-Atlantic hydrothermal vents. *Biological Bulletin* 196, 265-272.
- Macena, B. C. L. and Hazin, F. H. V. (2016). Whale shark (*Rhincodon typus*) seasonal occurrence, abundance and demographic structure in the Mid-Equatorial Atlantic Ocean. *PLoS ONE* 11(10), e0164440.
- Maldonado, M., Ribes, M. and Van Duyl, F. C. (2012). Nutrient fluxes through sponges: biology, budgets, and ecological implications. *Advances in Marine Biology* 62, 114-182.
- Mannocci, L., Monestiez, P., Spitz, J. and Ridoux, V. (2015). Extrapolating cetacean densities beyond surveyed regions: Habitat-based predictions in the circumtropical belt. *Journal of Biogeography* 42, 1267-1280.
- Mansfield, K. L., Wyneken, J., Porter, W. P. and Luo, J. (2014). First satellite tracks of neonate sea turtles redefine the 'lost years' oceanic niche. *Proceedings of the Royal Society Biological Sciences* 281, 20133039.
- Mapstone, G. M., Corbari, L. and Menot Lenaick (2017). Two deep-living rhodaliids (Cnidaria, Siphonophora) from the Mid-Atlantic Ridge. *Marine Biology Research* 5(10), 486 - 493.
- Marra, P. P., Norris, R. D., Haig, S. M., Webster, M. and Royle, A. J. (2006). Migratory connectivity. In: Crooks, Kr. and Sanjayan, M (Eds.), *Connectivity Conservation*. Cambridge: Cambridge University Press, pp. 157-183.
- Martynov, A. V. and Litvinova, N. M. (2008). Deep-water Ophiuroidea of the northern Atlantic with descriptions of three new species and taxonomic remarks on certain genera and species. *Marine Biology Research* 4(1-2), 76-111.

- Matabos, M., Cuvelier, D., Brouard, J., Shillito, B., Ravaux, J., Zbinden, M., Barthelemy, D., Sarradin, P. M. and Sarrazin, J. (2015). Behavioural study of two hydrothermal crustacean decapods: *Mirocaris fortunata* and *Segonzacia mesatlantica*, from the Lucky Strike vent field (Mid-Atlantic Ridge). *Deep-Sea Research II* 121, 146-158.
- Mauchline, J. and Gordon, J. D. M. (1991). Oceanic pelagic prey of benthopelagic fish in the benthic boundary layer of a marginal oceanic region. *Marine Ecology Progress Series* 74, 109-15.
- Maury, O., Gascuel, D., Marsac, F., Fonteneau, A. and Rosa, A. L. D. (2001). Hierarchical interpretation of nonlinear relationships linking yellowfin tuna (*Thunnus albacares*) distribution to the environment in the Atlantic Ocean. *Canadian Journal of Fisheries and Aquatic Sciences* 58(3), 458-469.
- Maxwell, S. M., Hazen, E. L., Bograd, S. J., Halpern, B. S., Breed, G. A., Nickel, B. and Al, E. (2013). Cumulative human impacts on marine predators. *Nature Communications* 4, 2688.
- McClellan, C. M. and Read, A. J. (2007). Complexity and variation in loggerhead sea turtle life history. *Biology Letters* 3(6), 592-594.
- Meier, D. V., Pjevac, P., Bach, W., Markert, S., Schweder, T., Jamieson, J., Petersen, S., Amann, R. and Meyerdierks, A. (2019). *Environmental Microbiology* 21(2), 682-701.
- Mestre, M., Rui-Gonzalez, C., Logares, R., Duarte, C. M., Gasol, J. M. and Sala, M. M. (2018). Sinking particles promote vertical connectivity in the ocean microbiome. *PNAS* 115(29), E6799-E6807.
- Metaxas, A. (2011). Spatial patterns of larval abundance at hydrothermal vents on seamounts: evidence for recruitment limitation. *Marine Ecology Progress Series* 437, 103-117.
- Meyer, J. L., Jaekel, U., Tully, B. J., Glazer, B. T., Wheat, C. G., Lin, H.-T., Hsieh, C.-C., Cowen, J. P., Hulme, S. M., Girguis, P. R. and Huber, J. A. (2016). *Scientific Reports* 6, 22541.
- Meysman, F. J. R. (2018). Cable bacteria take a new breath using long-distance electricity. *Trends in Microbiology* 26, 411-422.
- Miller, J. E. and Pawson, D. L. (1990). Swimming sea cucumbers (Echinodermata, Holothuroidea): A survey, with analysis of swimming behavior in four bathyal species. *Smithsonian Contributions to Marine Science* 35. 18 pp.
- Miller, P. I., Read, J. F. and Dale, A. C. (2013). Thermal front variability along the North Atlantic Current observed using microwave and infrared satellite data. *Deep-Sea Research II* 98, 244-256.
- Mironov, A. N. (2006). Echinoids from seamounts of the north-eastern Atlantic; onshore/offshore gradients in species distribution. In: Mironov, A. N., Gebruk, A. V. and Southward, A. J. (Eds.), *Biogeography of the North Atlantic Seamounts*. Moscow: KMK Scientific Press Ltd., 97-133.
- Mironov, A. N. (2008). Pourtalesiid sea urchins (Echinodermata: Echinoidea) of the northern Mid-Atlantic Ridge. *Marine Biology Research* 4(1-2), 3-24.
- Mironov, A. N. and Gebruk, A. V. (2006a). Introduction. In: Mironov, A. N., Gebruk, A. V. and Southward, A. J. (Eds.), *Biogeography of the North Atlantic Seamounts*. Moscow: KMK Scientific Press Ltd., 4-5.
- Mironov, A. N. and Gebruk, A. V. (2006b). Biogeography of the Reykjanes Ridge, the northern Atlantic. In: Mironov, A. N., Gebruk, A. V. and Southward, A. J. (Eds.), *Biogeography of the North Atlantic Seamounts*. Moscow: KMK Scientific Press Ltd., 6-21.

- Moalic, Y., Desbruyeres, D., Duarte, C. M., Rozenfeld, A., Bachraty, C. and Arnaud-Haond, S. (2012). Biogeography revisited with network theory: Retracing the history of hydrothermal vent communities. *Systematic Biology* 61(1), 127-137.
- Moberg, F. and Folke, C. (1999). Ecological goods and services of coral reef ecosystems. *Ecological Economics* 29, 215-233.
- Molodtsova, T. N. (2013). Deep-sea mushroom soft corals (Octocorallia: Alcyonacea: Alcyoniidae) of the Northern Mid-Atlantic Ridge. *Marine Biology Research* 9(5-6), 488-515.
- Molodtsova, T. N. (2016). New records of *Heteropathes* Opresko, 2011 (Anthozoa: Antipatharia) from the Mid-Atlantic Ridge. *Marine Biodiversity*, 1-8.
- Molodtsova, T. N., Galkin, S. V. and Dobretsova, I. (2014). Preliminary data on fauna of inactive hydrothermal sulfide fields on the Mid Atlantic Ridge at 12°58'-13°31'N. *World Conference on Marine Biodiversity*, 12-16 October 2014, Qingdao, China.
- Molodtsova, T. N., Galkin, S. V., Kogylansky, S. G., Simakova, U. V., Vedenin, A. A., Dobretsova, I. G. and Gebruk, A. V. (2017). First data on benthic and fish communities from the Mid-Atlantic Ridge, 16°40'-17°14'N. *Deep-Sea Research II* 137, 69-77.
- Molodtsova, T. N., Sanamyan, N. P. and Keller, N. (2008). Anthozoa from the northern Mid-Atlantic Ridge and Charlie-Gibbs Fracture Zone. *Marine Biology Research* 4(12), 112-113.
- Morato, T., Cleary, J., Taranto, G. H., Bilan, M., Barros, I., Vandeperre, F., Pham, C. K., Dunn, D. C., Colaco, A. and Halpin, P. N. (2016). Updated data report: Strategic Environmental Management Plan for deep seabed mineral exploitation in the Atlantic Basin (SEMPIA II). Pre-Workshop Data Report. IMAR Instituto do Mar & the Marine Geospatial Ecology Lab, Duke University. Horta, Portugal. 143 pp.
- Morato, T., Lemey, E., Menezes, G., Pham, C. K., Brito, J., Soszynski, A., Pitcher, T. J. and Heymans, J. J. (2016). Food-web and ecosystem structure of the open-ocean and deep-sea environments of the Azores, NE Atlantic. *Frontiers in Marine Science* 3, 245.
- Morato, T., Miller, P. I., Dunn, D. C., Nicol, S. J., Bowcott, J. and Halpin, P. N. (2018). A perspective on the importance of oceanic fronts in promoting aggregation of visitors to seamounts. *Fish and fisheries* 17(4), 1227-1233.
- Morineaux, M., Nishi, E., Ormos, A. and Mouchel, O. (2010). A new species of *Phyllochaetopterus* (Annelida: Chaetopteridae) from deep-sea hydrothermal Ashadze-1 vent field, Mid-Atlantic Ridge: taxonomical description and partial COI DNA sequence. *Cahiers de Biologie Marine* 51, 239-248.
- Morrison, C. L., Baco, A. R., Nizinski, M. S., Coykendall, D. K., Demopoulos, A. W. J., Cho, W. and Shank, T. M. (2017). Population Connectivity of Deep-Sea Corals. In: Hourigan, T. F., Etnoyer, P. J. and Cairns, S. D. (Eds.), *The state of deep-sea coral and sponge ecosystems of the United States*. NOAA Technical Memorandum, NMFS-OHC, Silver Spring, MD. 30p.
- Morrison, C. L., Ross, S. W., Nizinski, M. S., Brooke, S., Waller, R. G., Johnson, R. L., King, T. L. (2011). Genetic discontinuity among regional populations of *Lophelia pertusa* in the North Atlantic Ocean. *Conservation Genetics* 12(3), 713-729.
- Mortensen, P. B., Buhl-Mortensen, L., Gebruk, A. V. and Krylova E. M. (2008). Occurrence of deep-water corals on the Mid-Atlantic Ridge based on MAR-ECO data. *Deep-Sea Research II* 55, 142-152.

- Murina, V. V. (2008). New records of Echiura and Sipuncula in the North Atlantic Ocean, with the description of a new species of *Jacobia*. *Marine Biology Research* 4(1-2), 152-156.
- Murton, B. J., Lehrmann, B., Dutrieux, A. M., Martins, S., Gil de la Iglesia, A., Stobbs, I. J., Barriga, F. J. A. S., Bialas, J., Dannowski, A., Vardy, M. E., North, L. J., Yeo, I. A. L. M., Lusty, P. A. J. and Petersen, S. (2019). Geological fate of seafloor massive sulphides at the TAG hydrothermal field (Mid-Atlantic Ridge). *Ore Geology Reviews* 107, 903-925.
- Murton, B. J., Klinkhammer, G., Becker, K., Briais, A., Edge, D., Hayward, N., Mitchell, I., Rouse, I., Rudnicki, M., Sayanagi, K., Sloan, H., and Parson, L. (1994). Direct evidence for the distribution and occurrence of hydrothermal activity between 27°N - 30°N on the Mid-Atlantic Ridge. *Earth and Planetary Science Letters* 125(1-4), 119-128.
- Musyl, M. K., Brill, R. W., Boggs, C. H., Curran, D. S., Kazama, T. K. and Seki, M. P. (2003). Vertical movements of bigeye tuna (*Thunnus obesus*) associated with islands, buoys, and seamounts near the main Hawaiian Islands from archival tagging data. *Fisheries Oceanography* 12(3), 152-169.
- Nakamura, I. (1985). FAO species catalogue. Billfishes of the World. An annotated and illustrated catalogue of marlins, sailfishes, spearfishes and swordfishes known to date. *FAO Fisheries Synopsis* 125(5), 65 pp.
- Nicol, S., Bowie, A., Jarman, S., Lannuzel, D., Meiners, K. M. and Van Der Merwe, P. (2010). Southern Ocean iron fertilization by baleen whales and Antarctic krill. *Fish and Fisheries* 11(2), 203-209.
- Niedzielski, T., Høines, Å., Shields, M. A., Linley, T. D. and Priede, I. G. (2013). A multi-scale investigation into seafloor topography of the northern Mid-Atlantic Ridge based on geographic information system analysis. *Deep-Sea Research II* 98, 231-243.
- Odisi, E. J., Silvestrin, M. B., Takahasi, R. Y. U., da Silva, M. A. C. and Lima, A. O. D. S. (2012). Bioprospection of cellulolytic and lipolytic South Atlantic deep-sea bacteria. *Electronic Journal of Biotechnology* 15(5).
- Olabarria, C. (2005). Patterns of bathymetric zonation of bivalves in the Porcupine Seabight and adjacent abyssal plain, NE Atlantic. *Deep-Sea Research I* 52, 15-31.
- O'Leary, J. K., Micheli, F., Aioldi, L., Boch, C., De Leo, G., Elahi, R., Ferretti, F., Graham, N. A. J., Litvin, S. Y., Low, N. H., Lummis, S., Nickols, K. J. and Wong, J. (2017). The resilience of marine ecosystems to climate disturbances. *Bioscience* 67(3), 208-220.
- O'Mullan, G. D., Maas, P. A. Y., Lutz, R. A. and Vrijenhoek, R. C. (2001). A hybrid zone between hydrothermal vent mussels (Bivalvia: Mytilidae) from the Mid-Atlantic Ridge. *Molecular Ecology* 10, 2819-2831.
- Opdal, A. F., Godø, O. R., Bergstad, O. A. and Fiksen, Ø. (2008). Distribution, identity, and possible processes sustaining meso- and bathypelagic scattering layers on the northern Mid-Atlantic Ridge. *Deep-Sea Research II* 55, 45-58.
- Orcutt, B. N., Sylvan, J. B., Rogers, D. R., Delaney, J., Lee, R. W. and Girguis, P. R. (2015). Carbon fixation by basalt-hosted microbial communities. *Frontiers in Microbiology* 6, 904.
- Osinga, R., Armstrong, E., Burgess, J. G., Hoffmann, F., Reitner, J., Schumann-Kindel, G. (2001). Sponge-microbe associations and their importance for sponge bio process engineering. *Hydrobiologia* 461, 55-62.
- Pawson, D. L. and Foel, E. J. (1986). *Peniagone leander* new species, an abyssal benthopelagic sea cucumber

- (Echinodermata: Holothuroidea) from the eastern Central Pacific Ocean. *Bulletin of Marine Science* 38, 293-299.
- Pearcy, W. G. and Brodeur, R. D. (2009). Nekton. In: *Encyclopedia of Ocean Sciences (Second Edition)*. Academic Press. 1-7.
- Peña, M. (2019). Mesopelagic fish avoidance from the vessel dynamic positioning system. *ICES Journal of Marine Science* 76, 734-742.
- Pereira, J. G. (1995). Etat d'exploitation du stock de patudo. *Collective Volume of Scientific Papers ICCAT* 44(2), 272-280.
- Pereira, J. N., Neves, V. C., Prieto, R., Silva, M. A., Cascao, I., Oliveira, C., Cruz, M. J., Medeiros, J. V., Barreiros, J. P., Porteiro, F. M. and Clarke, D. (2011). Diet of mid-Atlantic Sowerby's beaked whales *Mesoplodon bidens*. *Deep-Sea Research I* 58(11), 1084-1090.
- Perez, J. A., Alves, E. D., Clark, M. R., Bergstad, O. A., Gebruk, A., Cardoso, I. A., Rogacheva, A. (2012). Patterns of life on the southern Mid-Atlantic Ridge: Compiling what is known and addressing future research. *Oceanography* 25(4), 16-31.
- Perner, M., Bach, W., Hentscher, M., Koschinsky, A., Garbe-Schonberg, D., Streit, W. R. and Strauss, H. (2009). Short-term microbial and physico-chemical variability in low-temperature hydrothermal fluids near 5S on the Mid-Atlantic Ridge. *Environmental Microbiology* 11(10), 2526-2541.
- Perner, M., Kuever, J., Seifert, R., Pape, T., Koschinsky, A., Schmidt, K., Strauss, H. and Imhoff, J. F. (2007). The influence of ultramafic rocks on microbial communities at the Logatchev hydrothermal field, located 15N on the Mid-Atlantic Ridge. *FEMS Microbial Ecology* 61, 97-109.
- Pershing, A. J., Christensen, L. B., Record, N. R., Sherwood, G. D. and Stetson, P. B. (2010). The impact of whaling on the ocean carbon cycle: why bigger was better. *PLoS ONE* 5(8), e12444.
- Petersen, J. M., Ramette, A., Lott, C., Cambon-Bonavita, M. A., Zbinden, M. and Dublier, N. (2010). *Environmental Microbiology* 12(8), 2204-2218.
- Petersen, J. M., Zielinski, F. U., Pape, T., Seifert, R., Moraru, C., Amann, R., Hourdez, S., Girguis, P. R., Wankel, S. D., Barbe, V., Pelletier, E., Fink, D., Borowski, C., Bach, W. and Dubilier, N. (2011). Hydrogen is an energy source for hydrothermal vent symbioses. *Nature* 476, 176-180.
- Pham, C. K., Vandeperre, F., Menezes, G., Porteiro, F., Isidro, E. and Morato, T. (2015). The importance of deep-sea vulnerable marine ecosystems for demersal fish in the Azores. *Deep-Sea Research I* 96, 80-88.
- Pierrot-Bults, A. C. (2008). A short note on the biogeographic patterns of the Chaetognatha fauna in the North Atlantic. *Deep Sea Research II* 55(1-2), 137-141.
- Pietsch, T. W. (2009). *Oceanic anglerfishes, extraordinary diversity in the deep sea*. University of California Press, 557 pp.
- Piontkovski, S. Q., O'Brien, T. D., Umani, S. F., Krupa, E. G., Stuge, T. S., Balymbetov, K. S., Grishaeva, O. V. and Kasymov, A. G. (2006). Zooplankton and the North Atlantic Oscillation: a basin-scale analysis. *Journal of Plankton Research* 28(11), 1039-1046.
- Plum, C., Pradillon, F., Fujiwara, Y. and Sarrazin, J. (2017). Copepod colonization of organic and inorganic substrata at a deep-sea hydrothermal vent site on the Mid-Atlantic Ridge. *Deep-Sea Research II* 137, 335-348.
- Poli, A., Finore, I., Romano, I., Gioiello, A., Lama, L. and Nicolaus, B. (2017). Microbial diversity in extreme marine habitats and their biomolecules. *Microorganisms* 2, 25.
- Pond, D. W., Sargent, J. R., Fallick, A. E., Allen, C., Bell, M. V. and Dixon, D. R. (2000).

$\delta^{13}\text{C}$ values of lipids from phototrophic zone microplankton and bathypelagic shrimps at the Azores sector of the Mid-Atlantic Ridge. *Deep-Sea Research I* 47(1), 121-136.

Portail, M., Brandily, C., Cathalot, C., Colaço, A., Gelinas, Y., Husson, B., Sarradin, P.-M. and Sarrazin, J. (2018). *Deep-Sea Research I* 131, 101-120.

Porteiro, F., Gomes-Pereira, J. N., Pham, C., Tempera, F. and Santos, R. S. (2013). Distribution and habitat association of benthic fish on the Condor seamount (NE Atlantic, Azores) from *in situ* observations. *Deep Sea Research II* 98, 114-128.

Priede, I. G. (2017). *Deep-sea fishes: Biology, diversity, ecology and fisheries*. Cambridge University Press.

Priede, I. G., Bergstad, O. A., Miller, P. I., Vecchione, M., Gebruk, A., Falkenhaug, T., Billett, D. S. M., Craig, J., Dale, A. C., Shields, M. A., Tilstone, G. H., Sutton, T. T., Gooday, A. J., Inall, M. E., Jones, D. O. B., Martinez-Vicente, V., Menezes, G. M., Niedzielski, T., Sigurðsson, P., Rothe, N., Rogacheva, A., Alt, C. H. S., Abell, R., Brierley, A. S., Cousins, N. J., Crockard, D., Hoelzel, A. R., Høines, Å., Letessier, T. B., Read, J. F., Shimmield, T., Cox, M. J., Galbraith, J. K., Gordon, J. D. M., Horton, T., Neat, F. and Lorance, P. (2013a). Does presence of a Mid Ocean Ridge enhance biomass and biodiversity? *PLoS ONE* 8(5), e61550.

Priede, I. G., Billett, D. S. M., Brierley, A. S., Hoelzel, A. R., Inall, M., Miller, P. I., Cousins, N. J., Shields, M. A. and Fujii, T. (2013b). The ecosystem of the Mid-Atlantic Ridge at the sub-polar front and Charlie-Gibbs Fracture Zone; ECO-MAR project strategy and description of the sampling programme 2007 - 2010. *Deep-Sea Research II* 98, 220-230.

Priede, I. G., Osborn, K. J., Gebruk, A. V., Jones, D., Shale, D., Rogacheva, A. and Holland, N. D. (2012). Observations on

torquaratorid acorn worms (Hemichordata, Enteropneusta) from the North Atlantic with descriptions of a new genus and three new species. *Invertebrate Biology* 131(3), 244-257.

Putman, N. F., Verley, P., Shay, T. J. and Lohmann, K. J. (2012). Simulating transoceanic migrations of young loggerhead sea turtles: Merging magnetic navigation behavior with an ocean circulation model. *Journal of Experimental Biology* 215, 1863-1870.

Queiroz, N., Humphries, N. E., Mucientes, G., Hammerschlag, N., Lima, F. P., Scales, K. L., Miller, P. I., Sousa, L. L., Seabra, R. and Sims, D. W. (2016). Ocean-wide tracking of pelagic sharks reveals extent of overlap with longline fishing hotspots. *PNAS* 113(6), 1582-1587.

Ramírez, I., Paiva, V. H., Fagundes, I., Menezes, D., Silva, I., Ceia, F. R. and Phillips, R. A. (2016). Conservation implications of consistent foraging and trophic ecology in a rare petrel species. *Animal Conservation* 19(2), 139-152.

Ramírez, I., Paiva, V. H., Menezes, D., Silva, I., Phillips, R. A., Ramos, J. A. and Garthe, S. (2013). Year-round distribution and habitat preferences of the Bugio petrel. *Marine Ecology Progress Series* 476, 269-284.

Ramiro-Sánchez, B., González-Irusta, J. M., Henry, L.-A., Cleland, J., Yeo, I., Xavier, J. R., Carreiro-Silva, M., Sampaio, I., Spearman, J., Victorero, L., Messing, C. G., Kazanidis, G., Roberts, J. M. and Murton, B. (2019). Characterization and mapping of a deep-sea sponge ground on the Tropic Seamount (Northeast Tropical Atlantic): Implications for spatial management in the High Seas. *Frontiers in Marine Science* 6, 278.

Ramos, R., Ramírez, I., Paiva, V. H., Militão, T., Biscoito, M., Menezes, D., Phillips, R. A., Zino, F. and González-solís, J. (2016). Global spatial ecology of three closely-

- related gadfly petrels. *Scientific Reports* 6, 23477.
- Read, J. F., Pollard, R. T., Miller, P. I. and Dale, A. C. (2010). Circulation and variability of the North Atlantic Current in the vicinity of the Mid-Atlantic Ridge. *Deep Sea Research Part I* 57(3), 307-318.
- Reed, D. C., Breier, J. A., Jiang, H., Anantharaman, K., Klausmeier, C. A., Toner, B. M., Hancock, C., Speer, K., Thurnherr, A. M. and Dick, G. J. (2015). Predicting the response of the deep-ocean microbiome to geochemical perturbations by hydrothermal vents. *The International Society for Microbial Ecology Journal* 9, 1857-1869.
- Reid, W. D. K., Wigham, B. D., McGill, R. A. R. and Polunin, N. V. C. (2012). Elucidating trophic pathways in benthic deep-sea assemblages of the Mid-Atlantic Ridge north and south of the Charlie Gibbs Fracture Zone. *Marine Ecology Progress Series* 463, 89-103.
- Renz, J. and Markhaseva, E. L. (2015). First insights into genus level diversity and biogeography of deep sea benthopelagic calanoid copepods in the South Atlantic and Southern Ocean. *Deep-Sea Research Part I* 105, 96-110.
- Reysenbach, A.-L., Longnecker, K. and Kirshtein, J. (2000). Novel bacteria and archaeal lineages from an *in-situ* growth chamber deployed at a Mid-Atlantic Ridge hydrothermal vent. *Applied and Environmental Microbiology* 66(9), 3798-3806.
- Richardson, D. E., Marancik, K. E., Guyon, J. R., Lutcavage, M. E., Galuardi, B., Lam, C. H., Walsh, H. J., Wildes, S., Yates, D. A. and Hare, J. A. (2016). Discovery of a spawning ground reveals diverse migration strategies in Atlantic bluefin tuna (*Thunnus thynnus*). *PNAS* 113(12), 3299-3304.
- Riehl, T., Lins, L. and Brandt, A. (2018). The effects of depth, distance and the Mid-Atlantic Ridge on genetic differentiation of abyssal and hadal isopods (Macrostyliidae). *Deep-Sea Research Part II* 148, 74-90.
- Riesgo, A., Pérez-Portela, R., Pita, L., Blasco, G., Erwin, P. and López-Legentil, S. (2016). Population structure and connectivity in the Mediterranean sponge *Ircinia fasciculata* are affected by mass mortalities and hybridization. *Heredity* 117(6), 427.
- Riesgo, A., Taboada, S., Pérez-Portela, R., Melis, P., Xavier, J. R., Blasco, G. and López-Legentil, S. (2019). Genetic diversity, connectivity and gene flow along the distribution of the emblematic Atlanto-Mediterranean sponge *Petrosia ficiformis* (Haplosclerida, Demospongiae). *BMC Evolutionary Biology* 19, 24.
- Rizzo, L. Y. and Schulte, D. (2009). A review of humpback whales' migration patterns worldwide and their consequences for gene flow. *Journal of the Marine Biological Association of the United Kingdom* 89, 995-1002.
- Roberts, J. M., Henry, L. A., Long, D. and Hartley, J. P. (2008). Cold-water coral reef frameworks, megafaunal communities and evidence for coral carbonate mounds on the Hatton Bank, north east Atlantic. *Facies* 54, 297-316.
- Robinson, C., Steinberg, D. K., Anderson, T. R., Aristegui, J., Carlson, C. A., Frost, J. R., Ghiglione J.-F., Hernandez-Leond, S., Jackson, G. A., Koppelman, R., Queguiner, B., Ragueneau, O., Rassoulzadegan, F., Robison, B. H., Tamburini, C., Tanaka, T., Wishner, K. and Zhang, J. (2010). Mesopelagic zone ecology and biogeochemistry - a synthesis. *Deep Sea Research Part II* 57, 1504-1518.
- Robson, J., Sutton, R. T., Archibals, A., Cooper, F., Christensen, M., Gray, L. J., Holliday, N. P., Macintosh, C., McMillan, M., Moat, B., Russo, M., Tilling, R., Carslaw, K., Desbruyeres, D., Embury, O., Feltham, D. L., Grosvenor, D. P., Josey, S., King, B., Lewis, A., McCarthy, G. D., Merchant, C., New, A.

- L., O'Reilly, C. H., Osprey, S. M., Read, K., Scaife, A., Shepherd, A., Sinha, B., Smeed, D., Smith, D., Ridout, A., Woolings, T. and Yan, M. (2018). Recent multivariate changes in the North Atlantic climate system, with a focus on 2005–2016. *International Journal of Climatology* 38, 5050–5076.
- Roe, H. S. J. (1988). Midwater biomass profiles over the Madeira Abyssal Plain and the contribution of copepods. *Hydrobiologia*, 167/168, 169–181.
- Roe, H. S. J., Billett, D. S. M. and Lampitt, R. S. (1990). Benthic/midwater interactions on the Madeira Abyssal Plain; evidence for biological transport pathways. *Progress in Oceanography* 24, 127–140.
- Rogacheva, A. (2012). Taxonomy and distribution of the genus *Kolga* (Elpidiidae: Holothuroidea: Echinodermata). *Journal of the Marine Biological Association of the United Kingdom* 92(5), 1183–1193.
- Rogacheva, A., Gebruk, A. and Alt, C. H. S. (2012). Swimming deep-sea holothurians (Echinodermata: Holothuroidea) on the northern Mid-Atlantic Ridge. In: Kroh, A., Reich, M. (Eds.), *Echinoderm Research 2010: Proceedings of the Seventh European Conference on Echinoderms. Zoosymposia* 7, 213–224.
- Rogacheva, A., Gebruk, A. and Alt, C. H. S. (2019). Swimming deep-sea holothurians (Echinodermata: Holothuroidea) on the northern Mid-Atlantic Ridge. *Zoosymposia* 7.
- Rogacheva, A., Gebruk, A., Alt, C. H. S. (2013). Holothuroidea of the Charlie Gibbs Fracture Zone area, northern Mid-Atlantic Ridge. *Marine Biology Research* 9(5–6), 587–623.
- Rogers, A. D., Tyler, P. A., Connelly, D. P., Copley, J. T., James, R., Larter, R. D., Linse, K., Mills, R. A., Garabato, A. N., Pancost, R. D., Pearce, D. A., Polunin, N. V., German, C. R., Shank, T., Boersch-Supan, P. H., Alker, B. J., Aquilina, A., Bennett, S. A., Clarke, A., Dinley, R. J., Graham, A. G., Green, D. R., Hawkes, J. A., Hepburn, L., Hilario, A., Huvenne, V. A., Marsh, L., Ramirez-Llodra, E., Reid, W. D., Roterman, C. N., Sweeting, C. J., Thatje, S. and Zwirglmaier, K. (2012). The discovery of new deep-sea hydrothermal vent communities in the southern ocean and implications for biogeography. *PLoS Biology* 10, e1001234.
- Rommevaux, C., Henri, P., Degboe, J., Chavagnac, V., Lesongeur, F., Godfroy, A., Boulart, C., Destrigneville, C. and Castillo, A. (2019). Prokaryote communities at active chimney and *in-situ* colonization devices after a magmatic degassing event (37N MAR, EMSO-Azores Deep-Sea Observatory). *Geochemistry, Geophysics, Geosystems* 20(6), 3056–3089.
- Rona, P. A. et al. (1982). *EOS Transactions of the American Geophysical Union: Fall Meeting 1982*, 63, 1014.
- Rona, P. A., Bostrom, K. and Epstein, S. (1980). Hydrothermal quartz vug from the Mid-Atlantic Ridge. *Geology* 8(12), 569–572.
- Rona, P. A., Hannington, M. D., Raman, C. V., Thompson, G., Tivey, M. K., Humphris, S. E., Lalou, C. and Petersen, S. (1993). Active and relict sea-floor hydrothermal mineralization at the TAG hydrothermal field, Mid-Atlantic Ridge. *Economic Geology* 88(8), 1989–2017.
- Rona, P. A., Harbison, R. N., Bassinger, B. G., Scott, R. B. and Nalwark, A. J. (1976). Tectonic fabric and hydrothermal activity of Mid-Atlantic Ridge crest (lat 26N). *The Geological Society of America Bulletin* 71(8), 1515–1525.
- Rona, P. A., Seilacher, A., de Vargas, C., Gooday, A. J., Bernhard, J. M., Bowser, S., Vetriani, C., Wirsén, C. O., Mullineaux, L., Sherrell, R., Grassle, F. J., Low, S. and Lutz, R. A. (2009). *Paleodictyon nodosum*: A living fossil on the deep-sea floor. *Deep-Sea Research III* 56, 1700–1712.

- Rooker, J. R., Bremer, J. R. A. B., Block, B. A., Dewar, H., de Metrio, G., Corriero, A., Kraus, R. T., Prince, E. D., Rodriguez-Marin, E. and Secor, D. (2007). Life history and stock structure of Atlantic bluefin tuna (*Thunnus thynnus*). *Reviews in Fisheries Science* 15(4), 265–310.
- Roper, C. F. E. and Brundage, N. L. (1972). Cirrate octopods with associated deep-sea organisms: New biological data based on deep-benthic photographs. *Smithsonian Contributions to Zoology* 121, 1–46.
- Roper, C. F. E. and Vecchione, M. (1997). *In-situ* observation test hypotheses of functional morphology in *Mastigoteuthis. Vie et Milieu* 47(2), 87–93.
- Roper, C. F. E. and Young, R. E. (1975). Vertical distribution of pelagic cephalopods. *Smithsonian Contributions to Zoology* 209, 1–51.
- Rosa, R., Dierssen, H. M., Gonzalez, L. and Seibel, B. A. (2008). Large-scale diversity patterns of cephalopods in the Atlantic open ocean and deep sea. *Ecology* 89(12), 3449–3461.
- Rossby, T. (1999). On gyre interactions. *Deep Sea Research II* 46(1–2), 139–164.
- Røstad, A., Kaartvedt, S. and Aksnes, D. L. (2016). Light comfort zones of mesopelagic acoustic scattering layers in two contrasting optical environments. *Deep-Sea Research I* 113, 1–6.
- Roussel, E. G., Konn, C., Charlou, J.-L., Donval, J.-P., Fouquet, Y., Querellou, J., Prieur, D. and Cambon Bonavita, M.-A. (2011). Comparison of microbial communities associated with three Atlantic ultramafic hydrothermal systems. *FEMS Microbial Ecology* 77, 647–665.
- Ruppert, E. E., Fox, R. S. and Barnes, R. D. (2004). *Invertebrate Zoology*. Seventh Edition.
- Rybakova, E. and Galkin, S. (2015). Hydrothermal assemblages associated with different foundation species on the East Pacific Rise and Mid-Atlantic Ridge, with a special focus on mytilids. *Marine Ecology* 36 (Supplement 1), 45–61.
- Samadi, S., Bottan, L., Macpherson, E., Richer de Forges, B. and Boisselier, M.-C. (2006). Seamount endemism questioned by geographic distribution and population genetic structure of marine invertebrates. *Marine Biology* 149, 1463–1475.
- Samadi, S., Schlacher, T. A. and Richer de Forges, B. (2007). Seamount benthos. In: Pitcher, T. J., Morato, T., Hart, P. J. B., Clark, M. R., Haggan, N. and Santos, R. S. (Eds.), *Seamounts: Ecology, Fisheries and Conservation*. Oxford: Blackwell, pp. 119–140.
- Sampaio, I., Carreiro-Silva, M., Freiwald, A., Menezes, G. and Grasshoff, M. (2019). Natural history collections as a basis for sound biodiversity assessments: Plexauridae (Octocorallia, Holaxonida) of the Naturalis CANCAP and Tyro Mauritania II expeditions. *ZooKeys* 870, 1–32.
- Sampaio, I., Freiwald, A., Porteiro, F. M., Menezes, G. and Carreiro-Silva, M. (2019a). Census of Octocorallia (Cnidaria: Anthozoa) of the Azores (NE Atlantic): a nomenclature update. *Zootaxa* 4550(4), 451–498.
- Santelli, C. M., Edgcomb, V. P., Bach, W. and Edwards, K. J. (2009). The diversity and abundance of bacteria inhabiting seafloor lavas positively correlate with rock alteration. *Environmental Microbiology* 11(1), 86–98.
- Santos, M. B., Pierce, G. J., Herman, J., Lopez, A., Guerra, A., Mente, E. and Clarke, M. R. (2001). Feeding ecology of Cuvier's beaked whale (*Ziphius cavirostris*): a review with new information on the diet of this species. *Journal of the Marine Biological Association of the United Kingdom* 81, 1–12.

- Association of the United Kingdom 81(4), 687-694.
- Sarrazin, J., Cuvelier, D., Peton, L., Legendre, P. and Sarradin, P. M. (2014). High-resolution dynamics of a deep-sea hydrothermal vent mussel assemblage monitored by the EMSO-Azores MoMAR observatory. *Deep-Sea Research I* 90, 62-75.
- Scales, K. L., Miller, P. I., Hawkes, L. A., Ingram, S. N., Sims, D. W. and Votier, S. C. (2014). On the Front Line: frontal zones as priority at sea conservation areas for mobile marine vertebrates. *Journal of Applied Ecology* 51(6), 1575-1583.
- Schaefer, K. M., Fuller, D. W. and Block, B. A. (2009). Vertical movements and habitat utilization of skipjack (*Katsuwonus pelamis*), yellowfin (*Thunnus albacares*), and bigeye (*Thunnus obesus*) tunas in the equatorial eastern Pacific Ocean, ascertained through archival tag data. In: *Tagging and tracking of marine animals with electronic devices*. Dordrecht: Springer, 121-144.
- Schorr, G. S., Falcone, E. A., Moretti, D. J. and Andrews, R. D. (2014). First long-term behavioral records from Cuvier's beaked whales (*Ziphius cavirostris*) reveal record-breaking dives. *PLoS ONE* 9(3), e92633.
- Scott, J. J., Breier, J. A., Luther, G. W. 3rd and Emerson, D. (2015). Microbial iron mats at the Mid-Atlantic Ridge and evidence that Zetaproteobacteria may be restricted to iron-oxidizing systems. *PLoS ONE* 10(3), e0119284.
- Sen, A., Podowski, E. L., Becker, E. L., Shearer, E. A., Gartman, A., Yucel, M., Hourdez, S., Luther, G. W. 3rd and Fisher, C. R. (2014). Community succession in hydrothermal vent habitats of the Eastern Lau Spreading Center and Valu Fa Ridge, Tonga. *Limnology and Oceanography* 59(5), 1510-1528.
- Sequeira, A., Mellin, C., Rowat, D., Meekan, M. G. and Bradshaw, C. J. A. (2012). Ocean-scale prediction of whale shark distribution. *Diversity and Distributions* 18, 504-518.
- Shao, Z., Cui, Z., Dong, C., Lai, Q. and Chen, L. (2010). Analysis of a PAH-degrading bacterial population in subsurface sediments on the Mid-Atlantic Ridge. *Deep-Sea Research I* 57, 724-730.
- Shields, A. and Blanco-Perez, R. (2013). Polychaete abundance, biomass and diversity patterns at the Mid-Atlantic Ridge, North Atlantic Ocean. *Deep-Sea Research II* 98, 315-325.
- Silantyev, S. (2008). Russia National News. *InterRidge News* 17, online supplement, 39-41.
- Silva, M. A., Borrell, A., Prieto, R., Gauffier, P., Berube, M., Palsbol, P. J. and Colaco, A. (2019). Stable isotopes reveal winter feeding in different habitats in blue, fin and sei whales migrating through the Azores. *Royal Society Open Science* 6, 181800.
- Sievert, S. and Vetriani, C. (2012). Chemoautotrophy at deep-sea vents: Past, present, and future. *Oceanography* 25(1), 218-233.
- Skomal, G. B., Braun, C. D., Chisholm, J. H. and Thorrold, S. R. (2017). Movements of the white shark *Carcharodon carcharias* in the North Atlantic Ocean. *Marine Ecology Progress Series* 580, 1-16.
- Snelgrove (2010). *Discoveries of the Census of Marine Life: making ocean life count*. Cambridge: Cambridge University Press, 270 pp.
- Søiland, H., Budgell, W. P. and Knutsen, Ø. (2008). The physical oceanographic conditions along the Mid-Atlantic Ridge north of the Azores in June - July 2004. *Deep-Sea Research II* 55(1-2), 29-44.
- Souto, J. and Albuquerque, M. (2019). Diversity and community structure of

- Cheilostomata (Bryozoa) from the Hayes Fracture Zone, Mid-Atlantic ridge. *Deep Sea Research Part I: Oceanographic Research Papers* 147, 32-53.
- Sperling, A. T., Neilson, J. D., Carruthers, E. H. and Stone, H. H. (2005). Compilation and analyses of Canadian conventional tagging data for swordfish (*Xiphias gladius*), 1961-2004. *Collective Volume of Scientific Papers ICCAT* 58, 1483-1494.
- Spitz, J., Cherel, Y., Bertin, S., Kiszka, J., Dewez, A. and Ridoux, V. (2011). Prey preferences among the community of deep-diving odontocetes from the Bay of Biscay, Northeast Atlantic. *Deep-Sea Research I* 58, 273-282.
- St. John, M. A., Borja, A., Chust, G., Heath, M., Grigorov, I., Mariani, P., Martin, A. P. and Santos, R. (2016). A dark hole in our understanding of marine ecosystems and their services: perspectives from the mesopelagic community. *Frontiers in Marine Science* 3, 31.
- St. Laurent, L. C. and Thurnherr, A. M. (2007). Intense mixing of lower thermocline water on the crest of the Mid-Atlantic Ridge. *Nature* 448(7154), 680-683.
- Stevick, P. R., Bouveret, L., Gandilhon, N., Rinaldi, C., Broms, F., Carlson, C., Kennedy, A., Ward, N. and Wenzel, F. (2018). Migratory destinations and timing of humpback whales in the southeastern Caribbean differ from those off the Dominican Republic. *Journal of Cetacean Research and Management* 18, 127-133.
- Sudarikov, S. M., Ashadze, A. M., Stepanova, T. V., Nesheretov, A. B., Vorobiov, P. V., Kasabov, R. V. and Guinikov, A. S. (1990). Hydrothermal activity and ore-forming in the rift zone of the Mid-Atlantic Ridge (new data). *Translations (Doklady) of the U.S.S.R. Academy of Science: Earth Science Section* 311, 89-93.
- Sumida, P. Y. G., Alfaro-Lucas, J. M., Shimabukuro, M., Kitazato, H., Perez, J. A., A., Soares-Gomes, A., Toyofuku, T., Lima, A. O. S., Ara, K. and Fujiwara, Y. (2016). Deep-sea whale fall fauna from the Atlantic resembles that of the Pacific Ocean. *Scientific Reports* 6, 22139.
- Sutton, T. T., Clark, M. R., Dunn, D. C., Halpin, P. N., Rogers, A. D., Guinotte, J., Bograd, S. J., Angel, M. V., Perez, J. A. A., Wishner, K., Haedrich, R. L., Lindsay, D. J., Drazen, J. C., Vereshchakam, A., Piatkowski, U., Morato, T., Błachowiak-Samołyk, K., Robison, B. H., Gjerder, K. M., Pierrot-Bults, A., Bernalt, P., Reygondeau, G. and Heino, M. (2017). A global biogeographic classification of the mesopelagic zone: An aid for marine conservation planning. *Deep-Sea Research I* 126, 85-102.
- Sutton, T. T. and Hopkins, T. L. (1996). Species composition, abundance, and vertical distribution of the stomiid (Pisces: Stomiiformes) fish assemblage of the Gulf of Mexico. *Bulletin of Marine Science* 59, 530-42.
- Sutton, T. T., Porteiro, F. M., Heino, M., Byrkjedal, I., Langhelle, G., Anderson, C. I. H., Horne, J., Soiland, H., Falkenhaug, T., Godo, O. R. and Bergstad, O. A. (2008). Vertical structure, biomass and topographic association of deep-pelagic fishes in relation to a mid-ocean ridge system. *Deep-Sea Research II* 55, 161-184.
- Sutton, T. T. and Sigurðsson, T. (2008). Vertical and horizontal distribution of mesopelagic fishes along a transect across the northern Mid-Atlantic Ridge. *ICES CM, 2008/C (16)*, 1-12.
- Suzuki, Y., Inagaki, F., Takai, K., Nealson, K. H. and Horikoshi, K. (2004). Microbial diversity in inactive chimney structures from the deep-sea hydrothermal systems. *Microbial Ecology* 47(2), 186-196.
- Sy, A. (1988). Investigation of large-scale circulation patterns in the central North Atlantic: The North Atlantic Current, the Azores Current, and the Mediterranean Water plume in the area of the Mid-

- Atlantic Ridge. *Deep Sea Research A* 35(3), 383–413.
- Sy, A., Schauer, U. and Meincke, J. (1992). The North Atlantic Current and its associated hydrographic structure above and eastwards of the Mid-Atlantic Ridge. *Deep Sea Research Part A* 39(5), 825–853.
- Sylvan, J. B., Toner, B. M. and Edwards, K. J. (2012). Life and death of deep-sea vents: bacterial diversity and ecosystem succession on inactive hydrothermal sulphides. *mBio* 3(1), e00279-11.
- Tabachnick, K. R. and Collins, A. G. (2008). Glass sponges (Porifera, Hexactinellida) of the northern Mid-Atlantic Ridge. *Marine Biology Research* 4, 25–47.
- Tabachnick, K. R. and Mensheninia (2013). New data on glass sponges (Porifera, Hexactinellida) of the northern Mid-Atlantic Ridge. Part 2. Aphrocallistidae, Euretidae, Euplectellidae and Rossellidae (with descriptions of two new species of *Sympagella*). *Marine Biology Research* 9(5–6), 469–487.
- Tchesunov, A. V. (2015). Free-living nematode species (Nematoda) dwelling in hydrothermal sites of the North Mid-Atlantic Ridge. *Helgoland Marine Research* 69, 343–384.
- Tempera, F., Atchoi, E., Amorim, P., Gomes-Pereira, J., Gonçalves, J. (2013). *Atlantic Area Marine Habitats. Adding new Macaronesian habitat types from the Azores to the EUNIS Habitat Classification*. Mesh Atlantic Technical Report, 4/2013. IMAR/DOP-UAç, Horta, 126 pp.
- Tempera, F., Carreiro-Silva, M., Jakobsen, K., Porteiro, F. M., Braga-Henriques, A. and Jakobsen, J. (2015) An Eguchipsammia (Dendrophylliidae) topping on the cone. *Marine Biodiversity* 45(1), 3–4.
- Tempera, F., Giacomello, E., Mitchell, N., Campos, A. S., Braga-Henriques, A., Bashmachnikov, I., Martins, A., Mendonça, A., Morato, T., Colaco, A., Porteiro, F. M., Catarino, D., Gonçalves, J., Pinho, M. R., Isidro, E. J., Santos, R. S. and Menezes, G. (2012). Mapping the Condor seamount seafloor environment and associated biological assemblages (Azores, NE Atlantic). In: Baker, E., Harris, P. (Eds.), *Seafloor Geomorphology as Benthic Habitat: Geohab Atlas of Seafloor Geomorphic Features and Benthic Habitats*. New York: Elsevier, 807–818.
- Teixeira, S., Cambon-Bonavita, M. A., Serrao, E. A., Desbruyeres, D. and Arnaud-Haond, S. (2010). Recent population expansion and connectivity in the hydrothermal shrimp *Rimicaris exoculata* along the Mid-Atlantic Ridge. *Journal of Biogeography* 38(3), 564–574.
- Thoma, J. N., Pante, E., Brugler, M. R. and France, S. C. (2009). Deep-sea octocorals and antipatharians show no evidence of seamount-scale endemism in the NW Atlantic. *Marine Ecology Progress Series* 397, 25–35.
- Thornalley, D. J. R., Oppo, D. W., Ortega, P., Robson, J. I., Brierley, C. M., Davis, R., Hall, I. R., Moffa-Sánchez, P., Rose, N. L., Spooner, P. T., Yashayaev, I. and Keigwin, L. D. (2018). Anomalously weak Labrador Sea convection and Atlantic overturning during the past 150 years. *Nature* 556, 227–232.
- Thurber, A. R., Sweetman, A. K., Narayanaswamy, B. E., Jones, D. O. B., Ingels, J. and Hansman, R. I. (2014). Ecosystem function and services provided by the deep sea. *Biogeosciences* 11, 3941–3963.
- Tozer, B., Sandwell, D. T., Smith, W. H. F., Olson, C., Beale, J. R. and Wessel, P. (2019). Global bathymetry and topography at 15 arc sec: SRTM15+. *Earth and Space Science* 6, 1847–1864.
- Turnipseed, M., Jenkins, C. D. and Van Dover, C. L. (2004). Community structure in Florida Escarpment seep and Snake

- Pit (Mid-Atlantic Ridge) vent mussel beds. *Marine Biology* 145, 121–132.
- Van der Heijden, K., Petersen, J. M., Dubilier, N. and Borowski, C. (2012). Genetic connectivity between North and South Mid-Atlantic Ridge chemosynthetic bivalves and their symbionts. *PLoS one* 7(7), e39994.
- Van Dover, C. L. (2019). Inactive sulphide ecosystems in the deep sea: a review. *Frontiers in Marine Science* 6, 461.
- Van Dover, C. L. (2011). Mining seafloor massive sulphides and biodiversity: what is at risk? *ICES Journal of Marine Science* 68, 341–348.
- Van Dover, C. L. (1995). Ecology of Mid-Atlantic Ridge hydrothermal vents. In: Parson, L. M., Walker, C. L. and Dixon, D. R. (Eds.), *Hydrothermal vents and processes*. Geological Society Special Publication 87, 257–294.
- Van Dover, C. L., Berg, C. J. Jr. and Turner, R. D. (1988). Recruitment of marine invertebrates at deep-sea hydrothermal vents on the East Pacific Rise and Galapagos spreading center. *Deep Sea Research Part A* 35(10–11), 1833–1849.
- Van Dover, C. L. and Doerries, M. B. (2005). Community structure in mussel beds at Logatchev hydrothermal vents and a comparison of macrofaunal species richness on slow- and fast-spreading mid-ocean ridges. *Marine Ecology* 26, 110–120.
- Van Dover, C. L., German, C. R., Speer, K. G., Parson, L. M. and Vrijenhoek (2002). Evolution and biogeography of deep-sea vent and seep invertebrates. *Science* 295, 1253–1257.
- Van Dover, C. L., Arnaud-Haond, S., Gianni, M., Helmreich, S., Huber, J. A., Jaeckel, A. L., Metaxas, A., Pendleton, L. H., Petersen, S., Ramirez-Llodra, E., Steinberg, P. E., Tunnicliffe, V. and Yamamoto, H. (2018). Scientific rationale and international obligations for protection of active hydrothermal vent ecosystems from deep-sea mining. *Marine Policy* 90, 20–28.
- Van Dover, C. L. and Trask, J. (2000). Diversity at deep-sea hydrothermal vent and intertidal mussel beds. *Marine Ecology Progress Series* 195, 169–178.
- Vaudo, J. J., Byrne, M. E., Wetherbee, B. M., Harvey, G. M. and Shivji, M. S. (2017). Long-term satellite tracking reveals region-specific movements of a large pelagic predator, the shortfin mako shark, in the western North Atlantic Ocean. *Journal of Applied Ecology* 54, 1765–1775.
- Vecchione, M., Bergstad, O. A., Byrkjedal, I., Falkenhaug, T., Gebruk, A. V., Godø, O. R., Gislason, A., Heino, M., Høines, A. S., Menezes, G. M. M., Piatowski, U., Priede, I. G., Skov, H., Søiland, H., Sutton, T. and de Lange Wenneck, T. (2010b). Biodiversity patterns and processes on the Mid-Atlantic ridge. In: McIntyre, A. D. (Ed.), *Life in the World's Oceans: Diversity, Distribution and Abundance*, Wiley-Blackwell, 103–121.
- Vecchione, M. and Roper, C. F. E. (1991). Cephalopods observed from submersibles in the western North Atlantic. *Bulletin of Marine Science* 49(1–2), 433–445.
- Vecchione, M., Roper, C. F. E., Widder, E. A. and Frank, T. M. (2002). *In-situ* observations on three species of large-finned deep-sea squids. *Bulletin of Marine Science* 71(2), 893–901.
- Vecchione, M. and Young, R. E. (1997). Aspects of the functional morphology of cirrate octopods: Locomotion and feeding. *Vie et Milieu* 47(2), 101–110.
- Vecchione, M., Young, R. E. and Pietkowski, U. (2010a). Cephalopods of the northern Mid-Atlantic Ridge. *Marine Biology Research* 6(1), 25–52.
- Vereshchaka, A. L., Vinogradov, G. M., Lein, A. Y., Dalton, S. and Dehairs, F. (2000). Carbon and nitrogen isotopic composition

- of the fauna from the Broken Spur hydrothermal vent field. *Marine Biology* 136, 11-17.
- Vic, C., Gula, J., Roullet, G. and Pradillon, F. (2018). Dispersion of deep-sea hydrothermal vent effluents and larvae by submesoscale and tidal currents. *Deep-Sea Research I* 133, 1-18.
- Villanueva, R., Segonzac, M. and Guerra, A. (1997). Locomotion modes of deep-sea cirrate octopods (Cephalopoda) based on observations from video recordings on the Mid-Atlantic Ridge. *Marine Biology* 129, 113-122.
- Vinogradov, G. M. (2005). Vertical distribution of macroplankton at the Charlie-Gibbs Fracture Zone (North Atlantic), as observed from the manned submersible Mir-1. *Marine Biology* 146, 325-331.
- Vinogradov, M. E., Vereshchaka, A. L., Shushkina, E. A. (1996). Vertical structure of the zooplankton communities in the oligotrophic areas of the Northern Atlantic, and influence of the hydrothermal vent. *Okeanolgiya* 36, 71-79.
- Virgili, A. (2018). *Modelling distributions of rare marine species: the deep-diving cetaceans*. Agricultural sciences. Université de La Rochelle, 2018. English. NNT: 2018LAROS003. Tel-02009798.
- Virgili, A., Authier, M., Boisseau, O., Cañadas, A., Claridge, D., Cole, T., Corkeron, P., Dorémus, G., David, L., Di-Méglia, N., Dunn, C., Dunn, T. E., García-Barón, I., Laran, S., Lauriano, G., Lewis, M., Louzao, M., Mannocci, L., Martínez-Cedeira, J., Palka, D., Panigada, S., Petteg, E., Roberts, J. J., Ruiz, L., Saavedra, C., Santos, M. B., Van Canneyt, O., Vázquez Bonales, J. A., Monestiez, P. and Ridoux, V. (2019). Combining multiple visual surveys to model the habitat of deep-diving cetaceans at the basin scale: Large-scale modelling of deep-diving cetacean habitats. *Global Ecology and Biogeography* 28, 300-314.
- Vrijenhoek, R. C. (2010). Genetic diversity and connectivity of deep-sea hydrothermal vent metapopulations. *Molecular Ecology* 19, 4391-4111.
- Visser, F., Hartman, K. L., Pierce, G. J., Valavanis, V. D. and Huisman, J. (2011). Timing of migratory baleen whales at the Azores in relation to the North Atlantic spring bloom. *Marine Ecology Progress Series* 440, 267-279.
- Waller, R. G. and Tyler, P. A. (2005). The reproductive biology of two deep-water, reef-building scleractinians from the NE Atlantic Ocean. *Coral Reefs* 24, 514-522.
- Watling, L., Guninotte, J., Clark, M. R. and Smith, C. R. (2013). A proposed biogeography of the deep ocean floor. *Progress in Oceanography* 111, 91-112.
- Webster, M. S., Marra, P. P., Haig, S. M., Bensch, S. and Holmes, R. T. (2002). Links between worlds: unraveling migratory connectivity. *Trends in Ecology and Evolution* 17, 76-83.
- Wheeler, A. J., Murton, B., Copley, J. T., Lim, A., Carlsson, J., Collins, P. C., Dorschel, B., Green, D., Judge, M., Nye, V., Benzie, J., Antoniacomi, A., Coughlan, M. and Morris, K. (2013). Moytirra: Discovery of the first known deep-sea hydrothermal vent field on the slow-spreading Mid-Atlantic Ridge north of the Azores. *Geochemistry Geophysics and Geosystems* 14(10), 4170-4184.
- Wenzel, F. W., Polloni, P. T., Craddock, J. E., Gannon, D. P., Nicolas, J. R., Read, A. J. and Rosel, P. E. (2013). Food habits of Sowerby's beaked whales (*Mesoplodon bidens*) taken in the pelagic drift gillnet fishery of the western North Atlantic. *Fishery Bulletin* 111(4), 381-389.

- Whitehead, H. (1982). Populations of humpback whales in the northwest Atlantic. *Reports of the International Whaling Commission* 32, 345-53.
- Wishner, K. F. (1980a). The biomass of the deep-sea benthopelagic plankton. *Deep-Sea Research* 27A, 203-216.
- Wishner, K. F. (1980b). Aspects of the community ecology of deep-sea, benthopelagic plankton, with special attention to gymnopleid copepods. *Marine Biology* 60, 179-187.
- Wissak, M., Neumann, C., Jakobsen, J. and Freiwald, A. (2009). The 'living-fossil community' of the cyrtocrinid *Cyathidium foresti* and the deep-sea oyster *Neopycnodonte zibrowii* (Azores Archipelago). *Palaeogeography, Palaeoclimatology, Palaeoecology* 271(1-2), 77-83.
- Yahagi, T., Fukumori, H., Warén, A. and Kano, Y. (2019). Population connectivity of hydrothermal-vent limpets along the northern Mid-Atlantic Ridge (Gastropoda: Neritimorpha: Phenacolepadidae). *Journal of the Marine Biological Association of the United Kingdom* 99(1), 179-185.
- Yahel, G., Whitney, F., Reiswig, H. M., Eerkes-Medrano, D. I. and Leys, S. P. (2007). In situ feeding and metabolism of glass sponges (Hexactinellida, Porifera) studied in a deep temperate fjord with a remotely operated vehicle. *Limnology and Oceanography* 52, 428-440.
- Yesson, C., Taylor, M. L., Tittensor, D. P., Davies, A. J., Guinotte, J., Baco, A., Black, J., Hall-Spencer, J. M. and Rogers, A. D. (2012). Global habitat suitability of cold-water octocorals. *Journal of Biogeography* 39, 1278-1292.
- Young, R. E., Vecchione, M. and Donovan, D. (1998). The evolution of coleoid cephalopods and their present biodiversity and ecology. *South African Journal of Marine Science* 20, 393-420.
- Young, R. E., Vecchione, M. and Piatkowski, U. (2006). *Promachoteuthis sloani*, a new species of the squid family Promachoteuthidae (Mollusca: Cephalopoda). *Proceedings of the Biological Society of Washington* 119(2), 287-292.
- Zagaglia, C. R., Lorenzetti, J. A. and Stech, J. L. (2004). Remote sensing data and longline catches of yellowfin tuna (*Thunnus albacares*) in the equatorial Atlantic. *Remote Sensing of the Environment* 93(1-2), 267-281.
- Zbinden, M., Le Bris, N., Gaill, F. and Compere, P. (2004). Distribution of bacteria and associated minerals in the gill chamber of the vent shrimp *Rimicaris exoculata* and related biogeochemical processes. *Marine Ecology Progress Series* 284, 237-251.
- Zekely, J., Van Dover, C. L., Nemeschkal, H. L. and Bright, M. (2006a). Hydrothermal vent meiobenthos associated with mytilid mussel aggregations from the Mid-Atlantic Ridge and the East Pacific Rise. *Deep-Sea Research Part I* 53, 1363-1378.
- Zekely, J., Sorensen, M. and Bright, M. (2006b). Three new nematode species (Monhysteridae) from deep-sea hydrothermal vents. *Meiofauna Marina* 15, 25-42.
- Zeppilli, D., Bellec, L., Cambon-Bonavita, M.-A., Decraemer, W., Fontaneto, D., Fuchs, S., Gayet, N., Mandon, P., Michel, L. N., Portail, M., Smol, N., Sorensen, M. V., Vanreusel, A. and Sarrazin, J. (2019). Ecology and trophic role of *Oncholaimus dyvae* sp. nov. (Nematoda: Oncholaimidae) from the lucky strike hydrothermal vent field (Mid-Atlantic Ridge). *BMC Zoology* 4(6).
- Zeppilli, D., Vanreusel, A., Pradillon, F., Fuchs, S., Mandon, P., James, T. and Sarrazin, J. (2015). Rapid colonisation by nematodes on organic and inorganic substrata deployed at the deep-sea Lucky Strike hydrothermal vent field (Mid-Atlantic

- Ridge). *Marine Biodiversity* 45(3), 489–504.
- Zhang, L., Kang, M., Xu, J., Xu, J., Shuai, Y., Zhou, X., Yang, Z. and Ma, K. (2016). Bacterial and archaeal communities in the deep-sea sediments of inactive hydrothermal vents in the Southwest India Ridge. *Scientific Reports* 6, 25982.
- Zhang, X., Fang, J., Bach, W., Edwards, K. J., Orcutt, B. N. and Wang, F. (2016). Nitrogen stimulates the growth of subsurface basalt-associated microorganisms at the western flank of the Mid-Atlantic Ridge. *Frontiers in Microbiology* 7, 633.
- Zuercher, R. and Galloway, A. W. E. (2019). Coastal marine ecosystem connectivity: pelagic ocean to kelp forest subsidies. *Ecosphere* 10(2), e02602.
- Zylinski, S. and Johnsen, S. (2011). Mesopelagic cephalopods switch between transparency and pigmentation to optimize camouflage in the deep. *Current Biology* 21, 1937–1941.

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