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Deep-sea ecosystems of the North Atlantic Ocean: discovery, status, function and future challenges

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ABSTRACT

The North Atlantic is an ocean basin with a diversity of deep-sea ecosystems. Here we provide a summary of the topography and oceanography of the North Atlantic including the Gulf of Mexico and Caribbean Sea, provide a brief overview of the history of scientific research therein, and review the current status of knowledge of each of 18 pelagic and benthic deep-sea ecosystems, with a particular focus on knowledge gaps. We analyse biodiversity data records across the North Atlantic and highlight spatial data gaps that could provide important foci for future expeditions. We note particular data gaps in EEZs of nations within and bordering the Caribbean Sea. Our data provide a baseline against which progress can be tracked into the future. We review human impacts caused by fishing, shipping, mineral extraction, introduction of substances, and climate change, and provide an overview of international, regional and national measures to protect ecosystems. We recommend that scientific research in the deep sea should focus on increasing knowledge of the distribution and the connectivity of key species and habitats, and increasing our understanding of the processes leading to the delivery of ecosystem services. These three pillars - distribution, connectivity, ecosystem function - will provide the knowledge required to implement conservation and management measures to ensure that any deep-sea development in the future is sustainable. Infrastructure and capacity are unevenly distributed and implementation of strategies that will lead to more equitable deep-sea science is required to ensure that essential science can be delivered.

1. Introduction

The North Atlantic Ocean, lying between Europe to the East and North America to the west, is, in places, one of the best studied expanses of ocean on the planet. Nevertheless, its deeper parts are still considerably less studied than shallower regions, and some areas have never been explored. There is also a disparity of wealth among nations with deep ocean within their Exclusive Economic Zones (EEZs) that has impacted the intensity of scientific discovery within territorial waters. At the same time, human activities are increasing and expanding, and areas once thought to be beyond the reach of human impact are now subjected to anthropogenic pressures which may irrevocably alter ecosystems.

In the context of the UN Decade of Ocean Science for Sustainable Development (the Ocean Decade), we review the biological diversity of the North Atlantic deep sea. The overarching objectives of the Ocean Decade are to identify and generate required ocean data; increase the capacity to generate, understand, manage, and use ocean knowledge for sustainable development, including conservation; build comprehensive understanding of the ocean and ocean governance systems; and to increase the use of ocean knowledge. These objectives all hinge on first identifying which data are required (Muller-Karger et al., 2025).

In this review a major aim is to present a gap analysis of biodiversity research and discovery by collating available information on deep-sea (>200 m depth) benthic and pelagic macro- and megafaunal diversity of the North Atlantic, including the Gulf of Mexico and Caribbean Sea. We further review the literature on the ecosystems present to identify non-spatial knowledge gaps. We summarize information on key human activities in the area and present an overview of international policies and international and national area-based management measures. Finally, based on the collated data and knowledge, we present research priorities that can guide North Atlantic deep-sea research through the UN Decade of Ocean Sciences for Sustainable Development and beyond.

2. Geographic setting

The Atlantic Ocean contains numerous geomorphological features that have led to great biological diversity in the region, from pole to pole and from coastal zones to the deep ocean. This study focuses on the biodiversity of the deep North Atlantic Ocean including the Caribbean Sea and Gulf of Mexico (Fig. 1). The southern boundary of the study area stretches from the entrance of the Mediterranean Sea to the South-eastern boundary of the Caribbean (this is the northern boundary of the complementary review by Bridges et al., 2023). Here, we summarize general aspects of the diversity of organisms beyond continental shelves in the water column and on the ocean bottom. Detailed bathymetric mapping, an important foundation for mapping marine life and to understand marine biodiversity, is pursued separately by the Seabed2030 project (Mayer et al., 2018). Below we describe the extent of the North Atlantic study area.

2.1. Northern boundary

The northern boundary of the study region follows the 67° parallel from Baffin Island in Canada, around Greenland, to Norway. The “North Atlantic Gateway” (Jöst et al., 2019) between the North Atlantic Ocean and the Arctic Ocean (whose deep sea was reviewed by Ramirez-Llodra et al., 2024) reaches across from the east coast of Greenland to Iceland,

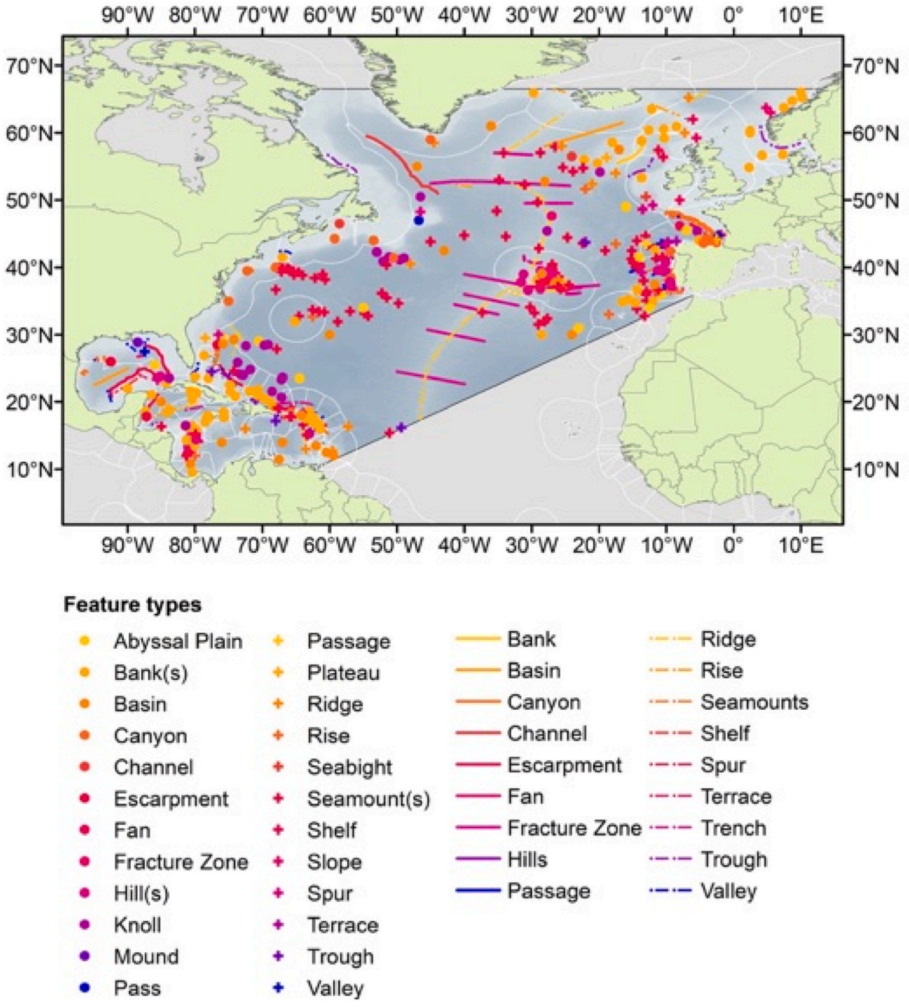

Fig. 1. Panel 1. Major topographic features of the North Atlantic deep ocean in the area of interest.

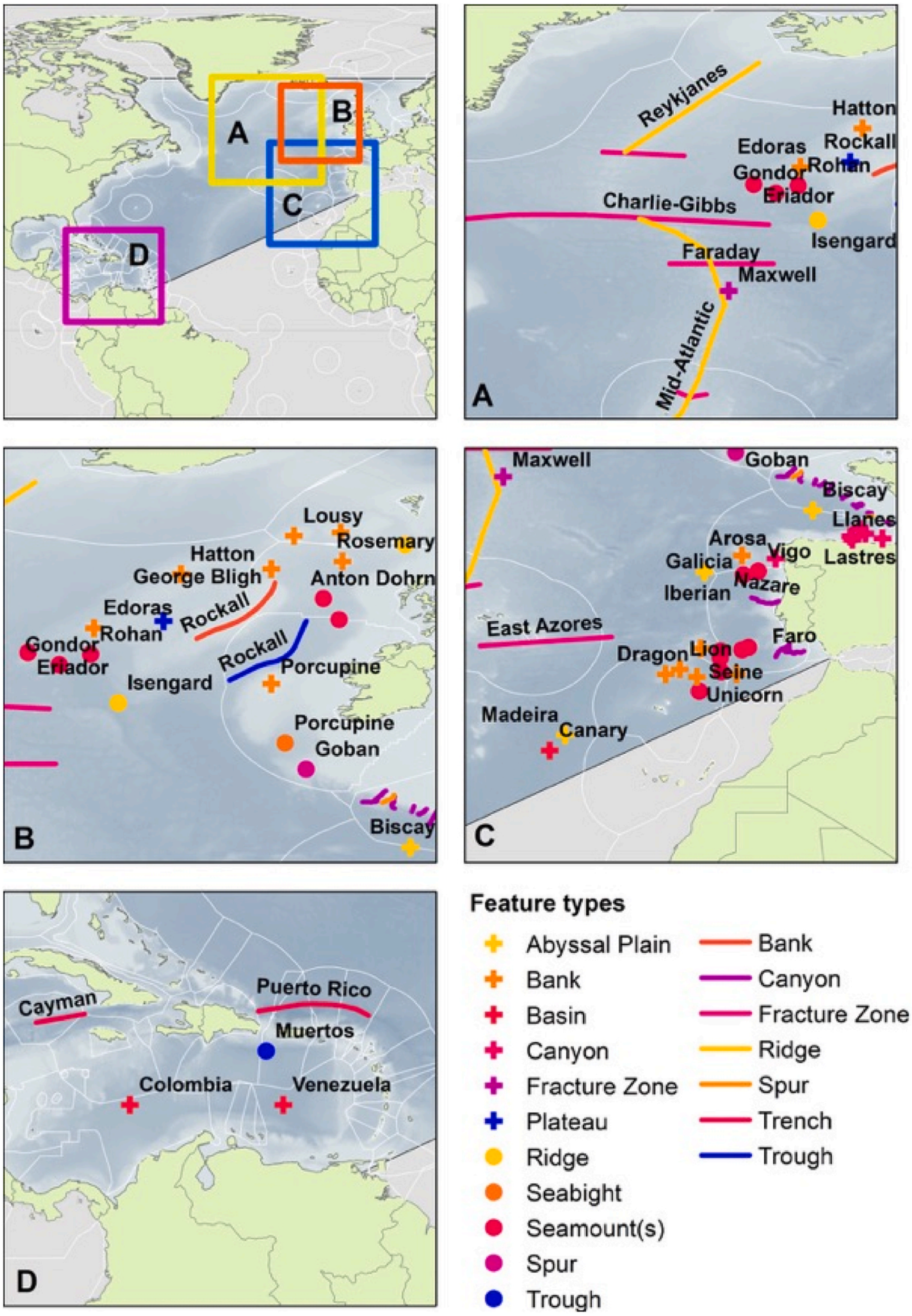

Fig. 1. Panel 2. Focus on named features of topographically diverse areas from Panel 1.

extends southeast through the Faroe Islands to the north coast of Scotland, and across to the Norwegian coast. East of Iceland, the Faroe Shetland Channel directs Arctic water south and west, with occasional overflows recorded along the Wyville-Thomson Ridge (Vlasenko and Stashchuk, 2018). Davis Strait, between Baffin Island and Greenland, separates the Labrador Sea from Baffin Bay and forms a second connection to the Arctic. The density differential of the Arctic cold water is responsible for the world's largest underwater waterfall at the Denmark Strait Overflow, with water falling 3.5 km (Jochumsen et al., 2012; Saberi et al., 2020). The geology of the region is complex with highly variable rapidly changing flow. The Denmark Strait Overflow Water forms the starting point of North Atlantic Deep Water, which feeds into the Deep Western Boundary Current and is an important component of the Atlantic Meridional Overturning Circulation (AMOC) (Rhein et al., 2015).

The AMOC moves water, salt, heat, nutrients, carbon, and marine life around the Atlantic (McCarthy et al., 2020). It transports shallow warm water that enters the Atlantic from the Indian Ocean (southernmost boundary) and flows in a general northward direction. In return, cold deep water that originated in the Arctic flows in a general southward direction (McCarthy et al., 2017). The deep water enters the North Atlantic through Denmark Strait (Jochumsen et al., 2017) and the Faroe-Bank Channel (Hansen et al., 2016). The AMOC is significant in the global ocean's heat transport, with the highest transport occurring at ~30°N. The consensus is that the AMOC has rapidly changed during specific periods in the Earth's history. There is active research and discussions on AMOC variability due to climate change (e.g., McCarthy et al., 2020; Kilbourne et al., 2022; and many others).

Additional details of the geology and oceanography of this region are included in the "Eastern Margin" section below.

2.2. Western margin

The western boundary of the study area is the Atlantic coasts of North, Central and South America. This includes the Gulf of Mexico (Gulf of America) and the Caribbean Sea (Fig. 1).

The Caribbean Sea is a semi-enclosed basin in the western tropical Atlantic Ocean, bounded in the West by Mexico and Central America, to the south by South America, and to the North and East by the Greater and Lesser Antilles, respectively. The Caribbean Sea encompasses a variety of bathymetric features. These include part of the Caribbean Plate. The basin is bound by the Lesser Antilles volcanic arc and the Barbados Accretionary Prism to the east, and the inactive volcanic arc of the Greater Antilles to the north. There are also several ridges (Aves, Beata, Nicaragua Rise, Cayman) and seamounts. The Muertos Trough is located in the north-central Caribbean. The Cayman Trough, located between Cuba and Jamaica, is the deepest known depth in the Caribbean Sea at 7535 m. Immediately to the north of the Caribbean, at the plate boundary zone between the Caribbean and subducting North American Plate, is the Puerto Rico Trench, with a depth of 9200 m (Lutz and Ginsburg, 2007).

The water within the Caribbean Sea is considered homogenous below 2000 m, with weak stratification between 1200 and 2000 m and stronger stratification at depths shallower than 1200 m (Gordon, 1967). The surface circulation is marked by the strong geostrophic Caribbean Current, the presence of multiple cyclonic and anticyclonic eddies that enter from the Atlantic across the Lesser Antilles, and a marked seasonal inflow of Orinoco River and some Amazon River water (Muller-Karger et al., 1989; Muller-Karger and Aparicio, 1994; Astor et al., 2003). A substantial amount of sediment enters the Caribbean through numerous passages between the Antilles (see references in Muller-Karger et al., 1989). This material sinks off the continental shelf of the Southeastern Caribbean. The waters that enter the Caribbean Basin through the Antilles Arc flow west-northwestward and over the Aves and Beata Ridges. The Beata Ridge extends south-southwest from Cape Beata on the island of Hispaniola and divides the Caribbean Sea into two abyssal plains, namely the Colombian Basin and Venezuelan Basin (Edgar et al., 1973).

The continental slope of Central America extends over 3800 km on the Western and Southwestern Caribbean ecoregions (Spalding et al., 2007). There are numerous canyons and gullies along the slope that are influenced by high runoff (Chérubin et al., 2008; OSPESCA, 2011; Cambronero-Solano et al., 2019). The width of the continental shelf of the southern Caribbean Sea varies widely, facilitating wind-driven or topographic upwelling, and also transport of terrigenous sediments (Rueda-Roa and Muller-Karger, 2013). These processes deliver inorganic and organic material to the deep seafloor via sedimentation and turbidity currents (Heezen et al., 1955; Thunell et al., 2007, 2008; Ojeda et al., 2020). Turbidity currents originating from river mouths, such as those of the Magdalena and Sixaola rivers in the south, transport material into submarine canyons (Chollett et al., 2012). The northern region is characterized by the Swan Islands Transform Fault, which marks the boundary between the North American and Caribbean plates (Rosencrantz and Mann, 1991). This area features diverse geological and topographic characteristics, including a deep reef wall and various outcrops and escarpments. Geological formations consist of limestone above approximately 400–450 m depth and basalt below this, and may be exposed or covered with sediment (Etnoyer et al., 2022).

Approximately 40 % of the Caribbean Current recirculates towards the southwestern Caribbean, forming the Colombia-Panama cyclonic gyre. Surface currents in this area are influenced by rotating eddies from the Caribbean Current, which interact with numerous seamounts and atolls around the San Andrés, Providencia, and Santa Catalina archipelago (Idárraga-García and León, 2019). The main water masses in the region are Caribbean Surface Water, which is shallow (50–75 m) with low salinity, Subtropical Subsurface Water (150–200 m) with higher salinity, and Subantarctic Intermediate Water (600–900 m) with the lowest salinity; the deepest parts are mainly characterized by North Atlantic Deep Water (CORALINA-INVEMAR, 2012).

The Caribbean Sea has numerous passages that connect it with the Atlantic Ocean. In addition to the Grenada Passage and numerous smaller channels among the Lesser Antilles, there are two large and very deep passages among the Greater Antilles: the Windward Passage west of Hispaniola, and the Mona Passage east of Hispaniola. The deepest is the Anegada-Jungfern Passage complex, between the British Virgin Islands and Sombrero (Anguilla), with a sill depth of 1915 m (Muller-Karger et al., 1989; Fratantoni et al., 1997; Lutz and Ginsburg, 2007). The structure of the flow through these passages is complex and not well characterized (Wilson and Johns, 1997; Johns et al., 2002). Most deep water exits through the Yucatan Strait into the Gulf of Mexico, with bi-directional flow documented through this strait (Gordon, 1967; Sturges, 2005; Sheinbaum et al., 2002; Vazquez et al., 2023; and many others).

While there are only limited studies of the vertical particulate flux to the benthos in the Caribbean Sea, the CARIACO Ocean Time-Series Station provided sediment trap measurements between 1994 and 2017 in the Cariaco Basin (Thunell et al., 2008; Goñi, et al., 2009; Lorenzoni et al., 2012; Montes et al., 2013; Muller-Karger et al., 2019; Ojeda et al., 2020). These studies concluded that ballasting due to inorganic matter is important in the delivery of organic carbon to the bottom, that there is an approximate exponential decay with depth in the flux of particulate organic matter, and that, typically, the benthic particulate organic flux at about 1300 m is about 1–3 % of surface primary productivity. The sediment flux and decomposition rates in the anoxic Cariaco Basin were in general consistent with organic sediment flux observations in aerobic environments (Thunell et al., 2007). High rates of organic carbon sinking and deposition are thus expected under the strong wind-driven upwelling zone of the southern-central margin of the Caribbean Sea, where high surface productivity occurs.

The Gulf of Mexico is a semi-enclosed sea bounded by the United States of America, Mexico, and Cuba (Davis, 2017; McKinney et al., 2021). Galloway (2008) and Davis (2017) provide comprehensive overviews of the benthic habitats and sediment depositional environments of the Gulf of Mexico. The sediment types vary within the basin. More sandy sediments are found in the east near the Florida Keys, by the Mississippi Delta, and to the south, just north of the Yucatan Peninsula (Davis, 2017). In the deeper part of the Gulf, terrigenous and hemipelagic muds dominate. Patches of sand have been detected from core sampling, thought to be a result of slumps in shallower water (Balsam and Beeson, 2003). There are some hard substrata bounding the Gulf to the East along the Florida Platform and to the South along the Yucatan Peninsula. In the North, the primary form of hard substratum is authigenic carbonate related to present and past hydrocarbon seep activity. There are a few areas of outcropping salt along the Sigsbee Escarpment.

The dominant oceanographic current in the Gulf of Mexico is the Loop Current. This warm current enters the Gulf from the Caribbean Sea through the Yucatan Channel. It travels north and then east, looping back on itself to then exit the Gulf through the Straits of Florida to merge with the Gulf Stream. The Loop Current typically extends from the surface to approximately 800 m depth. The Loop Current follows a cycle in which it can penetrate north into the Gulf of Mexico, often as far as the Mississippi Delta (Weisberg and Liu, 2017; Muller-Karger, 2000). These large intrusions lead to the shedding of warm anticyclonic eddies (Lugo-Fernández et al., 2016). These Loop Current anticyclonic eddies can exceed 300 km in diameter, and can influence the benthic boundary layer on the continental slope to depths greater than 1000 m (Hamilton, 2007). They are also accompanied by several cyclonic eddies of varying diameter. The large anticyclones typically drift west across the Gulf (Lindo-Atichati et al., 2012; Muller-Karger et al., 2015). Some anticyclonic eddies have higher chlorophyll concentration around their outer edges, and may advect highly productive shelf waters, including the Mississippi plume, into the interior of the Gulf (Biggs and Muller-Karger, 1994; Muller-Karger et al., 2015; Le Hénaff et al., 2019; Damien et al., 2021). The material advected from the continental shelves contributes to the flux of particulate organic carbon reaching the bottom of the Gulf of Mexico (Biggs et al., 2008).

There are several other important islands and archipelagos in the North Atlantic that provide habitats for deep ocean biota, including the Bahamas and Bermuda. The Bahamas comprises over 700 islands on large and shallow carbonate platforms that are interspersed by several deep channels and basins in a tropical-subtropical setting (Helim and Masaferro, 1997; many others). Shipley et al. (2024) provide an overview of the geological setting and a review of the biology, biodiversity, and particulate carbon flux of the twilight zone and deep benthos of the Bahamas. Bermuda is a subtropical group of islands in the western North Atlantic (approximately 32.3°N, 64.8°W) on a carbonate platform sitting on an ancient volcanic peak (Coates et al., 2013). Bermuda is the site of one of the longest oceanographic time series at the Bermuda Atlantic Time-Series and of vertical carbon flux observations by sediment traps, from the surface to over 3000 m depth (Deuser et al., 1988, 1990; Steinberg et al., 2001; Conte and Weber, 2014).

2.3. Eastern margin

The eastern region of the North Atlantic study area (Fig. 1) includes the Mid-Atlantic Ridge and the African Continental Margin. The Canary Basin reaches its deepest point at the Madeira Abyssal Plain. Bounded by the Seewarte seamounts on the west and by the African continental rise in the east, the Madeira Abyssal Plain is located about 1000 km west of the African continental Margin. It extends for approximately 300–500 km north-south and less than about 200 km east-west. Its northern region is marked by a series of small scarps (Heezen et al., 1959; Alibés et al., 1996; Mason, 2009).

A group of abyssal hills divides the Madeira Plain from the Cape Verde plain, which has an area of about 520,000 km^2 (Heezen et al., 1959). The Africa continental margin flanking the basin is uniform. The width of the shelf ranges between 20 and 120 km, while the slope width ranges from 800 km at Cape Verde to only 80 km at Casablanca (Heezen et al., 1959). The margin is cut by several canyon systems, the major ones being the Timiris and Kayar Canyons near Cape Verde, and the Agadir Canyon southwest of Cape Ghir (Mason, 2009; Valdés and Déniz-González, 2015). The Canary basin hosts four archipelagos which together comprise Macaronesia: (from south to north) Cape Verde, Canary Islands, Madeira, and Azores.

Along the Moroccan shelf, the Northwest African margin transitions into the Gulf of Cádiz margin, located where the African and the Eurasian plates meet. Here, the Strait of Gibraltar separates the Atlantic from the Mediterranean Sea, with relatively warm, surface water flowing eastwards from the Atlantic into the Mediterranean, while warm, saline intermediate and deep water from the Mediterranean flows in the opposite direction. After exiting through the Strait of Gibraltar, this Mediterranean Water sinks along the slope and forms a neutrally buoyant plume centered approximately at 1000 m depth. The sinking water entrains North Atlantic Central Water, generating Mediterranean Outflow Water (MOW) (De Pascual-Collar et al., 2019). As MOW spreads through the Gulf of Cádiz, bottom topography and mixing cause it to split into two main branches: an upper branch located between 500 and 800 m depth and a lower branch located between 800 and 1200 m depth (Gasser et al., 2017). Both branches represent cores of maximum temperature and salinity. Ambar et al. (2002, 2008) reported a third shallow core at a depth of less than 600 m.

After passing Cape São Vincente (the southwestern tip of Portugal), the MOW turns northward, travelling along the western margin of the Iberian Peninsula. There it is trapped in an anticyclonic rotation in the Tagus Basin (Daniault et al., 1994). It then assumes two main pathways: poleward along the western European continental slope, entering the Bay of Biscay and continuing northward to the Porcupine Bank and Rockall Trough at 53°N; and westward towards the central Atlantic (De Pascual-Collar et al., 2019). This system is known as the Mediterranean Undercurrent. Deep mesoscale eddies can facilitate south and southwestward transport of Mediterranean Water (Armi and Zenk, 1984).

The Atlantic portion of the Iberian margin is formed by the Algarve, the Portuguese, the Galician, and the Cantabrian continental margins (Maestro et al., 2013; García et al., 2015). The width of the continental shelf on the Iberian Margin facing the North Atlantic ranges from 56 to 70 km on the western Cantabrian and Portuguese margin to 2–3 km in the Gibraltar Strait. The depth of the shelf break is also variable, from 70 m in the Gulf of Cadiz, down to 200 m in some areas of the Cantabrian margin (Maestro et al., 2013). The principal canyon systems occurring in the Algarve margin are, from east to west, the Faro, Portimão and Lagos Canyons, opening into the respective valleys. The Faro Valley merges with the Portimão Valley, which together with the Lagos valley opens into the Horseshoe Abyssal Plain (4800 m; Mulder et al., 2006; García et al., 2015). The plain is associated with the Horseshoe Seamount Chain, which includes the Coral Patch, Ampère, and Seine Seamounts in the south, the Unicorn, Dragon, Lion and Josephine Banks in the west, and the Gorringe, Hirondelle II, Gettysberg and Ormonde Seamounts in the north (Lebreiro et al., 1997; Christiansen et al., 2015). Along the Portuguese margin, the slope is incised by the São Vincente, Setúbal-Lisbon, and Cascais Canyons which feed into the Horseshoe and Tagus Abyssal Plains (Allin et al., 2016). In the northern part of the margin, the Nazaré, Porto, and Aveiro Canyons open onto the Iberian Abyssal Plain (5300 m; García et al., 2015; Allin et al., 2018; Weaver et al., 2000). Heading northwards, the main canyons cutting the slope of the Galician margin are the Pontevedra, Arousa, Muros, Muxía and Laxe Canyons, which converge on the lower slope, open into the Galicia Interior Basin, and feed the Valle-Inclán Channel, which extends to the Biscay Abyssal Plain (García et al., 2015). Northward towards Ortegal Spur, the A Coruña and Ferrol Canyons dissect the slope and also open onto the Biscay Abyssal Plain. West from the Galicia Interior Basin (3000–4000 m) and facing towards the Iberian Abyssal Plain are the Galicia Bank and the associated Vigo, Vasco da Gama, and Porto Seamounts (Berthois et al., 1965; Mauffret et al., 1978; Roberts and Kidd, 1984; Mougenot et al., 1986; García et al., 2015). The Cantabrian margin includes de Avilés, Santander, Torrelavega, Lastres, and Llanes Canyon systems. These open onto the Biscay Abyssal Plain (García et al., 2015) together with Le Danois Bank, a striking morphological bank whose presence creates an intra-slope basin (Ercilla et al., 2008).

The Biscay Abyssal Plain is the oceanic portion of the Bay of Biscay, an engulfment located between Spain and France. The average depth of the plain is about 4500 m, although the depth decreases to about 2000 m in the proximity of submarine rises (Pascual et al., 2004). On its northern side, the plain is delimited by the French Atlantic margin, divided into the Celtic Margin in the north, and the Armorican and Aquitaine Margins in the south (Bourillet et al., 2006). The Aquitaine Margin extends from Capbreton Canyon to Conti Spur, the Armorican margin to the Berthois Spur, and the Celtic Margin to the Goban Spur (Bourillet et al., 2006). The shelf in the Aquitaine margin is narrow (~70 km) and is incised by the Capbreton and Cap-Ferret Canyons, which come together to form the Cap-Ferret Canyon system. The shelf then widens in the Armorican margin (~200 km) characterized by several spurs and canyons forming five main drainage basins: Rochebonne (from Oleron to Sables d'Olonnes canyons), Gascogne (Yeu to Belle-île canyons), southern Brittany (Blavet to Audierne canyons), western Brittany (Douarnenez to Brest canyons), and La Chapelle (Guilcher to Blackmud canyons) (Zaragosi et al., 2001; Bourillet et al., 2006; Van Den Beld et al., 2017). In the Celtic Margin, the shelf is ~250 km wide and is incised by two major canyons, Shamrock and Whittard, the main features of the Petite Sole and Grande Sole drainage basins (Bourillet et al., 2006).

Morrissey et al. (2023) reviewed the geomorphology and oceanography of the Irish-Scottish margin. This extends from the Whittard Canyon to the Wyville-Thomson Ridge and can be divided into three main regions: the Porcupine Seabight, the Western-Irish margin, and the Hebridean margin. The Porcupine Seabight is located north of the Goban

Spur. It hosts the Gollum Channel, which opens into the Porcupine Abyssal Plain, and coral carbonate mound provinces including the Hovland, Belgica, and Moira Mounds (Huvenne et al., 2005; Wheeler et al., 2005, 2011; Sacchetti et al., 2012). In the north, the Porcupine Seabight is delimited by the Porcupine Bank, a plateau about 200–400 m depth, characterized by the presence of mounds, and with a western margin incised by several canyons (Thébaudeau et al., 2016). The western Irish margin extends to the Donegal-Barra Fan, a composite fan that is characterized by important mass transport deposit events and which opens onto the Rockall Trough (Roy et al., 2020). The Rockall Trough is a bathymetric depression that ranges between 1000 and 3500 m depth and contains three seamounts: (from south to north) Rosemary Bank, Anton Dohrn Seamount, and Hebrides Terrace Seamount (Howe et al., 2006; Henry et al., 2014; Davies et al., 2015). The Rockall Trough is delimited in the north by the Wyville-Thomson Ridge, a continuation of the Hebridean margin that separates the Rockall Trough from the Faroe-Shetland Channel.

In terms of water masses, the northern Rockall Trough is mostly occupied by Wyville-Thomson Overflow Water, with a lower depth branch below 1500 m (Morrissey et al., 2023). In the west, a series of banks (Bill Bailey's Bank, Lousy Bank, George Bligh Bank, Hatton Bank, and Edoras Bank) interspersed with channels separate the Rockall Trough from the Iceland Basin (Roberts et al., 1983; Johnson et al., 2010). Labrador Sea Water, formed through deep convection in the Labrador Sea and characterized by low temperature, low salinity and high oxygen levels (Bashmachnikov et al., 2015), enters here and recirculates in the northern Rockall Trough at depths of 1600 to 2200 m, flowing south-west towards the Porcupine Seabight and Bay of Biscay (van Aken, 2000; Kieke et al., 2009; Liu and Tanhua, 2021). Below 2200 m is North Atlantic Deep Water (NADW) generated by deep convection in the Greenland Sea. NADW propagates southward through the Denmark Strait and the eastern side of Iceland (Hansen and Østerhus, 2000). It is observed throughout the Atlantic between 1000 and 4000 m depth (Bashmachnikov et al., 2015). The deepest parts of NADW interact with Antarctic Bottom Water and are modified through diapycnal mixing (van Aken, 2000; Orsi et al., 2001). The Rockall Trough is also crossed by the Modified North Atlantic Water, a homogeneous water mass that is mixed north of the Porcupine Bank and which reaches the Nordic Seas (Holliday et al., 2000, 2008; Morrissey et al., 2023). East of Hatton and Edoras Banks is the Rockall Plateau, characterized by two main features: the Rockall Bank, containing the Logachev Mounds province, and the Fangorn Bank volcanic complex (Morrissey et al., 2023). Southward of these banks are three seamounts: Eriador, Gondor and Rohan, which are flanked on the east by the Isengard Ridge, in the north by the Rockall Plateau, and in the south by the Porcupine Seabight.

2.4. Mid Atlantic Ridge

South of Iceland, the Reykjanes Ridge, the northernmost part of the Mid Atlantic Ridge (MAR), forms a geologically-active spreading axis. From there, the MAR extends in a southwest direction and gradually increases in depth from 200 to 2700 m by the Bight Fracture Zone at 57°N. This may be the southern limit of the influence of the Iceland mantle plume hotspot (Martinez et al., 2020; Le Saout et al., 2023). Further south, the ridge axis trends in a more southerly direction to the Charlie Gibbs Fracture Zone at 52–53°N. This Fracture Zone offsets the ridge axis by 350 km to the east. South of the Charlie Gibbs Fracture Zone, the MAR axis runs southeast, past the Faraday Fracture Zone at 49.7°N to the Maxwell Fracture Zone at 47.8°N, with an axial valley depth reaching 3700 m. At the Maxwell Fracture Zone, the ridge is affected by the Azores mantle plume hotspot (Peyve et al., 2023). There, the MAR axis turns to the south through the Kurchatov Fracture Zone at 40.5°N and becomes shallower towards the Azores Plateau.

The MAR is influenced by the Azores magma hotspot south of the Azores Plateau. V-shaped propagating ridge sections indicate that flow of hotspot material occurs along the axis (Vogt, 1976). The axis in this area runs southwest and becomes deeper past the Pico Fracture Zone at 37.5°N to the Oceanographer Fracture Zone at 35°N (both fracture zones have an irregular bathymetry that reaches depths greater than 3000–4000 m; https://www.ngdc.noaa.gov/gazetteer/view/home accessed 7 April 2025). Further south, the MAR is segmented by several major fracture zones (Hayes, 33.5°N; Atlantis, 30.1°N; Kane, 23.7°N; Fifteen-twenty, 15.3°N; Vema, 10.7°N). The Romanche Fracture Zone then offsets the ridge axis by 900 km to the east between 2°N and 2°S. The Romanche Fracture Zone creates a trough more than 7000 m deep that allows a current of 3.6 Sv to flow from the western to the eastern Atlantic basin (Schlitzer et al., 1985). These features effectively divide the northern hemisphere MAR from the southern hemisphere MAR.

The Azores Archipelago (centered approximately at 36° 39' N, 25° 31' W) defines an EEZ that covers an area of more than 950,000 km^2. The archipelago consists of nine volcanic islands. The northernmost, Flores and Corvo Islands, are associated with the North America plate. The central (Faial, Pico, São Jorge, Terceira and Graciosa) and eastern islands (São Miguel and Santa Maria) lie where the Eurasian and Nubian (African) plates meet. The islands themselves are the emergent portions of an enormous submarine volcanic platform. The Azores region is delimited to the south by the East Azores Fracture Zone, and the Terceira Axis to the northwest (Machado, 1957). The Azores EEZ includes more than 460 seamount-like features (Morato, 2019). Ocean circulation patterns are complex, with unstable eddies resulting from the interaction of the more northerly North Atlantic Current (or North Atlantic Drift) with the more southerly Azores Current (AzC) (Santos et al., 1995; Alves and Colin de Verdière, 1999; Johnson and Stevens, 2000; Bashmachnikov et al., 2009, 2015). Originating southeast of the Grand Banks as a branch of the Gulf Stream, the AzC flows southeastward towards the MAR. It crosses the MAR at approximately 34°N, southwest of the Azores Islands (Käse and Siedler, 1982; Gould, 1985). The AzC then continues eastward, as a zonal jet, towards the Gulf of Cadiz (Volkov and Fu, 2010), transporting around 10–12 Sv mainly in the upper 1000 m of the ocean (Käse and Siedler, 1982; Gould, 1985; Sy, 1988; Stramma and Müller, 1989; Pingree et al., 1999). The AzC establishes the northern boundary of the North Atlantic Subtropical Gyre (Juliano and Alves, 2007). It separates the colder Eastern North Atlantic Central Waters, which occupy depths between 100 and 600 m, from warmer and more saline Subtropical waters (Martins et al., 2008). In general, the AzC displays intricate mesoscale variations, featuring meandering patterns and the development of westward-spreading eddies due to the current's baroclinic instability (Kielmann and Käse, 1987; Alves and Colin de Verdière, 1999). The AzC bifurcates into three main branches: the easternmost stretches into the Canary Basin, playing a role in the formation of the Canary Current (Stramma, 1984; New et al., 2001); the more westerly branches circulate back into the North Atlantic Current (NAC; Maillard and Käse, 1989).

The AzC forms the northeast segment of the North Atlantic Subtropical Gyre (Gould, 1985; Jia, 2000; Lamas et al., 2010; Silva-Fernandes and Peliz, 2020; Frazão et al., 2022). It also may play a role in contributing to MOW (Zenk, 1975; Rhein and Hinrichsen, 1993; Volkov and Fu, 2010; Huertas et al., 2012). The Azores Counter Current (AzCC) is identified as a westward counterflow (Onken, 1993; Cromwell et al., 1996), located north of the AzC within the 36°–38°N latitude range. Primarily observed in subsurface layers, the AzCC reaches its peak intensity at depths ranging from 200 to 500 m (Onken, 1993; Cromwell et al., 1996; Comas-Rodríguez et al., 2011; Carracedo et al., 2014). This current reaches its maximum intensity during spring and, according to Alves et al. (2002), its transport ranges from 2 to 5 Sv. Closer to the Iberian Peninsula, the Portugal Current is characterized by a weak and broad flow to the south, extending some 300 km beyond the shelf (Stramma, 1984; Martins et al., 2002). It contributes to the Canary Current.

Several water masses are recognised in this region. The upper layer (500–1000 m) is predominantly occupied by the North Atlantic Central

Water (NACW; Pollard et al., 1996). NACW is divided into two sub-domains: Eastern North Atlantic Central Water and Western North Atlantic Central Water (Harvey, 1982). The sources and characteristics of these water masses have been reviewed in multiple studies (McCartney, 1982; Pollard and Pu, 1985; Harvey and Arhan, 1988; Paillet and Arhan, 1996; van Aken, 2001; Palma et al., 2012; Lázaro et al., 2013; Liu and Tanhua, 2021).

The intermediate layers (700–1500 m depth) encompass Subarctic Intermediate Water (SAIW), Antarctic Intermediate Water (AAIW), and Mediterranean Water (Bashmachnikov et al., 2015). The SAIW, characterized by cold, oxygenated fresher waters, forms in the northern branch of the NAC, west of the MAR. It is formed by mixing of NACW (warm and salty water transported by the NAC) and Labrador Sea Water (LSW; Read, 2000; Garcia-Ibanez et al., 2015), and descends to depths of 700 to 1000 m at its southern boundary (McCartney and Talley, 1982; Harvey and Arhan, 1988; Tsuchiya, 1989; Arhan, 1990; Arhan et al., 1994). AAIW forms in the area of the Antarctic polar frontal zone (Schmitz, 1996) and moves northward (Bashmachnikov et al., 2015). In the North Atlantic, it is found between 700 and 900 m, characterized by a minimum of salinity, oxygen, and a maximum of silicates (Schmitz, 1996). In the Azores region, the AAIW has different characteristics than at its region of origin (2.2 °C and salinity 33.8), leading to its designation as modified AAIW (mAAIW) (Pérez et al., 1998, 2001; Álvarez et al., 2004).

Highly saline and warm water spreading westwards from the Mediterranean reaches the Azores Rise with a core at 800–1000 m. Deeper fractions, potentially mixed with NADW, spread south of the AzC at depths of 1000–1200 m (Harvey and Arhan, 1988; Iorga and Lozier, 1999; van Aken, 2000). The influence of Mediterranean Water is most notable between 700 and 1500 m, with some weak influence observed from 500 to 3000 m depth (Tsuchiya et al., 1992; Arhan et al., 1994). In the Azores, LSW, which crosses the MAR in the region of the Charlie-Gibbs fracture zone (Straneo, 2003), is found at depths of 1200–2500 m (Harvey and Arhan, 1988).

The ocean climatology in the Azores is characterized by spatial, seasonal, and interannual variability typical of mid-latitudes (Stramma and Siedler, 1988; Valente, 2013). The northernmost islands are under the influence of the southward branches of the NAC, which bring colder, less saline and possibly more productive waters to the Azores region (Narciso et al., 2016). In the South, the Azores Current is a quasi-permanent feature forming a thermohaline front which separates these northern waters from warmer and more saline southern water masses (Juliano and Alves, 2007). These factors also influence the biological oceanographic processes around the Azores archipelago (Palma et al., 2012).

The deep North Atlantic Ocean receives a supply of particulate organic carbon as a result of the seasonal primary productivity of overlying surface waters (Deuser et al., 1988, 1990; Conte and Weber, 2014). The presence of the Mid-Atlantic Ridge does not enhance surface primary production (Priede et al., 2022). However, the amount of particulate organic matter reaching the floor of the North Atlantic is typically 1.3 to 3.0 times greater on the MAR as a result of the shorter vertical transport distance from the surface relative to adjacent abyssal regions. This is one of the drivers for increased biological diversity on the MAR (Priede et al., 2022).

3. Historical overview

Deep-sea biology as a discipline is relatively new, yet there have been dramatic discoveries that changed fundamental concepts in ecology, evolution and the origin of life. At the dawn of the 19th Century, official navigation charts were being published by the major maritime nations, but the ocean depths remained largely unknown. First unequivocal evidence of life in the deep sea came from stalked crinoids *Cenocrinus asterius* retrieved from the Caribbean in 1761 and 1762 (Etter and Hess, 2015) and the description of 21 deep-sea fish species and their depth zonation off Nice in the Western Mediterranean by Risso (1810, 1820, 1826). Studies in the Atlantic Ocean revealed deep-sea fishes off Madeira (Lowe, 1833, 1843-1860; Johnson, 1862, 1863), molluscs at 915 m with living foraminifera at 1920 m under the Gulf Stream (Pourtalès, 1854), and hundreds of species living at 360–820 m depth off Norway (Sars, 1872). du Bocage and de Brito Capello (1864) described new species of deep-water sharks captured by a commercial fishery off Setubal on deep-sea floor areas featuring sponge beds (Wright, 1870). A controversial scientific hiatus was created by Forbes (1844) who postulated a "*Zero of Animal Life probably about 300 fathoms*" (550 m) based on diminishing abundance of biota with depth in the Aegean Sea (Anderson and Rice, 2006). Nevertheless, Charles Wyville Thomson, a student of Forbes inspired by the work of Michael Sars off Norway, began a series of expeditions around Scotland and Ireland on board the HMS *Lightning* in 1868 followed by the HMS *Porcupine* in 1869 and 1870. These cruises revealed the presence of life down to 4454 m including "particularly great living masses of *Lophohelia prolifera*" (now *Desmophyllum pertusum* (Linnaeus, 1758)) on the eastern flank of the Rockall Bank. The book, "*The Depths of the Sea*" (Thomson, 1873) describing the results from these voyages was a best-seller setting the stage for a golden age of deep-sea exploration.

3.1. Global/transatlantic expeditions

In 1854, Matthew Maury published the first deep bathymetric chart of the North Atlantic Ocean (Murray and Hjort, 1912) suggesting unobstructed abyssal plains that he dubbed a "*telegraphic plateau*" suitable for laying cables. Surveys for the first transatlantic telegraph cables followed in 1856 and 1857 (Hanley, 2014). In view of these new developments and the success of *HMS Porcupine* voyages, Charles Wyville Thomson was granted the *HMS Challenger* by the British government for a global expedition to investigate the deep sea. During 1873, the *Challenger* crossed the North Atlantic Ocean twice sampling at over 100 stations, defining the general shape of the ocean basin, finding that life existed on the seafloor at all depths, and describing numerous new species. Reports were edited by John Murray. From 1884 to 1900, the United States Commission of Fish and Fisheries' vessel *RV Albatross* performed over 1700 dredges, beam trawls, surface and mid-water tow net deployments, temperature measurements, and depth soundings from Newfoundland south along the coast of the US, including the Gulf of Mexico, and then into the Caribbean Sea and beyond into the Pacific Ocean (Townsend, 1901). The German Deep-Sea Expedition followed in 1898–1899 led by Carl Chun on board the *SS Valdivia* and used novel techniques to sample the deep pelagic fauna but took few samples in the North Atlantic. Surveys ranged from coastal down to 4173 fathoms deep (7,632m) and revealed many different species, sediment types, bathymetric features, and temperatures (Townsend, 1901). John Murray returned to the North Atlantic Ocean in 1910 with Johan Hjort on board the Norwegian steamship *Michael Sars* and revealed the ubiquity of deep pelagic species (Hjort, 1911) and for the first time showed the presence of a mid-ocean ridge dividing the Atlantic into two basins, East and West (Murray and Hjort, 1912). Subsequent expeditions from both sides of the Atlantic explored these deep basins during a golden age of deep-sea research (see regional accounts below) but the rough terrain of the Mid-Atlantic Ridge remained largely inaccessible until new technologies became available in the 1980s.

The first general bathymetric chart of the oceans was first published in 1904, with the support of H.S.H. Prince Albert I of Monaco. The second edition, with more detail of the deep ocean basins, was initiated in 1912, but not completed until 1930 (Anonymous, 1936), prior to the widespread use of echo-sounding. These early bathymetric maps were remarkable in the compilation of thousands of physical sounding measurements, but misrepresented the deep-sea floor as more or less smooth. The true rugosity of the deep sea was disclosed over the next century by data from new sounding technologies compiled in editions of GEBCO, General Bathymetric Charts of the Ocean.

Two World Wars and political and economic crises in the early 20th Century created a hiatus in deep-sea research from 1914 to 1947 (Mills, 1983). However, there were exceptions, firstly voyages of the *Dana* (1920–1922) led by Johannes Schmidt that discovered the mesopelagic spawning site of European and American eels in the Sargasso Sea (Schmidt, 1923) and secondly, bathysphere dives by William Beebe and Otis Barton off Bermuda down to 923 m, making the first direct observations of mesopelagic fauna and their bioluminescence (Beebe, 1934).

After World War II, there was a resurgence in deep-sea research beginning with the Swedish Deep-Sea Expedition of the *Albatross* (1947–1948) that circumnavigated the globe and, in the Atlantic Ocean, retrieved polychaetes and holothurians by trawling down to 7900 m depth in the Puerto Rico Trench. This was followed by the Danish circumglobal *Galathea* (1951–1952) expedition but sampling in the North Atlantic was limited.

From 1947 to 1949, the *RV Atlantis* of Woods Hole Oceanographic Institution undertook three expeditions across the Atlantic Ocean that measured the bathymetry using a continuous echosounder, under the direction of Maurice Ewing and Bruce Heezen. Those echosounder records, compiled by Marie Tharp with bathymetric data from other sources (Doel et al., 2006) culminated in the publication of the first physiographic map of the North Atlantic in 1957 (Heezen et al., 1959). The topographic artist, Heinrich Berann, used these to produce the iconic three-dimensional images of the Atlantic Ocean floor depicting the mid-ocean ridge, seamounts, continental slopes and abyssal plains (National Geographic, 1968). The theory of continental drift, plate tectonics and the concept of seafloor spreading (Dietz, 1961) provided the framework for understanding the origin of these features. Improved benthic sampling equipment such as box corers and multi-corers began to enable quantitative samples of soft sediment areas (Gage and Tyler, 1991).

From the 1960s, mobile human occupied vehicles such as the French bathyscaphe *Archimède* and US DSV *Alvin* became available, followed by remotely operated vehicles (ROVs). From the 1980s satellite technology began to provide remote sensing imagery of the surface ocean (Gower, 1981; MacDonald and Priede, 1983) and through GPS, precise navigation enabled research on difficult topography such as coral mounds, canyons, seamounts and the mid ocean ridge previously avoided by most research cruises.

The vivid representation of the Atlantic Ocean floor by the National Geographic (1968) inspired a generation of scientists but was based on artistic interpolation with little or no direct evidence of existence or location of some features. As more bathymetry data became available, the GEBCO 5th edition at a scale of 1:10,000,000 was published in 1982 providing a more definitive framework for research (GEBCO, 2003). Satellite altimetry data combined with shipborne soundings enabled Smith and Sandwell (1997) to produce a world map at 2-min grid resolution resulting in the familiar maps used today with discrimination of the distribution of seamounts (Yesson et al., 2011) and other features that are continually updated in digital form.

Modern expeditions after World War II aided with sonar and submersibles informed the interpretation of observations from earlier expeditions. The ecology of the deep sea as a vast food-limited environment with episodic and uneven distribution of food falling to the sea floor became central to interpreting processes from static observations. The inevitable discovery of hydrothermal vents from oceanography modelling of chemical mass balance changed the understanding of energy sources and sinks in the deep-sea environment (Weiss et al., 1977), with profound insights into the metabolic diversity of marine organisms (Somero, 1992).

3.2. Eastern Atlantic expeditions

Pioneering work by Sars (1872), Thomson (1873) and others in the northeast Atlantic established the science of deep-sea biology and this continued to be an important region for research over the subsequent 150 years.

After the *Challenger* expedition, in 1880 John Murray with Captain Thomas Tizard surveyed the Faroe-Shetland channel and confirmed the presence of a physical barrier between the Norwegian Sea and Atlantic Ocean to the south, later named the Wyville-Thomson Ridge. In 1895 and 1896 the Danish HDMS *Ingolf* expedition explored the deep sea off Iceland, west, south and southeast Greenland, and the Faroe Islands, and visited the Wyville-Thomson Ridge (Wandel, 1898; Anonymous, 1900). Fine mesh was used for the first time to sieve animals from the sediment, resulting in very rich collections of smaller organisms and numerous benthic species (e.g., Hansen, 1916) that evidenced distinctively different bottom faunas in the cold Arctic water to the north compared with Atlantic waters to the south (Anonymous, 1900).

Oceanography in France began with voyages of the *Travailleur* and *Talisman* (1880–1883) organised by Leopold Folin and Alphonse Milne-Edwards exploring the Northeast Atlantic and parts of the Mediterranean (Milne-Edwards, 1882, 1883), discovering 176 new species and the first samples of pressure tolerant bacteria in sediments laying the foundations of deep-sea microbiology (Dolan, 2020). These expeditions inspired Albert I, the Prince of Monaco, to equip his yacht the *Hirondelle* as a research vessel for a series of voyages during 1885–1888. From 1891 a new vessel *Princess Alice* worked in deeper water setting fish traps at 5285 m depth, followed by the *Princess Alice II* (1898–1910) and *Hirondelle II* from 1911. When work was ended by war, systematic studies had been made of the eastern Atlantic from the Cape Verde Islands to Spitzbergen. The ships and equipment commissioned by Albert I were of the highest standard enabling sampling on the seafloor and at all mid-water depths. Samples were frozen on board resulting in decades of scientific publications from staff and visiting scientists at the Institut Océanographique, Monaco, founded in 1906 (Mills, 1983).

The German FS *Meteor* Expedition, or Deutsche Atlantische Expedition (1925–1927), used new echo sounding technology and mainly surveyed the South Atlantic but discovered the Great Meteor Seamount in the North Atlantic 1000 km south of the Azores.

The Porcupine Seabight and northern Bay of Biscay areas of the Northeast Atlantic were visited during subsequent years by a variety of vessels but most of these expeditions obtained only small numbers of samples (see Le Danois, 1948; Rice, 1986; Rice et al., 1991). In 1948, Le Danois produced an account of the continental slope fauna off the coasts of north-western Europe, based on these earlier cruises and on his experience of working with samples collected from off the coasts of Spain, France, and Ireland by vessels of the French ’Office Scientifique et Technique de Peches Maritime’ (Rice et al., 1991).

Bathyal and abyssal work continued in the Northeast Atlantic in the 1970s and 1980s with the French BIOGAS programme in the Bay of Biscay beginning in 1972 (Laubier and Monniot, 1985) and the Scottish Marine Biological Association’s time series sampling programme in the Rockall Trough (Gage et al., 1980). The Porcupine Seabight again became a focus for intensive study between 1977 and 1986 by the Institute of Oceanographic Sciences (Rice et al., 1991). During the 1970s, standardised deep-sea bottom trawl techniques were developed that enabled quantitative surveys of four regions of Northeast Atlantic slope from the shelf edge to the abyssal plains in the Rockall Trough, Porcupine Seabight, Morocco and Northwest Africa, which were compiled into the Atlas of deep-living demersal fishes of the North Atlantic by Haedrich and Merrett (1988). The BIOFAR (Biology of the Faeroes) project in 1987–1990 extensively augmented knowledge of the benthic fauna of the northern-most part of the study area (Nørrevang et al., 1994; e.g. Sneli et al., 2005).

3.3. Mid-Atlantic Ridge expeditions

The first evidence of the presence of the ridge in the Mid Atlantic came from soundings by the *USS Dolphin* in 1853, which were incorporated into the chart by Maury (1855) and named the Dolphin Rise to the north and southwest of the Azores. Soundings by the *USS Arctic* from

Newfoundland to Ireland in 1856 along a possible route for trans-Atlantic submarine telegraph cable, indicated that this feature extended further while soundings from *HMS Challenger* in 1873 provided evidence of the further extent of the feature south to 21°N.

In 1911 the steamship *Michael Sars* of the Norwegian Board of Fisheries undertook a research cruise led by Johan Hjort and Challenger veteran John Murray to investigate deep-sea life in the north Atlantic, including the Mid-Atlantic Ridge (Murray and Hjort, 1912). More than a hundred species were described from specimens collected during the voyage, and Murray and Hjort's account notes that "the most striking feature of the Atlantic Ocean is certainly the low central ridge (dividing the ocean into eastern and western deep basins)", which is annotated with a margin note as the "Mid-Atlantic ridge".

More detailed bathymetry of the ridge was provided by the research ship *Meteor*, which was equipped with an echosounder, during the Deutsche Atlantische Expedition of 1925–1927. Bathymetric transects across the Atlantic by the *Meteor* provided sufficient resolution to reveal its median valley, although this was not recognised until Marie Tharp compiled echosounder records for the region in 1952 (Tharp and Frankel, 1986).

The 1947 to 1949 RV *Atlantis* expeditions and the Heezen et al. (1959) physiographic map of the North Atlantic Ocean provided the first comprehensive representation of the northern Mid-Atlantic Ridge completed in 1957. The first seafloor images of the deeply submerged Mid-Atlantic Ridge were obtained in 1959 by Jacques Cousteau and colleagues using a camera sled deployed from the research ship *Calypso* while crossing the Atlantic *en route* to the First International Oceanographic Congress in New York. Cousteau had been skeptical of the median rift valley posited by Tharp and Heezen, but the footage obtained by his team's *Troika* camera sled confirmed its existence, and Cousteau presented the imagery at the Congress (Tharp and Frankel, 1986).

The first Human-Occupied Vehicle (HOV) dives to the Mid-Atlantic Ridge took place in 1973–74 during Project FAMOUS (the French-American Mid-Ocean Undersea Study), southwest of the Azores at latitude 36° 50' N. The bathyscaphe *Archimède* made seven dives to the ridge (Bellaiche et al., 1974), and *DSV Alvin* and the submersible *Cyana* also made several dives (Hammond, 1975), collecting geological samples and imagery to investigate seafloor spreading processes (Ballard et al., 1975).

Interest in the biota of the Mid-Atlantic Ridge was stimulated by the discovery of active hydrothermal venting and vent-associated fauna in 1985 at latitude 26°N and depth 3600 m by a camera sled deployed from the *RV Researcher* (Rona et al., 1986). This first vent field to be found on a slow-spreading mid-ocean ridge was in the median valley of the Mid-Atlantic Ridge at the TAG (Trans-Atlantic Geotraverse) site, previously hypothesised to be an active hydrothermal field from manganese-encrusted seafloor samples collected by dredge in 1972–73 (Scott et al., 1974).

Further exploration and sampling of the biota of hydrothermal vent fields on the northern Mid-Atlantic Ridge has continued since the 1980s, using HOVs and Remotely Operated Vehicles (ROVs) to address scientific questions that span marine biology and Earth sciences (e.g. Karson and Brown, 1988; Murton et al., 1995; Langmuir et al., 1997; Gebruk et al., 2000; Fabri et al., 2011; Wheeler et al., 2013).

Meanwhile there have been few investigations of the non-chemosynthetic biota of the northern Mid-Atlantic Ridge except for studies such as Copley et al. (1996) that described megafauna of the Reykjanes ridge opportunistically collected by rock dredges during a geological survey. Notably, the Atlas of deep-living demersal fish of the North Atlantic Basin (Haedrich and Merrett, 1988) showed no data from the Mid-Atlantic Ridge. Systematic biological surveys of the wider Mid-Atlantic Ridge did not begin until the Census of Marine Life (2000–2010), aided by a new generation of research ships with dynamic positioning, ROVs, and real-time swath bathymetry displays that could target trawls and other sampling equipment precisely onto sites of interest in the rugged topography of the ridge as exemplified by the MAR-ECO (Gebruk et al., 2010) and ECOMAR (Priede et al., 2013a) programmes.

3.4. *Western Atlantic expeditions*

The first significant sampling of the Western Atlantic deep-sea basin was by Louis François de Pourtalès of the US Coast Survey. After initial findings of life in 1853 (Pourtalès, 1854), further sampling revealed a diversity of deep-sea fauna under the Gulf Stream (Pourtalès, 1867). Together with Louis Agassiz in 1868 on board the steamer *Bibb*, Pourtalès dredged between Florida Keys and Grand Bahama and found abundant fauna down to 946 m (Mills, 1983).

Alexander Agassiz, the son of Louis, was the naturalist for three cruises between 1877 and 1880 on board US Coast and Geodetic Survey Steamer *Blake* that sampled the sea floor from the Gulf of Mexico, the Caribbean Sea, the Straits of Florida and along the coast of the USA to Georges Bank, trawling down to 3567 m and showing that the deep-sea fauna begins at 549–640 m depth (Agassiz, 1888). During 1880–1903 the US Commission of Fish and Fisheries Schooner *Fish Hawk* and Steamer *Albatross* conducted extensive deepwater surveys off the US Atlantic and Gulf of Mexico coasts providing the basis of much of the early taxonomic work on deepwater species in the region.

In the 1960s the bathymetry of the Northwest Atlantic Ocean floor became sufficiently known to allow detailed systematic sampling of fauna of soft sediments. Sanders et al. (1965) established the Gay Head to Bermuda transect with stations at depths from 97 to 5001 m that were sampled using a modified anchor dredge. Studies along this transect and elsewhere with improved sampling gear began to reveal extraordinary biodiversity in the abyss of the same order of magnitude as shallow tropical marine environments (Hessler and Sanders, 1967). Further quantitative sampling of sediment infauna using box corers across the Northwest Atlantic basin over subsequent decades culminated in the postulation by Grassle and Maciolek (1992) that there may be over 10 million species in the deep sea.

In 1983, with the establishment of the Exclusive Economic Zone in the US and its territories, efforts were increased to explore, survey and sample this area under the auspices of the US Geological Survey (USGS) (EEZ-SCAN 85 Scientific Staff, 1987). The Institute of Oceanographic Sciences (UK) was contracted to map the seafloor from the 200 m depth contour out to the EEZ boundary using their GLORIA (Geological LOng-Range Inclined Asdic) sidescan and other equipment that provided seismic-reflection profile data and total-magnetic-field data under Program EEZ-SCAN (EEZ-SCAN 85 Scientific Staff, 1987).

First investigations of hadal habitats in the Puerto Rico Trench began with dives by the French bathyscaphe *Archimède* (Pérès, 1965) which was followed by trawl sampling by the *RV John Elliot Pillsbury* and *RV James M. Gilliss* during the University of Miami deep-sea expeditions, 1969–1972 and the Russian *RV Akademik Kurchatov* in 1973 (Leal and Harasewych, 1999). The trench lies within the EEZs of Puerto Rico and the US Virgin Islands so was mapped by the EEZ-SCAN program (1982–1987) which showed the trench to be a deeper than 8000 m strike-slip zone between the Caribbean and North American plates. In the north, basement ridges emerge from the flat abyssal plain with massive scarps, slumps and ridges. The floor of the trench is made up of abyssal sediments and there are no scarp features in the south (EEZ-SCAN 85 Scientific Staff, 1987)

The HOV *DSRV Alvin* enabled experiments on the deep-sea benthos such as the first measurements of deep-sea benthic community respiration (Smith and Teal, 1973) and recolonisation following artificial disturbance (Grassle, 1977). The onset in 1985 of sewage disposal from New York city at Deep-Water Dumpsite 106 (DWD-106) at 2500 m depth brought into sharp focus the need to protect the recently discovered biodiversity when it was shown that sewage-derived organic matter entered the benthic food web (Van Dover et al., 1992).

Cold-water coral mounds were first identified in the 1950s and 60s in the Gulf of Mexico (Moore and Bullis, 1960) and on the Blake Plateau

(Stetson et al., 1962) in echo soundings, dredges, and drop-camera surveys, and investigated more thoroughly in the 1980s and 90s as submersible technologies became more accessible (Reed et al., 2006; Cordes et al., 2008). Mullins et al. (1981) discovered living deep-water coral mounds at 1000–1300 m depth north of Little Bahama Bank and, in the following years, the extent and importance of this habitat around the Northwest Atlantic basin was gradually revealed using rapidly advancing remote camera and submersible technologies that allowed work in complex topography such as submarine canyons (Mortensen and Buhl-Mortensen, 2005).

During the 1970s and 1980s, standardised trawl surveys were conducted on the slopes of the Bahamas, mid-Atlantic Bight, southern New England Newfoundland, Denmark Strait and Irminger Sea providing the basis for the "*Summary Atlas of deep demersal fishes of the North Atlantic Basin*" (Haedrich and Merrett, 1988).

3.5. Wider Caribbean expeditions (including Gulf of Mexico)

The earliest explorations in the Caribbean were by Pourtalès in the 1860s, aboard the US Coast Survey Steamers *Corwin* and *Bibb,* and included discovery of deep-water corals off Cuba at 945 m. During the winter months of 1877–1879, Alexander Agassiz on the *Blake* made extensive surveys of the Gulf of Mexico and Caribbean Sea generating data for the first bathymetric charts of the area. Agassiz trawled to over 3500 m depth finding abundant fauna everywhere, observing calcareous oozes, pteropod remains, and presence of a rich variety of terrestrial remains (leaves, bamboo, sugar cane, land snail shells) at great depth leading to speculations on the sources of food supply to the deep sea (Mills, 1983). The steam yacht *Argo* from Liverpool, England visited the Caribbean, Gulf of Mexico and Florida in 1876 making biological collections (Higgin, 1877).

The US *RV Albatross I* was specially built for deep-sea dredging and conducted hydrographic and bathymetric surveys in the Caribbean Sea and Gulf of Mexico from 1884 to 1887 (Townsend, 1901). A number of expeditions passed through the area, including the French *Chazalie* Yacht (1893–1896), the Danish *Dana* and *Dana II* expeditions (1920–1930), the US *Carnegie* (1921–1930) that collected plankton in the Caribbean in 1928 (Dolan, 2011), and, in 1939, the *Velero III* undertook the Allan Hancock Expedition, exploring areas of the southern Caribbean off Venezuela, Colombia and Panama (Garth, 1945).

During the 1950 and 1960s, the United States Fish and Wildlife Service's *RV Oregon* and *RV Oregon II* began a series of systematic surveys throughout the Gulf of Mexico, Caribbean and neighboring seas mapping the seafloor, and collecting geological and biological deep-sea samples. A notable discovery in 1955 was one of the earliest examples of a massive deep-water coral reef 55 m high east of the Mississippi Delta (Moore and Bullis, 1960). During the 1960s, the University of Miami's Deep-Sea Expeditions on board *RV Pillsbury* resulted in a major series of taxonomic and biological reports and papers (e.g. Staiger, 1969; Hernández-Ávila, 2014).

Voyages by the *RV Eastward* (1970s), the *RV Akademik Vernadski* (early 1970s), and the *RV Columbus Iselin* (1970s and 1980s) contributed further biodiversity data (Lutz and Ginsburg, 2007; INVEMAR, 2010). In the early 1970s, the *RV Knorr* and *RV Atlantis II* collected hydrographic and midwater trawl samples throughout the Caribbean.[1]

The CAYTROUGH research programme in 1976–1977 (Ballard et al., 1979) investigated the geology of the Cayman Trough through several research cruises using rock dredging, camera sled deployments, and swath bathymetry mapping. The campaign also included dives by HOVs *Alvin* and *Trieste II* collecting samples and seafloor photographs, which approached the depth limits for those submersibles at that time (3600 m for *Alvin*, and 6000 m for the *Trieste II*).

In the early 1980s, the Norwegian research vessel *RV Dr Fridtjof Nansen* helped with providing detailed information within countries' EEZs, including in the Caribbean and off the North Coast of South America. In 2011, the Spanish research vessel *B/O Miguel Oliver* conducted a standardised bottom trawl survey along the Central American slope, from Panama to Belize, reaching depths of 1500 m. This expedition focused on characterizing the seafloor, demersal communities, and water column properties. The survey yielded significant findings, including reports of new species and extended distribution ranges for various demersal fauna (Brenes Rodríguez et al., 2017, Benavides-Morera and Campos-Calderón, 2019; Cambronero-Solano et al., 2019; Long et al., 2021a).

During the last three decades, Colombia has carried out biodiversity inventories on the seabed (200–4220 m) and in the mesopelagic zone (200–1000 m), despite challenges in terms of scientific capacity and the significant financial and logistical limitations that these expeditions require. Twenty-eight new species have been described and 700 species have been newly recorded for Colombian waters. INVEMAR has conducted more than thirty expeditions to study the biodiversity of the Colombian seabed, with different types of vessels and sampling methods from benthic trawls to remotely operated vehicles, characterizing marine benthic biodiversity (1995–2006; *BI Ancon*) and subsequently providing the environmental baseline for hydrocarbon exploration (2007–2024), an activity that requires the country to expand knowledge of the species living in these poorly known environments to ensure proper resource management. The samples collected in these expeditions are safeguarded in the Marine Natural History Museum of Colombia "MAKURIWA" of INVEMAR and most data are publicly accessible through the Marine Biodiversity Information System (SIBM), GBIF and OBIS.

In 1985, the USGS EEZ-SCAN Program's GLORIA side-scan sonar mapped the Gulf of Mexico, Puerto Rico and US Virgin Islands EEZs and the Mona Canyon, Venezuelan Basin, Muertos Trough and the Virgin Islands Trough, which separates St. Croix from the other US islands with depths down to 4000 m. Gulf of Mexico depths recorded during these surveys reached to 3600 m and the region was classified into three different zones: "a salt deformation province in the western section, the Mississippi Canyon and Fan system in the central section, and a carbonate province in the eastern section, which is separated from the terrigenous Mississippi Fan by the Florida Escarpment" (EEZ-SCAN 85 Scientific Staff, 1987). In addition, four submarine channels, extensive mass wasting, and several other interesting features were mapped (EEZ-SCAN 85 Scientific Staff, 1987).

Methane-seep ecosystems were first discovered in the Gulf of Mexico by geological surveys (Bernard et al., 1976), followed by geochemical characterization (Anderson et al., 1983) and the discovery of methane hydrate (Brooks et al., 1984). The first chemosynthetic cold-seep communities were discovered by submersible surveys along the Florida Escarpment (Paull et al., 1984) and by trawl surveys that collected "vent-type" taxa along the northern continental slope (Kennicutt et al., 1985) at depths from 350 m to 2200 m (Macdonald et al., 1990). Work on methane seeps and mud volcanoes expanded to the Barbados Accretionary Prism in the late 1980s (e.g., Faugères et al., 1990). This continued with the French submersible, *Nautile*, in the early 1990s as part of the DIAPISUB cruises (e.g., Olu et al., 1996, 1997).

The deep benthic fauna of the Northern Gulf of Mexico was systematically surveyed during 1964–1973 by voyages of the Texas A&M University *RV Alaminos* (Pequegnat, 1983). This study was followed by the Northern Gulf of Mexico continental slope survey (1983–1985) (Gallaway et al., 1987; Pequegnat et al., 1990) and the Deep Gulf of Mexico Benthos Project (2000–2002) (Powell et al., 2003; Rowe and Kennicutt, 2008). Data were extended to the entire Gulf of Mexico by a census of fishes in the southern Gulf by Ramírez et al. (2019).

Exploration of the central and southern Gulf of Mexico has been ongoing since the 1960s in collaborative efforts between USA and German scientists and institutions and among Mexican institutions (e.g.

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[1] https://repository.library.noaa.gov/view/noaa/43681/noaa_43681_DS1.pdf.

CIGoM and derived Atlases). These studies span deep-sea hydrographic conditions (Furey et al., 2018), oil and gas exploratory efforts (Colwell et al., 2021), biogeochemistry (Bosman et al., 2020) and biodiversity assessments (Wei et al., 2012; Quintanar Retama et al., 2023), including of cold-water corals (Hebbeln et al., 2014). The complex geomorphology of the deep Campeche knolls harbors diverse habitats (MacDonald et al., 2020) with natural hydrocarbon seep ecosystems and habitats that support cold seep fauna (Sahling et al., 2016).

The pelagic fauna of the Gulf of Mexico between 0 and 1500 m depth has been extensively studied since the Deepwater Horizon oil spill through three major research programs: ONSAP (2010–2015), DEEPEND (2015–2018), and DEEPEND|RESTORE (2019–2029) (Cook et al., 2020; Sutton et al., 2022), which provide a near-comprehensive census of the midwater micronektonic fishes, cephalopods, and crustaceans from the region, including the major taxa undertaking diel vertical migration. The Deep-C Consortium (2011–2014)[2] additionally investigated physical factors affecting the fate of released oil and dispersants to improve models in support of future responses. Prior to these programs, the Gulf pelagic fauna was sampled opportunistically by several researchers (Voss, 1956; Nafpaktitis and Gibbs Jr, 1977; Hopkins et al., 1996; Wormuth et al., 2000; Ross et al., 2010). Voss especially suggested more extensive methane seeps based on contaminated mud in deep trawls, thus this early research laid the foundation for later successful expeditions, changing views on the extent and influence of seeps and vents (Levin et al., 2016).

4. Spatial analysis of research activities to date

As detailed in Section 3, survey effort has varied in both time and space across the North Atlantic. In order to investigate this variation more fully, and to allow for efficient targeting of data gaps by future surveys, we conducted a spatial analysis of existing survey and record data.

4.1. Data methods

Data used for this review were compiled from open-access and private repositories referenced below and do not represent all data held for the region. Thus this exercise underestimates sampling effort. However, while the numbers of records may change with the addition of inaccessible datasets, overall patterns in sampling effort will likely remain similar.

4.1.1. Data extraction

Open-access data were compiled from the Ocean Biodiversity Information System (OBIS; www.iobis.org); and the Global Biodiversity Information Facility (GBIF; www.gbif.org, https://doi.org/10.15468/dl.htvbed). To represent the OBIS data, a subset of the Bridges and Howell (2025) dataset was used. Note that the citation for the GBIF dataset includes all the datasets extracted before data cleaning. These open-access datasets were also combined with several regional databases for the mapping effort (Table 1).

For all datasets, records were only retained when the depth value was greater than 200 m and position data were available. GBIF data were subjected to quality control criteria following Saeedi et al. (2020, 2022). Using custom R scripts in R Studio, all taxonomic names were matched against the World Register of Marine Species (WoRMS) and all records with invalid coordinate systems or coordinate uncertainty of more than 100 km were removed. Only data belonging to accepted marine species were retained. The packages used in this process were “rgbif” (Chamberlain and Boettiger, 2017; Chamberlain et al., 2024), “sf” (Pebesma and Bivand, 2023), “sp” (Bivand et al., 2013), “magrittr” (Bache and Wickham, 2022), “taxize” (Chamberlain and Szöcs, 2013), “obistools” and “robis” (Provoost and Bosch, 2018, 2022).

For trawl data from the ICES (International Council for the Exploration of the Sea) and GINR datasets, the mid- and start points were used, respectively – this was deemed acceptable given trawls do not span more than the 1° resolution used for mapping. All datasets were formatted in a one record per row table; in cases where quantities were represented as weights, percent-cover or SACFOR, a value of one was attributed equating to a single record.

4.1.2. Removing duplicate records

Combining datasets raises the possibility of duplication of records and consequent over-estimation of sample effort. While the regional databases here typically do not submit their data to OBIS or GBIF, confirmed by the database managers, ICES records originating from the MAREANO dataset were removed manually. Duplication between OBIS and GBIF was identified based on matching dataset_id, decimalLatitude, decimalLongitude, and depth, with the GBIF records being removed when there was a match (Saeedi, 2024).

4.1.3. Separating benthic and pelagic data

All data from the ICES VME, GINR, UNINMAR, CONABIO and MAREANO datasets were classified as benthic given their focus and collection methodologies (Table 1). Bridges and Howell (2025) propose a methodology to filter open-access databases into benthic and pelagic datasets based on multivariate clustering and the modelled relationship between seafloor depth and record depth using custom R scripts. Here, this methodology was applied to the GRIIDC, OBIS and GBIF datasets for the review focus area to separate the benthic and pelagic data.

4.1.4. Assigning size classes

On the assumption that most records in the benthic data are of adult specimens (plankton tows would fall in the pelagic dataset), data can be broadly sorted into size classes based on taxonomy. Taxonomic data (kingdom to species) for each record were extracted using the “taxize” package (Chamberlain and Szöcs, 2013). Expert knowledge was used to classify dominant groups as mega- or macrofauna (Table 2), with the corresponding size class added to the record table. This size-based classification is considered appropriate for the dataset given that the majority of benthic records (Table 2) originate from the MAREANO dataset, which is derived from video observations. Consequently, taxonomic groups such as foraminifera and hydroids included in the benthic category are likely to represent megafaunal specimens large enough to be detected by video imagery. Where the taxonomic resolution of the record was too coarse to define a dominant size class (e.g., Cnidaria), records were retained for overall mapping analyses, but were excluded from the mega- and macrofaunal specific maps.

Given the prevalence of plankton tow data in the pelagic dataset, it is not possible to use this method to discriminate between size classes, and thus the pelagic data are presented as single dataset containing all size classes.

4.2. Patterns in the benthic data

Spatial mapping of sampling effort in areas deeper than 200 m allowed for identification of understudied deep-water areas within the region. Patterns in sampling effort of benthic megafauna below 200 m show biases towards EEZs, with notably high record densities around Newfoundland in the west, and Norway and the United Kingdom in the east (Fig. 2). However, there are large spatial gaps in the EEZs of nations in and surrounding the Caribbean Sea. Large spatial gaps in available benthic megafaunal data also exist in the North American, Cabo Verde and Newfoundland Basins.

In comparison, sampling effort of benthic macrofaunal taxa below 200 m is considerably less both in terms of the spatial coverage and numbers of records per cell (Fig. 3). While the Norwegian EEZ and US east coast are again identified as effort hotspots, high sampling effort is

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[2] https://deep-c.coaps.fsu.edu/data.

Table 1
Details on each dataset used in the mapping exercise.

Dataset	Host	Gear type	Description	Citation/data URL	No. records		Download date
					Benthic	Pelagic	
ICES VME database	ICES	Trawl/video	The ICES VME database contains observations of Vulnerable Marine Ecosystem (VME) indicators and habitats in the North Atlantic. Data either comprise records for VME habitats or VME indicators and are compiled from both scientific survey and fisheries bycatch data.	https://vme.ices.dk/download.aspx	335,567	0	August 2023
MAREANO	IMR	Video	These data comprise quality-controlled MAREANO video analysis records from 2006 to 2020, as stored in the MAREANO MarVid database, together with field video logs from research cruises between 2021 and 2023 as stored in MAREANO's MarBunn database. Both databases can be accessed upon request to MAREANO (https://mareano.no/en/maps-and-data/biologiske-data).	https://mareano.no/kart-og-data	5,019,774	0	January 2024
Greenland	GINR	Trawl	The GINR dataset derives from the trawl bycatch-monitoring programme (Blicher and Hammeken Arboe, 2017) carried out by GINR where the data are currently held. Data used here were collected between 2015 and 2022.	Blicher and Hammeken Arboe (2017)	16,860	0	August 2023
GRIIDC	GRIIDC	N/A	GRIIDC records were sourced from the publicly accessible data management system developed to house data from Gulf of Mexico researchers. No date constraints were applied.	www.gulfresearchinitiative.org	15,301	26,627	August 2023
Bimini Biological Field Station - Shark Lab	Bimini Biological Field Station - Shark Lab	Deepwater longline	The Bimini Shark Lab has been collecting data on sharks since 1990. This deepwater dataset ran from 2005 to 2018. Depths were determined using a time-depth recorder (TDR) attached to the longline or estimated from charts. Data can be requested by contacting admin@biminisharklab.com.	https://www.biminisharklab.com/	122	0	September 2023
CONABIO	CONABIO	Trawl/core/multicorer/Boxcorer	CONABIO's data have a review process, with the objectives of standardizing, cleaning and completing the information. It is based on/and in equivalence with the Darwin Core standard	CONABIO (2021); http://www.biodiversidad.gob.mx/	222	0	February 2024
UNINMAR	UNINMAR	Benthic trawl/Multicorer/Boxcorer	UNINMAR has an internal database, structured on the DarwinCore standard, consulted through http://uninmar.icmyl.unam.mx/search?query=all. When the records are entered into the database, their taxonomy is validated through https://www.marinespecies.org/and, in case of discrepancies, the person responsible for the scientific collection is consulted, requesting their approval to update the information provided. The positioning information is validated through the relevant geographic information charts published by the National Institute of Statistics and Geography.	https://datosabiertos.unam.mx/	141	0	February 2024
OBIS	OBIS	N/A	These data are a subset of the global data (https://zenodo.org/records/15487410) mapped in Bridges and Howell, (2025). The quality control steps are outlined therein and we recommend readers refer to Bridges and Howell, (2025) for the full methodology.	Bridges and Howell, (2025)	1,149,380	709,538	June 2023
GBIF	GBIF	N/A	GBIF data were sourced from the open-access repository, accessible at www.gbif.org.	https://doi.org/10.15468/dl.htvbed	816,426	313,489	February 2024
Total					7,353,671	1,049,654	

also shown in the northern Gulf of Mexico. There are large spatial gaps in the southern Gulf of Mexico and in the EEZs of nations in and surrounding the Caribbean Sea. All sub-ocean basins (North American, Cape Verde, Newfoundland, West European and Canary) hold few benthic macrofaunal records.

While the number of benthic records presented here is roughly seven times the number of pelagic records (Table 1), pelagic data have comparatively vast spatial coverage, with some samples taken from most wider shelf and slope regions within the review area (Fig. 4). There tend to be fewer records in the EEZs of Caribbean nations as compared with other nations. Low effort areas are also identifiable along the mid-Atlantic ridge and around the southern Greenland coast.

4.3. *Stratification of data*

The number of benthic records from Areas Beyond National Jurisdiction (ABNJ) is far lower than from within EEZs (317,524 versus 6,970,631). Within EEZs, waters shallower than 500 m are most densely sampled, although there is a substantial peak in benthic record density at ~900 m (Fig. 5). For ABNJ, record density is highest at ~4250 m. We interpret this not as an indication that sampling efforts are preferentially targeted at this depth, but rather as a reflection of the underlying seafloor topography in ABNJ. Much of the ABNJ in the North Atlantic comprises abyssal plains, which are typically found between 3000 and 6000 m. Therefore, the peak in record density likely reflects the relative

Table 2
Taxonomic groups used to append size classes to the benthic data. Note that groupings reflect that the majority of records are derived from video observations (see text).

Taxonomic groups	Size class of benthic adults
Anthozoa, Bivalvia, Brachiopoda, Bryozoa, Cephalopoda, Chordata, Ctenophora, Decapoda, Echinodermata, Foraminifera, Gastropoda, Gnathostomata, Hydrozoa, Myxini, Polyplacophora, Porifera, Pycnogonida, Scaphopoda, Scyphozoa, Staurozoa, Thecostraca, Tunicata	Megafauna
Amphipoda, Annelida, Copepoda, Cumacea, Euphausiacea, Hemichordata, Isopoda, Mysida, Nematoda, Nemertea, Ostracoda, Phoronida	Macrofauna

availability of seafloor at these depths, rather than a specific research focus on this depth band (Fig. 5). The median benthic record depth across the region (including both EEZs and ABNJ) is 446 m.

The number of records per EEZ varies greatly across the region's bordering nations (Fig. 6), with 69.9 % of records located within the Norwegian EEZ. However, this is mostly due to the inclusion of the comprehensive MAREANO dataset in our analyses. If the Norwegian records are removed, the dominance of certain nations is still strong, with 44.8 % of the remaining records deriving from the Canadian EEZ. Although their smaller size should be taken into consideration, the EEZs of many Caribbean and southern Gulf of Mexico nations appear particularly undersampled, with the number of records orders of magnitude smaller (Fig. 6, note logarithmic scale), reflecting the patterns noted in spatial distribution (Figs. 2–4).

Examination of pelagic data from below 200 m shows a steep decline in the number of records with depth (Fig. 7). The trend is steady from the mesopelagic through to ~2500 m, at which point record numbers drop to near zero. This abrupt decline likely reflects both the logistical challenges and limited use of appropriate sampling gear, such as deep-towing plankton nets, at depths greater than 2000 m.

4.4. Conclusion of sampling effort to date

Despite the extensive history of deep-sea research (Section 3) and the efforts in recent decades, for example since the Census of Marine Life, to undertake more systematic sampling of the deep sea, many areas are yet to be sampled. The EEZs of many Caribbean nations appear particularly undersampled compared with other EEZs across the North Atlantic. Large data gaps exist for benthic mega- and macrofauna in several abyssal regions, especially to the west of the Mid-Atlantic Ridge, and records densities decrease with depth across the entire study area for both benthic and pelagic datasets. These data gaps underscore the need for more comprehensive sampling to achieve a robust understanding of the region's biodiversity and ecosystem dynamics.

Nonetheless, intense survey of particular features and areas such as the Porcupine Seabight, Norwegian slope, southern Labrador Sea, and the northern region of the Gulf of Mexico has led to considerable understanding of particular ecosystems, knowledge of which are elaborated in the next sections.

5. Broad-scale biodiversity patterns and ecosystem function

The complete absence of ambient light, generally low primary production and overall biomass, and potential for wide dispersal have helped to create expectations of a low diversity and homogenous deep-sea environment (e.g. Snelgrove and Smith, 2002). Broadly speaking, the North Atlantic deep sea encompasses fewer biogeographic provinces than corresponding coastal environments. For example, the North Atlantic encompasses only five pelagic provinces (Northwest Atlantic Subarctic, North Atlantic Drift, Central North Atlantic, Mauritania/Cape Verde, and a portion of the Tropical and West Equatorial Atlantic; Sutton et al., 2017), lower bathyal environments (700–3000 m depth) include only two provinces (Northern Atlantic Boreal and North Atlantic), abyssal environments (3000–6000 m) and hadal environments (6000–10,000 m) encompass only one province each (North Atlantic

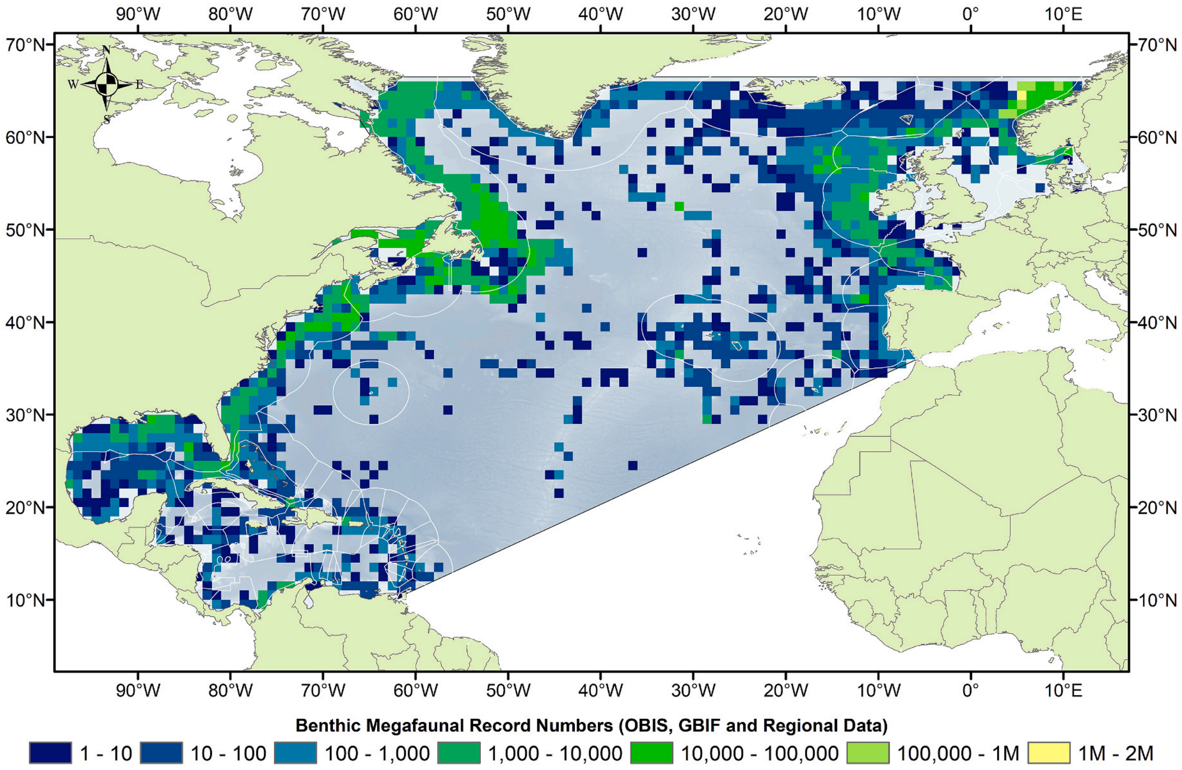

Fig. 2. Sum of benthic megafaunal records from deeper than 200 m per 1 × 1° grid cell for the North Atlantic and Gulf of Mexico. Data are classified into bins that incrementally increase by one order of magnitude and are indicated by colour. Data sources are presented in Table 1 and corresponding taxonomic groups in Table 2.

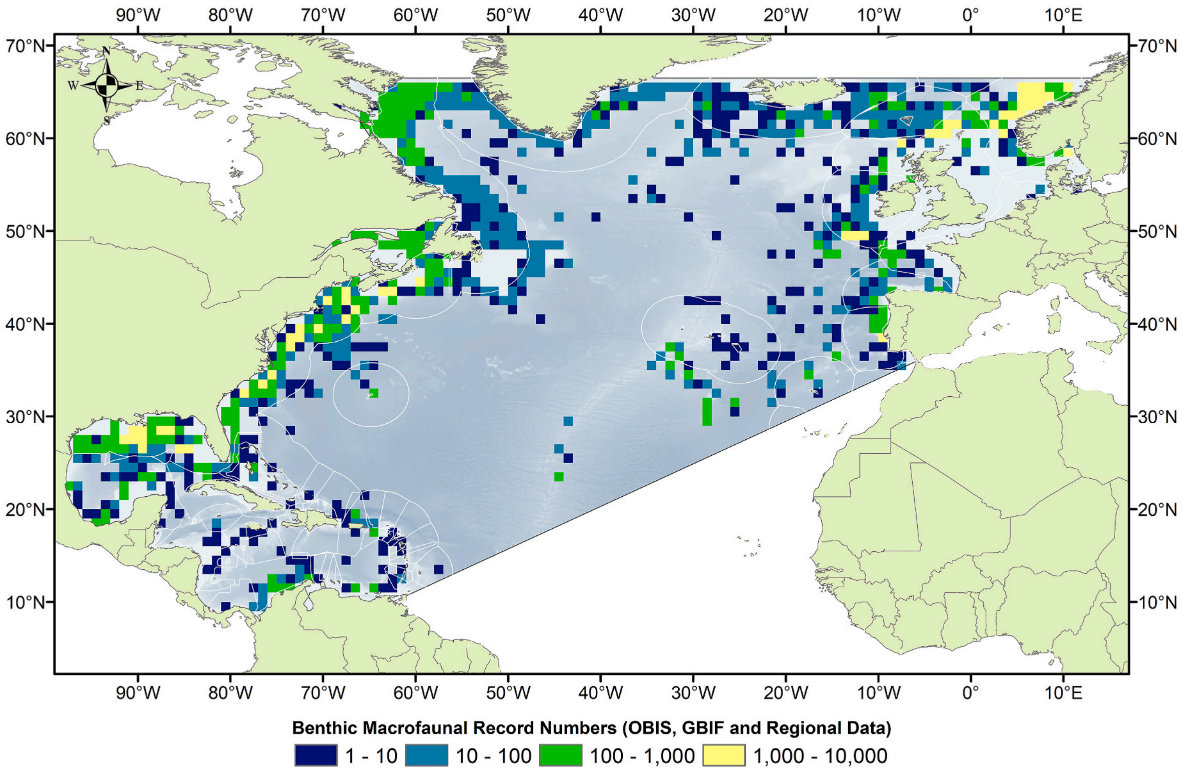

Fig. 3. Sum of benthic macrofaunal records from deeper than 200 m per 1 × 1° grid cell for the North Atlantic and Gulf of Mexico. Data are classified into bins that incrementally increase by one order of magnitude and are indicated by colour. Data sources are presented in Table 1 and corresponding taxonomic groups in Table 2.

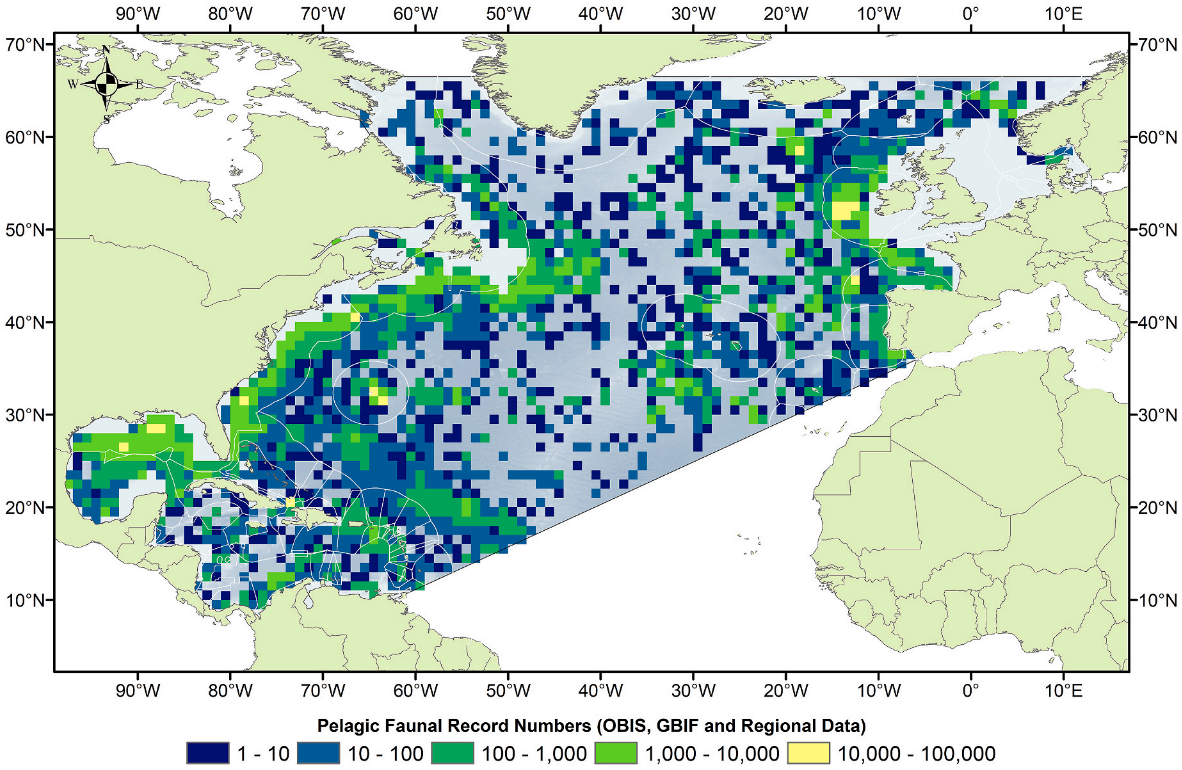

Fig. 4. Sum of pelagic records from deeper than 200 m per 1 × 1° grid cell for the North Atlantic and Gulf of Mexico. Data are classified into bins that incrementally increase by one order of magnitude and are indicated by colour. Data sources are presented in Table 1.

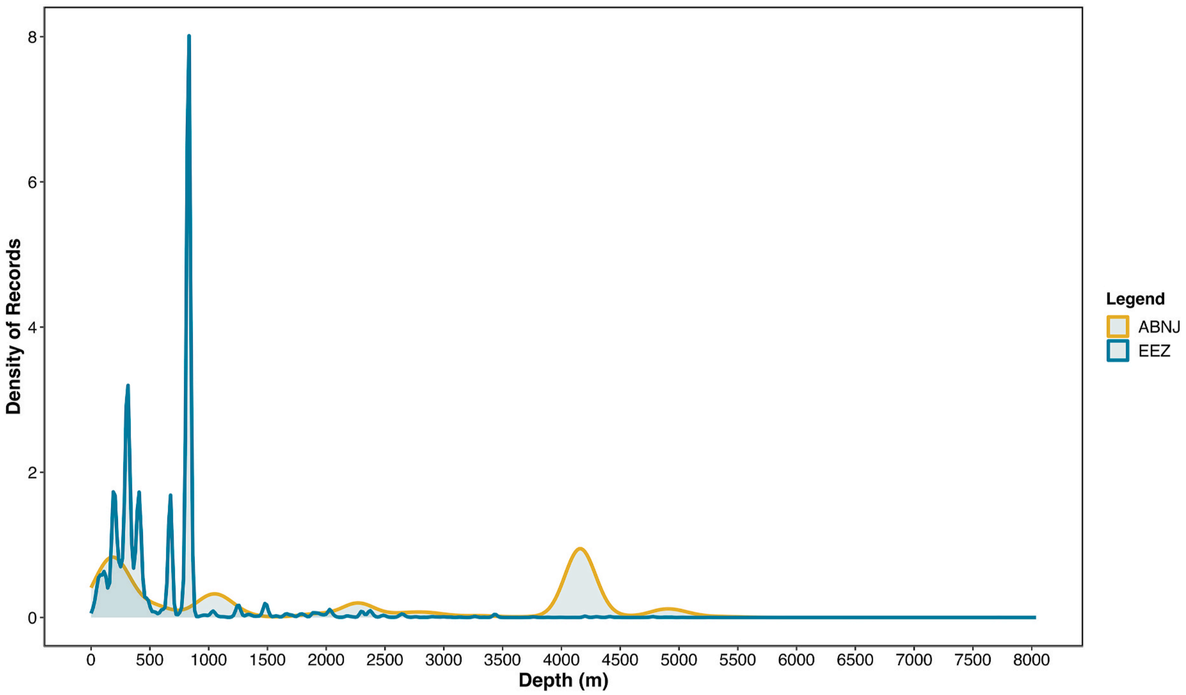

Fig. 5. Density of benthic records plotted by depth and area for the North Atlantic and Gulf of Mexico. Kernel density values were multiplied by 1000 for ease of reading. Values: Areas beyond national jurisdiction (ABNJ) n = 317,524; Exclusive economic zone (EEZ) n = 6,970,631. Data sources are presented in Table 1.

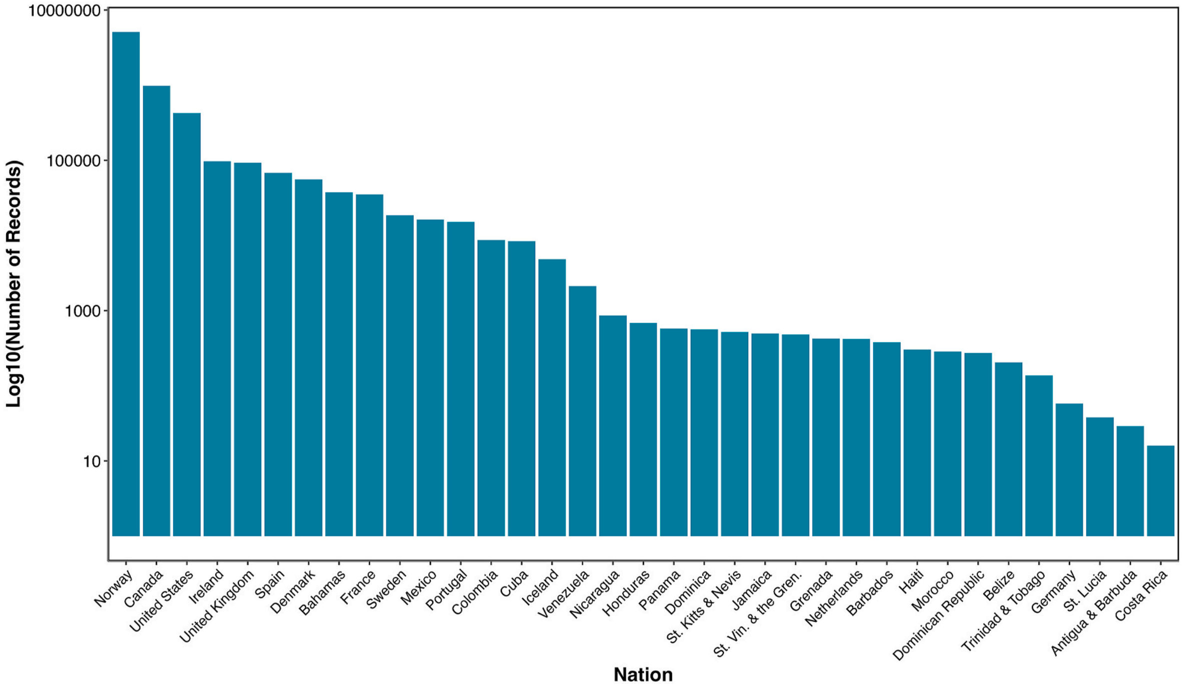

Fig. 6. Number of benthic records (log10) collected from deeper than 200 m *per* bordering nation in the North Atlantic and Gulf of Mexico. Data sources are presented in Table 1.

and Puerto Rico, respectively; Watling et al., 2013). However, recent taxon-specific studies have shown that the North Atlantic lower bathyal may require further division into eastern and western units and the boundary of the western Boreal Atlantic may require further adjustment (Watling and Lapointe, 2022). In comparison, shallow-water environments (bottom depths down to 200 m) across the same area encompass nine provinces, not only separating the Western from the Eastern side of the Atlantic basin but also including enclosed seas such as the Mediterranean and the Caribbean (Spalding et al., 2007).

Despite the massive geographic areas covered by these provinces, the biota within them are far from uniform, and scientists now recognize the deep sea as a species-rich biome that may rival even the most diverse habitats on Earth (Snelgrove and Smith, 2002). At large spatial scales of 10s–1000s of km, geomorphological features such as submarine canyons, mid-ocean ridges, hydrothermal vents, cold seeps, trenches, and seamounts create specialized habitats with relatively unique and

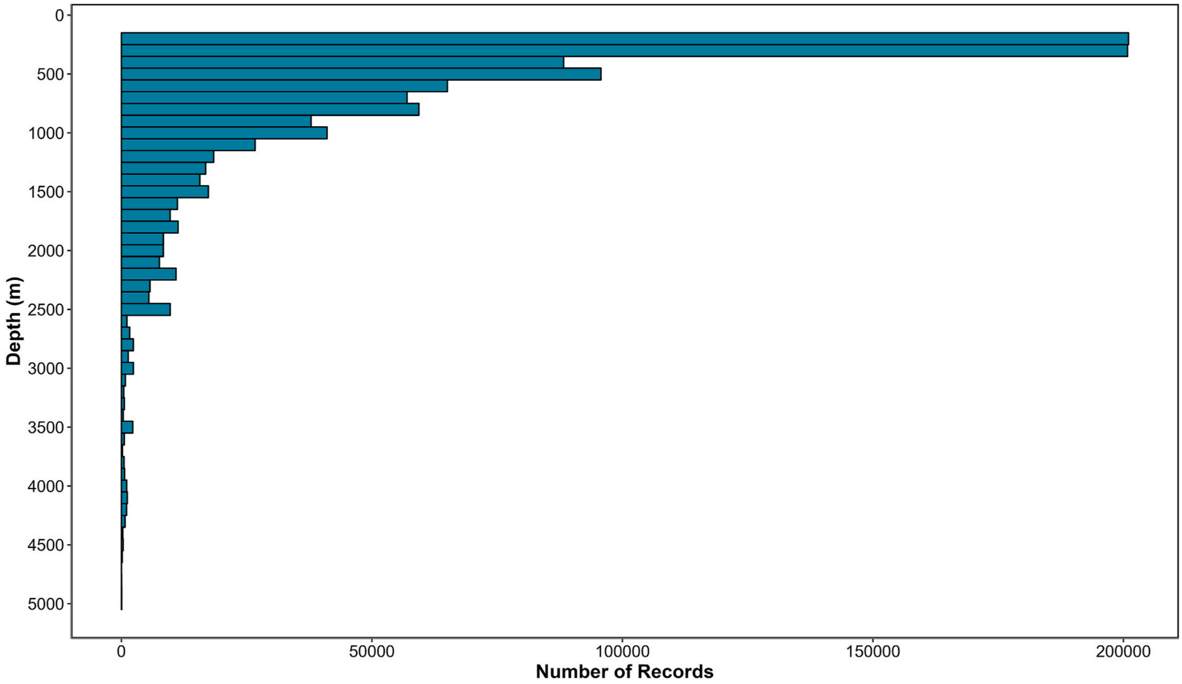

Fig. 7. Number of pelagic records from the North Atlantic and Gulf of Mexico across the bathymetric gradient in 100 m bins. Data sources are presented in Table 1.

habitat-specific biotas. At small spatial scales of centimeters to meters, living organisms such as cold-water corals and sponges provide habitat for fishes and smaller invertebrates. Many other variables add to this complexity; availability of organic matter typically decreases with depth, and circulation around geological features such as canyons adds further variability in terms of how organic matter settles to the bottom (Campanyà-Llovet et al., 2018). Chemoautotrophic habitats, including hydrothermal vents and cold seeps, also provide an alternative energy source that supports unique faunal assemblages.

The lack of obvious physical barriers to dispersal in the deep sea seems contrary to the high biodiversity of many deep-sea taxa. However, the "open" appearance of the deep sea belies differences in geological histories of ocean basins, physical complexity created by topographic features such as land masses and mid-ocean ridges, as well as large spatial distances and depth differences that create unseen barriers to dispersal (e.g. Cunningham and Collins, 1998; Etter et al., 2005). Indeed, accumulating research using genetic tools shows narrower distributions than previously thought, often along bathymetric gradients (corals, Quattrini et al., 2022; echinoderms, Cho and Shank, 2010; molluscs; Etter et al., 2005; Zardus et al., 2006). In contrast there can be strong connectivity over 1000s of km of ocean horizontally (Herrera et al., 2010; Etter et al., 2011). Thus there is a general pattern of greater vertical divergence, above and beyond that found horizontally over similar scales.

The North Atlantic represents just under half of all non-hydrothermal vent habitat population genomic studies in the deep-sea (Taylor and Roterman, 2017), although there are only relatively few in total; 77 papers covering 115 species in 2016, with an increase in research outputs in recent years as genomic sequencing has become cheaper and more widely available (Taboada et al., 2023). In fact, and despite considerable variability caused by differences in the life-histories of the various taxonomic groups, scales of dispersal and connectivity in the deep sea appear comparable to or only slightly larger than those in shallow water (Baco et al., 2016). Dispersal in many deep-sea benthic organisms occurs at the larval stage. Recent research created models of various larval swimming behaviors to investigate dispersal potential and found that vertical swimming can have a large impact on dispersal distance (Gary et al., 2020).

Regarding spatial patterns of diversity, Rex (1983) showed a bell-shaped pattern in macrofaunal biodiversity in relation to depth, peaking at intermediate depths between 1500 and 2500 m; Mokievsky et al. (2002) and Danovaro et al. (2010) reported a similar pattern for meiofauna. Bucklin et al. (2010a) reported that for zooplankton, biodiversity progressively increases from the continental shelf to a depth of 1000–2000 m and then gradually decreases to abyssal depths. Snelgrove and Smith (2002) reviewed studies on biodiversity in deep-sea benthos and potential drivers of patterns related to depth and latitude. Depth itself, presumably acts generally as a surrogate for variables closely linked to biology, such as food availability, temperature, or disturbance, and many factors other than depth come into play, blurring any simple generalization. For example, Levin and Gage (1998) reported highest biodiversity and biomass in surface waters of upwelling regions, typically decreasing at depths characterized by reduced oxygen. Wilson and Hessler (1987) and Brown and Thatje (2014) suggested that intermediate (bathyal) depths favor speciation, from which new species eventually spread to abyssal depths.

Rex et al. (1993) documented a latitudinal gradient in multiple groups of deep-sea macrofaunal invertebrates in the North Atlantic, though Woolley et al. (2016) note mid-latitude peaks for deep-sea ophiuroids. Deep-sea scientists have debated the drivers of deep-sea diversity patterns but most theories coalesce around intermediate levels of disturbance and available energy.

Overall, deep-sea research to date, which spans a wide range of habitats discussed below, demonstrates that, while regional scale patterns in species richness may relate to temperature and productivity (food availability), local-scale richness depends on a greater variety of variables that differ in importance within different habitats. The sections below elaborate on this idea.

Despite typically low process rates in most deep-sea environments relative to shallow water, the sheer vastness of the deep sea results in delivery of significant contributions of ecosystem functions and services at a global scale, particularly when considered over extended time scales of decades to hundreds of years. Key supporting services include large-scale cycling of major nutrients such as carbon and nitrogen, primary (chemosynthetic) and secondary production, and habitat provisioning for other species. Provisioning services encompass biological resources used for nutritional purposes (e.g. fish and shellfish) as well as genetic and mineral resources relevant to the biomedical and (bio)technology industry; whereas regulating services include bioremediation and climate regulation (La Bianca et al., 2023). Society increasingly recognizes the cultural significance of the deep sea, via educational, recreational, and spiritual elements, albeit intangible, and as an important component of deep-sea services from a socio-ecological perspective (see for instance Turner et al., 2020a). In the following sections we expand on these services and functions that vary in importance across the different habitat types, and for which the level of scientific knowledge exists (Table 3). We organize this discussion around IUCN Functional Typology,[3] which defines Ecosystem Functional Group as "a group of related ecosystems within a biome that share common ecological drivers, which in turn promote similar biotic traits that characterize the group."

5.1. Patterns within Ecosystem Functional Groups

5.1.1. Mesophotic ecosystems

Mesophotic ecosystems are light-dependent communities between shallow euphotic waters and the aphotic deep-sea, typically between 30 m and the depth at which photosynthetically active radiation is limited to 1 % of that at the surface (Ryther, 1956), which in clear water can extend below 150 m depth (Hinderstein et al., 2010). They support a variety of taxa, including sponges, octocorals, zooxanthellate corals, azooxanthellate corals, macroalgae and fishes (Lesser et al., 2009; Hinderstein et al., 2010; Bongaerts et al., 2010; Braga-Henriques et al., 2022). Some cold-water corals have their upper depth limit in the mesophotic, and we include the ecosystem here as a transition to the deep sea. Further information can be found in the comprehensive reviews of Loya et al. (2019) and Bell et al. (2024), the latter focusing on temperate mesophotic ecosystems, and on Mesophotic.org, a platform dedicated to mesophotic research around the world (Bongaerts et al., 2019).

The distribution of tropical and subtropical mesophotic ecosystems tends to mirror that of shallow-water coral reefs (Pyle and Copus, 2019); to date, in the North Atlantic, they are reported from Brazil, into the Gulf of Mexico, the Caribbean Sea, and north to Bermuda (Pyle and Copus, 2019; Bello Pineda et al., 2023); their composition and extent require further study (Gil-Agudelo et al., 2020) through collaborative efforts using state of the art infrastructure. In temperate waters, mesophotic ecosystems are known from the margins of the North Atlantic from Scotland to southern Portugal in the east, and from Newfoundland to the northern Gulf of Mexico in the west; and are also present in the Azores (Bell et al., 2024).

Despite significant research efforts in mesophotic ecosystems in recent years, they remain, like the deep sea, relatively unexplored in comparison to shallow-water ecosystems (Turner et al., 2019). There tends to be limited species overlap between mesophotic ecosystems and shallower depths (Lesser et al., 2019; Loya et al., 2019; Campoy et al., 2023; Diaz et al., 2023; Bell et al., 2024), and numerous new species of fishes, gorgonians, algae and cryptic invertebrates have been associated with advances in technical diving and improved ability to sample cryptic species (Loya et al., 2019).

Gaps persist in our fundamental knowledge of their distribution, environmental drivers, ecological and functional roles, connections to shallow-water ecosystems, and provisioning of ecosystem services (Turner et al., 2019). No studies have fully evaluated the ecosystem services provided by mesophotic ecosystems, however, experts predict they provide services unique to this ecosystem as well as many of the same services as shallow-water coral reefs (Holstein et al., 2019), including provisioning services (e.g., fish, shellfish, marine natural products), supporting services (e.g., feeding and nursery grounds), regulating services (e.g., coastal protection, carbon cycle), and cultural services (e.g., technical diving, deep-water sport fishing (Table 3; Tonin, 2018; Holstein et al., 2019; Micaroni et al., 2021; Campoy et al., 2023).

5.1.2. Continental and island slopes

Continental slopes comprise an integral component of continental margins and oceanic islands, forming the transition zone between the shelf break (c.a. 250 m depth) and abyssal plains (c.a. 3000 m). Though relatively featureless, these typically sedimented habitats include a variety of contrasting geomorphological structures and underwater features across the North Atlantic e.g., rocky outcrops, canyons, channels, landslides, coldwater coral mounds, and chemosynthetic environments (Gage and Tyler, 1991). We treat submarine canyons separately below, noting that although they represent a subset of continental slope habitats, they have received extra attention for their discontinuous and somewhat distinct processes and, in some cases, biota, thus meriting separate consideration.

Sedimentary habitats dominate continental slopes, and represent some of the best studied deep-sea habitats. Indeed, some of the first semi-quantitative deep-sea studies proposed biodiversity levels that rival some of the most diverse habitats on Earth (Sanders and Hessler, 1969), catalyzed considerable interest and debate (e.g. Dayton and Hessler, 1972; Grassle and Sanders, 1973), that accelerated with publication of the most detailed study of slope environments to date by Grassle and Maciolek, 1992). Detailed sampling of the New England continental slope led them to estimate that 10,000,000 species occur in the deep sea, again creating significant interest and debate (e.g. May, 1994). Small infaunal invertebrates such as polychaetes, crustaceans, and molluscs dominate sediments numerically, with epifauna such as sea pens, sponges, and anemones sometimes comprising significant biomass. Regional studies such as the BIOFAR (Marine Benthic Fauna of the Faroe Islands) (e.g., Freriksen et al., 1992; Klitgaard and Tendal, 2004) and BIOICE (e.g. (Dauvin et al., 2012), programs have added northern biogeographic coverage to studies of sedimentary environments of the eastern (e.g. Gooday et al., 2010) and western Atlantic (Rowe et al., 1982; Schaff and Levin, 1994; Blake and Grassle, 1994) sometimes extending from continental slopes to abyssal plains or from canyons too adjacent slopes (e.g. Duineveld et al., 2001; Ciraolo and Snelgrove, 2023). Collectively, these and other studies make the North Atlantic slope sedimentary environments among the best quantified of deep-sea habitats (e.g., Webb et al., 2010).

Burial and remineralization of large quantities of organic carbon occurs on continental slopes, derived from coastal and shelf-exported material and overlaying surface productivity. Organic carbon supply rate varies temporally, and decreases with distance from land and increases with water depth (Walsh, 1991). The pronounced environmental gradient observed on slopes associated with different water masses and depth-related changes in organic carbon flux to the seafloor, oxygen, and temperature conditions strongly affects the density, diversity, and distribution of fauna (Levin et al., 2001; Menot et al., 2010). Although the North Atlantic is one of the best-studied deep-sea regions globally, few consistent large-scale studies have assessed biodiversity across all components of the benthic and pelagic fauna.

Overall, continental slopes host highly diverse communities, particularly infaunal taxa, from microorganisms to meiofauna (i.e., Nematoda) and macrofauna (i.e., Polychaeta and Crustacea; e.g., Levin and Gage, 1998; Flach and de Bruin, 1999). For examples of habitats, see Fig. 8. In contrast, detritivores and predators dominate megafauna, including echinoderms, crustaceans, and fishes. As in other oceanic basins, the food supplied from both allochthonous and autochthonous sources decreases with increasing depth, contributing to species turnover, or species replacement along the continental slopes in the North Atlantic (e.g., Rowe et al., 1982; Carney, 2005; Rex et al., 2006; Stuart and Rex, 2008; Rowe and Kennicutt, 2008; Menot et al., 2010; Priede et al., 2010). The upper slope fauna usually defines a transitional zone with some similarities to shelf environments, but as depth increases, shifts in diversity and life-history traits typically occur. For example,

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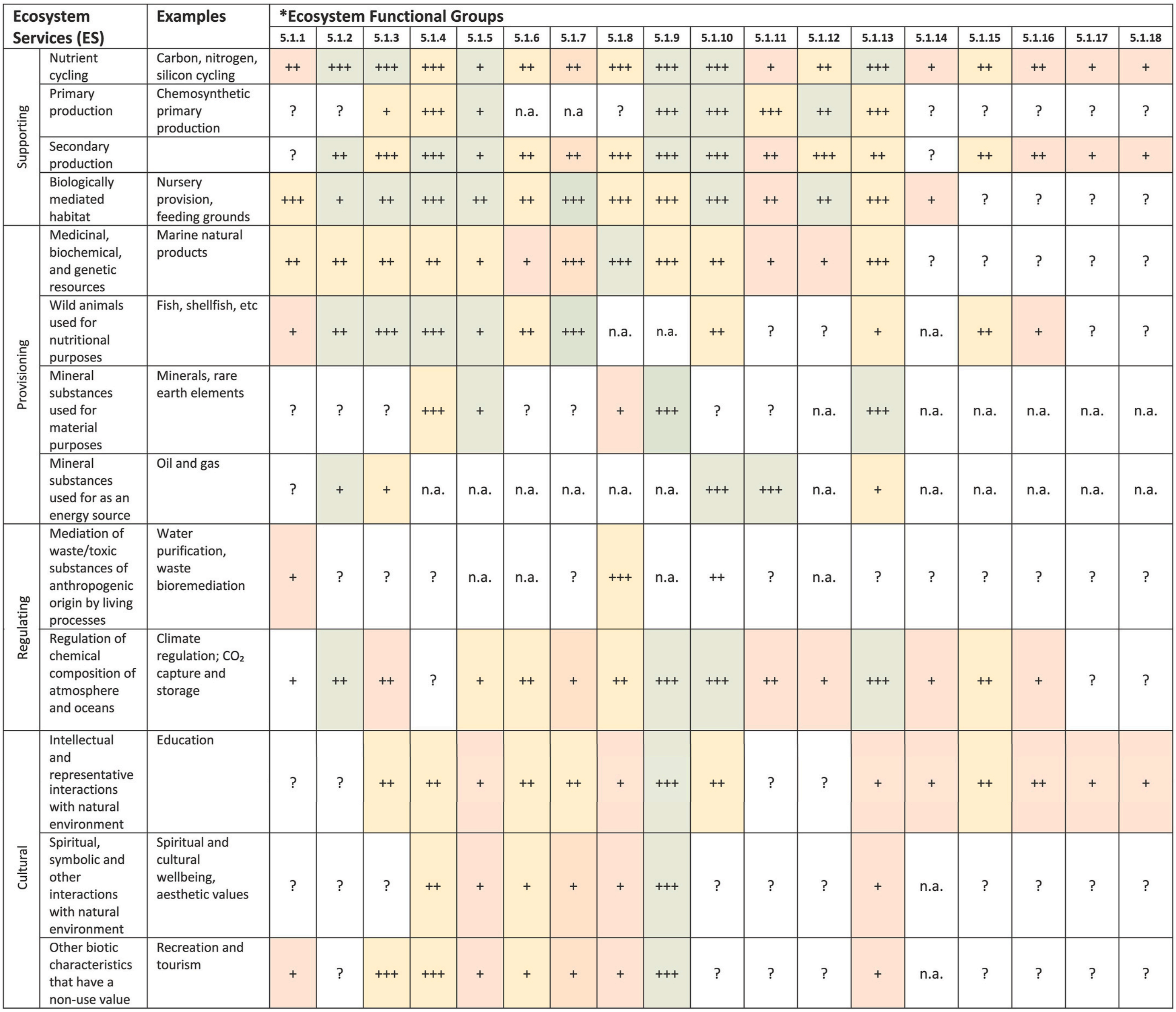
[3] https://global-ecosystems.org/page/typology.

Table 3
Ecosystem services (ES) provided by the different ecosystem functional groups (EFGs) of the North Atlantic. Ecosystem services and ecosystem functional groups follow the classifications by La Bianca et al. (2023) and Keith et al. (2022) respectively, with a few adaptations. Scores from + (somewhat relevant) to +++ (very relevant) provide an expert-based semi-quantitative assessment of how relevant a given ecosystem functional group is in terms of provision of a specific ES. n.a. indicates not applicable (when no evidence exists of the ES provided); and ? indicates high uncertainty (e.g. insufficient studies completed). Cell colours represent the relative knowledge/evidence level of a given ecosystem service for each functional – green (substantial existing knowledge); yellow (some knowledge); orange (poor to very poor existing knowledge).
***Ecosystem functional groups:** 5.1.1. – Mesophotic ecosystems; 5.1.2 – Continental and island slopes; 5.1.3 – Submarine canyons; 5.1.4 – Seamounts; 5.1.5 – Ridges; 5.1.6 – Carbonate mounds; 5.1.7 – Cold-water coral ecosystems; 5.1.8 – Sponge aggregations; 5.1.9 – Hydrothermal vents; 5.1.10 – Cold seeps; 5.1.11 – Asphalt volcanoes; 5.1.12 – Organic falls; 5.1.13 – Abyssal plains; 5.1.14 – Hadal trenches and troughs; 5.1.15 – Mesopelagic; 5.1.16 – Bathypelagic; 5.1.17 – Abyssopelagic; 5.1.18 – Hadopelagic.



Ecosystem Services (ES)		Examples	*Ecosystem Functional Groups																	
			5.1.1	5.1.2	5.1.3	5.1.4	5.1.5	5.1.6	5.1.7	5.1.8	5.1.9	5.1.10	5.1.11	5.1.12	5.1.13	5.1.14	5.1.15	5.1.16	5.1.17	5.1.18
Supporting	Nutrient cycling	Carbon, nitrogen, silicon cycling	++	+++	+++	+++	+	++	++	+++	+++	+++	+	++	+++	+	++	++	+	+
	Primary production	Chemosynthetic primary production	?	?	+	+++	+	n.a.	n.a	?	+++	+++	+++	++	+++	?	?	?	?	?
	Secondary production		?	++	+++	+++	+	++	++	+++	+++	+++	++	+++	++	?	++	++	+	+
	Biologically mediated habitat	Nursery provision, feeding grounds	+++	+	++	+++	++	++	+++	+++	+++	+++	++	++	+++	+	?	?	?	?
Provisioning	Medicinal, biochemical, and genetic resources	Marine natural products	++	++	++	++	+	+	+++	+++	+++	++	+	+	+++	?	?	?	?	?
	Wild animals used for nutritional purposes	Fish, shellfish, etc	+	++	+++	+++	+	++	+++	n.a.	n.a.	++	?	?	+	n.a.	++	+	?	?
	Mineral substances used for material purposes	Minerals, rare earth elements	?	?	?	+++	+	?	?	+	+++	?	?	n.a.	+++	n.a.	n.a.	n.a.	n.a.	n.a.
	Mineral substances used for as an energy source	Oil and gas	?	+	+	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	+++	+++	n.a.	+	n.a.	n.a.	n.a.	n.a.	n.a.
Regulating	Mediation of waste/toxic substances of anthropogenic origin by living processes	Water purification, waste bioremediation	+	?	?	?	n.a.	n.a.	?	+++	n.a.	++	?	n.a.	?	?	?	?	?	?
	Regulation of chemical composition of atmosphere and oceans	Climate regulation; CO_2 capture and storage	+	++	++	?	+	++	+	++	+++	+++	++	+	+++	+	++	+	?	?
Cultural	Intellectual and representative interactions with natural environment	Education	?	?	++	++	+	++	++	+	+++	++	?	?	+	+	++	++	+	+
	Spiritual, symbolic and other interactions with natural environment	Spiritual and cultural wellbeing, aesthetic values	?	?	?	++	+	+	+	+	+++	?	?	?	+	n.a.	?	?	?	?
	Other biotic characteristics that have a non-use value	Recreation and tourism	+	?	+++	+++	+	+	+	+	+++	?	?	?	+	n.a.	?	?	?	?

diversity of polychaete feeding guilds declines with depth (Carvalho et al., 2013). Several studies report a peak in species diversity in the mid-slope range (c.a. 1200–2000 m), with decreasing diversity below these depths and less marked changes (Rex, 1983; Stuart and Rex, 2008; Rowe and Kennicutt, 2008; Menot et al., 2010). For example, Rowe and Kennicutt (2008) reported a clear unimodal relation between the diversity of macrofaunal polychaetes, bivalves, and isopods across a wide depth range in the Gulf of Mexico. However, depth-related patterns in diversity across the Atlantic depend on the specific taxonomic group and the particular environmental conditions at local or regional scales (Menot et al., 2010; Levin et al., 2010). A study in the Faroe-Shetland region (NE Atlantic) for example, linked macrofaunal diversity to thermal regimes of different water masses (Narayanaswamy et al., 2010). In areas with low oxygen concentrations, an overall decrease in total macrofauna coincides with an increase in the abundance of species tolerant to low oxygen conditions (Levin and Gage, 1998).

Continental slope sediments play a pivotal role in delivering essential ecosystem services, such as nutrient cycling and carbon sequestration (Muller-Karger et al., 2005). This highly productive environment also supports economically important pelagic and demersal fisheries across

Fig. 8. Examples of habitats and fauna on continental slopes and abyssal plains. A) Aggregation of the hexactinellid sponge, *Pheronema carpenteri*; B) Roundnose grenadier; C) Chimaeridae; A, B & C from around 1100 m on the Porcupine Seabight, NE Atlantic, taken in 2011 from the JC062 expedition (credit: NERC CLASS); D) feeding traces and a deimatid holothurian at 4850 m depth on the Porcupine Abyssal plain, image taken in 2012 on the D377 Expedition (credit: NERC CLASS).

the whole Atlantic (Koslow, et al., 2000), yet many regions, from the Northeast Atlantic to the Grand Banks and the Flemish Cap in the Northwest Atlantic, show impacts of bottom-contact gear to depths greater than 1000 m (Eigaard et al., 2017; Vieira et al., 2018; Pham et al., 2019; Murillo et al., 2020). Among provisioning services, slopes host a large number of telecommunication cables laid on the seabed (Clare et al., 2023) and exploitation of oil and gas industries in these ecosystems is linked with chemosynthetic environments spread along the continental slopes, particularly off the Gulf of Mexico and North Sea (Cordes et al., 2016).

5.1.3. Submarine canyons

Submarine canyons are narrow, sinuous, steep-sided valleys incised into the continental shelf and slope of all continental margins (Shepard, 1972). They are major conduits for the transport of sediment and organic material (Jobe et al., 2011; Puig et al., 2014) from land and the shelf to the deep sea (Nittrouer and Wright, 1994). Submarine canyons are among the most energetic of oceanic environments, and their complex oceanographic processes (turbidity currents, internal waves, tidal flows) and topographic complexity result in high habitat heterogeneity (e.g., Amaro et al., 2016), including cliff walls (Huvenne et al., 2011; Johnson et al., 2013; Pearman et al., 2023), deep-sea coral reefs (Mortensen and Buhl-Mortensen, 2005; Morris et al., 2013; Davies et al., 2014; van den Beld et al., 2017), chemosynthetic ecosystems (Quattrini et al., 2015; Ross et al., 2015; Prouty et al., 2016; CSA Ocean Sciences Inc. et al., 2017), and soft sediment communities (Maurer et al., 1995; Cunha et al., 2011; Davies et al., 2014; Frutos and Sorbe, 2017; Ríos et al., 2022; Ciraolo and Snelgrove, 2023). The North Atlantic accounts for 16 % (1548) of the estimated 9477 large canyons globally (Harris and Whiteway, 2011). In the North Atlantic, canyons incise the continental margin shelf of Europe and East Coast of the US and Canada.

Many studies characterize submarine canyons as biodiversity hotspots with greater abundance and species richness compared with adjacent slope environments (De Leo et al., 2010; Cunha et al., 2011) enhancing fishing activities (Frutos and Sorbe, 2014; Ross et al., 2015; Almeida et al., 2017). The interaction of canyon topography with currents results in local upwelling of cold-nutrient rich waters (Hickey, 1995; Sobarzo et al., 2001) to the euphotic zone which supports enhanced primary production (Sobarzo et al., 2001; Amaro et al., 2015, 1016) attracting pelagic-associated secondary and tertiary consumers (Rennie et al., 2009). There is often enhanced zooplankton abundance at canyon heads (Greene et al., 1988; Allen et al., 2001; MacIsaac et al., 2014; Arriola-Pizano et al., 2022), while the upper section of shelf-incising canyons frequently supports cold-water coral communities (Whittard Canyon: Huvenne et al., 2011, Morris et al., 2013, Johnson et al., 2013; Norfolk Canyon: Brooke et al., 2017; Explorer Canyon: Davies et al., 2014; Corsair Canyon: Metaxas et al., 2019; Guy and Metaxas, 2022). Resuspended sediment is transferred along steep canyon walls by fast moving currents, and potentially concentrated by internal waves (Johnson et al., 2013) providing food and optimal condition for suspension feeders, including deep-sea corals.

Expansive soft-sediment habitats play an important role in submarine canyons, with some areas dominated by sediment-dwelling corals such as sea pens, gorgonians, and xenophyophores providing structural complexity for associated taxa, leading to increased biodiversity (Buhl-Mortensen et al., 2010; Cunha et al., 2011). Soft-sediment habitats that accumulate large quantities of organic material can support surface deposit feeders, such as holothurians; which provide important ecosystem functions by consuming and thus recycling large volumes of organic-rich seafloor matter (Amaro et al., 2010, 2015).

Despite growing research efforts on submarine canyons, especially in the North Atlantic, knowledge gaps on submarine canyon systems remain that reflect a lack of sampling for many canyons and lack of standardised methodologies, leading to incomparable data and lack of an integrated approach between disciplines (Huvenne and Davies, 2014).

5.1.4. Seamounts

Traditionally, seamounts are defined as undersea prominent topographic features whose summits rise at least more than 1000 m (Rogers, 2019) or 100 m above the surrounding seafloor (Pitcher et al., 2007; Yesson et al., 2011). Most seamounts are volcanic in origin and formed above largely stationary hotspots in the Earth's mantle (mantle plumes). As tectonic plates move over the hotspot, they carry the seamounts away from the magma source, thus forming a line of extinct volcanoes with monotonic age progression (Pitcher et al., 2007).

North Atlantic seamounts mostly occur along the Mid-Atlantic Ridge, with several additional chains in both the western and northeastern areas of the Atlantic (Clark et al., 2011). However, deformation along tectonic plate boundaries of the Greater-Lesser Antilles transition zone has produced numerous seamounts in the Caribbean (e.g., in the Anegada Passage), contributing to the environmental complexity of the deep-sea benthos (Auscavitch et al., 2020). Numerous volcanic seamounts around the San Andrés, Providencia, and Santa Catalina archipelago in the southwestern Caribbean link to seabed faults during Early Cenozoic times (Geister and Díaz, 2007; Idárraga-García and León, 2019). Normally these features represent oases of hard substrate surrounded by sedimentary habitat, especially in the case of increased currents, and these features may support a characteristic rich sessile fauna, such as sponges and corals.

According to accepted classification, summit depths of seamounts may be quite shallow (0–200 m), moderate in depth (200–800 m) or deep (800–3500m) (Clark et al., 2011). Many researchers consider seamounts as biodiversity hotspots (Rogers, 2019). Chlorophyll enhancement indicative of high primary production characterizes shallow seamounts that protrude to the photic zone (Leitner et al., 2020); this increased biomass may attract temporal or transient visitors such as commercial fishes, sharks, cetaceans, pinnipeds, and turtles that use seamounts for foraging, as spawning grounds, or as navigational waypoints (Morato et al., 2008; Rogers, 2019). Deeper seamounts (200–800 m) may trap vertically migrating zooplankton and nekton near the bottom, where fishes and invertebrates readily consume them (Pitcher et al., 2007; Clark et al., 2011). Fauna of deep (>800 m) seamounts normally benefit from the presence of hard substrate and enhanced hydrology.

Faunal composition of individual seamounts reflects historical and present-day processes and depends on many variables including water masses, concentration of dissolved oxygen, surface productivity and proximity to other seamounts, continental slope, and shelf habitats (Howell et al., 2010; Clark et al., 2011; Christiansen et al., 2015). Experts predict about 1426 seamounts in the North Atlantic based on 30 arc-sec bathymetry data, including 678 in Areas Beyond National Jurisdiction (Yesson et al., 2011). The best known seamount complexes and chains are the Great Meteor and Madeira-Tore seamount complexes in the Northeast Atlantic (Lima et al., 2020), and the New England and Corner Rise Seamounts in the Northwest Atlantic (Lapointe et al., 2020).

5.1.5. *Ridges*

The highly complex and dynamic geological systems of mid-ocean ridges form at the juncture of different tectonic plates, stretching 50,000–60,000 km across ocean basin floors (UNESCO, 2017). These prominent geological features can extend from shallow waters to bathyal depths, increasing environmental heterogeneity that significantly influences biological communities. They provide a wide range of habitats including fracture zones, small ridges, axial valleys, hills and seamounts (Harris et al., 2014; Alt et al., 2019). The presence of mid-ocean ridges affects ocean circulation, which can enhance biological productivity and subsequently influence the abundance and distribution patterns of various marine species (King et al., 2006; Bergstad et al., 2008). Additionally, mid-ocean ridges serve as hotspots of hydrothermal vents (see section 5.1.9), with the rift valleys of spreading ridges containing approximately 90 % of known or predicted hydrothermal vents (Harris et al., 2014). The productivity over mid-ocean ridges plays a crucial role in supporting diverse marine life.

The ongoing action of slow-spreading plate boundaries gives rise to the Mid-Atlantic Ridge, the largest mountain chain on Earth (Beaulieu et al., 2015). This volcanic mountain range runs ~16,000 km through the centre of the Atlantic Ocean from the Gakkel Ridge in the Arctic near Iceland in the north to the Bouvet Triple Junction in the Antarctic in the South. This review specifically focuses on the relatively well-studied MAR segment within the North Atlantic Ocean between the Reykjanes Ridge at 63.5°N and the Vema Fracture Zone at approximately 10° N.

The seafloor of the MAR in the North Atlantic spans thousands of meters of depth and encompasses varied seabed morphologies, providing an intricate patchwork of seafloor habitats. The ridge consists of an active slow-spreading centre and central rift valley, with its flanks largely consisting of sedimented gentle slopes and discontinuous plains (>95 %) alongside smaller areas of steeper hard substrate slopes (<5 %) (Niedzielski et al., 2013; Priede et al., 2013a, 2022; Harris et al., 2014). The northern region of the MAR contains 72 true seamounts with summit depths ranging 200–3000 m depth and nine major fracture zones (from South to North: Vema, Fifteen-Twenty, Kane, Atlantic, Hayes, Oceanographer, Pico, Kurchatov, Faraday, Charlie-Gibbs, and Bight). Additionally, it contains 25 visually confirmed active hydrothermal vent fields (described in section 5.1.8), alongside various smaller ridges, guyots, rift valleys, and canyons (Harris et al., 2014; InterRidge Database v3.4; GEBCO Undersea Feature Names Gazetteer). Sections 5.1.7-5.1.8 of this review discuss the biological communities associated with specific ridge features in more detail.

The majority of the northern MAR, particularly hard substrate on the ridge axis, lies within lower bathyal depths (800–3500 m depth) (Watling et al., 2013; Niedzielski et al., 2013). Most of the sedimented areas occur at abyssal depths (3500–6500 m), with a small proportion occurring at hadal depths (>6500 m) such as the Romanche Fracture Zone. The sedimented abyssal areas fall within the North Atlantic Abyssal Province, which also incorporates wider North Atlantic Ocean basins to the east and west (Watling et al., 2013).

Similar to other ocean ridges, the northern MAR is a prominent and complex topographic feature that alters ocean circulation, creating areas of high biomass over its summits and flanks (Priede et al., 2013b; Morato et al., 2021a). Several mechanisms contribute to the concentration of biomass over the northern MAR summits and flanks, including oceanic fronts (Scales et al., 2014; Morato et al., 2018a), topographical influences on water circulation (St Laurent and Thurnherr, 2007), and the subsequent upwelling of nutrient-rich deep water. The complex topography found in locations such as the Azores Triple Junction can lead to strong near-bed currents, which enhance the food supply for suspension-feeding cold-water corals and sponges (Mortensen et al., 2008; Braga-Henriques et al., 2013; Tempera et al., 2013; Morato et al., 2021a; Priede et al., 2022).

Predictive models propose that the MAR provides suitable habitat for a wide range of scleractinians and octocorals, with adjacent seamounts and continental slopes also offering suitable habitat for such corals, suggesting potential sharing of species among these seabed regions (Morato et al., 2020; Taranto et al., 2023). Indeed, MAR corals and anemones exhibit high affinities with wider Atlantic Ocean habitats (Molodtsova et al., 2008), as do hexactinellid sponges (Tabachnick and Collins, 2008) and demosponges (Cárdenas and Rapp, 2015). Amphi-Atlantic distributions characterize many of the species collected from the Reykjanes Ridge, encompassing multiple taxonomic groups such as Scleractinia, Cirripedia, Echinoidea, Asteroidea and Brachiopoda (Alt et al., 2013, 2019; Mironov and Gebruk, 2006).

North of the Azores, surface productivity above the MAR is high, supporting diverse assemblages of demersal fishes (Priede et al., 2022) and benthic invertebrates (Alt et al., 2019) on the ridge slopes. South of the Azores to the equator, productivity is much lower, and the benthic fauna is not well studied (Radziejewska et al., 2022).

The northern MAR contributes to multiple ecosystem services, largely through the provision of suitable habitat for specialized hydrothermal vent communities (see section 5.1.9) and taxonomic groups such as corals and sponges. Bioengineering corals and sponges provide three-dimensional habitat structure, increasing faunal biomass by three orders of magnitude (Henry and Roberts, 2007; Roberts et al., 2008; Beazley et al., 2013). These habitats provide key spawning, nursery, and feeding areas for fishes and invertebrates (Porteiro et al., 2013; Pham et al., 2015; Ashford et al., 2019). The calcium carbonate frameworks of deep-sea corals also provide key biogeochemical functions in the carbonate system and calcium balance (Moberg and Folke, 1999; Doney et al., 2009). The filtering action of sponges influences the microbial loop and benthic-pelagic coupling of carbon, alongside the nutrient cycles for phosphate, silicate, nitrate, nitrite, and ammonium (Yahel et al., 2007; Maldonado et al., 2012; Leys et al., 2018).

The European Union Horizon 2020 ATLAS project Vulnerable Marine Ecosystem (VME) database (Morato et al., 2018b), indicates a high probability of the northern MAR hosting VMEs, particularly in the Reykjanes Ridge and the Azores regions (Morato et al., 2021b). Not surprisingly, conservation prioritization approaches identified several areas within the northern MAR as priority locations for biodiversity conservation (Combes et al., 2021). These datasets also highlighted that the publicly available information about the MAR remains limited, particularly concerning patterns over space and time, biological connectivity, trophic relationships, broader ecosystem functions, and the impacts of anthropogenic activity (Weaver et al., 2019). Many existing studies suggest that we underestimate the biodiversity of the northern MAR, potentially as a consequence of under sampling the complex patchwork of MAR habitats. The better characterization of the section of the MAR between Iceland and the Azores compared with the area between the Azores and the Equator (Priede et al., 2022), reflects the focus of research projects such as MAR-ECO (Bergstad et al., 2008; Bergstad and Gebruk, 2008) and ECOMAR (Priede et al., 2013a). More recent European Union Horizon 2020 projects, such as ATLAS (Roberts and Morato, 2022), SponGES (Xavier et al., 2023), and iAtlantic (Roberts et al., 2023) have increased the knowledge base for the MAR, contributing to a more comprehensive understanding that extends beyond the section between Iceland and the Azores.

5.1.6. *Carbonate mounds*

Deep-water carbonate mounds occur in several forms, including mud mounds, plankton mounds, microbial mounds (Reijmer, 2021) but cold-water coral (CWC) carbonate mounds attract the most conservation interest, followed by those linked with hydrothermal and seeping processes.

CWC carbonate mounds are the most well known and are described by OSPAR as a “threatened and/or declining habitat” with the name “Carbonate Mounds” (OSPAR, 2010). Generally found at bathyal depths on continental shelves and shelf breaks, CWC carbonate mounds form raised ovoid topographic features tens to hundreds of meters high and across (Wheeler et al., 2007). Theories of mound genesis include a hydraulic theory associating hermatypic (=reef-building) corals and hydrocarbon seepage (Hovland, 1990), but more probably hydrodynamic conditions coupled with nutrient availability stimulate hermatypic coral build-up, trapping, and generating carbonate-rich sediments and lithified cements over hundreds or thousands of years with indications of glacial cycle influence (Roberts et al., 2006; Wheeler et al., 2007; Reijmer, 2021). Although CWC carbonate mounds occur globally, most mound provinces – sometimes containing tens of thousands of CWC carbonate mounds – have been discovered in the North Atlantic on the continental margins of Europe (Kenyon et al., 2003; Masson et al., 2003) and North America (Hebbeln et al., 2014; Gasbarro et al., 2022), likely reflecting bias in exploration and favorable environmental conditions (e.g. preservation of suitable oxy-thermal habitat and an especially deep aragonite saturation horizon) in these regions (Henriet et al., 2014; Hebbeln et al., 2016).

A variable and diverse array of substrates generally characterize CWC carbonate mounds as a result of the particular interplay of scleractinian coral framework - growth with hydrodynamic and sedimentary processes at each site (Huvenne et al., 2005). Consequently, the biodiversity associated with CWC carbonate mounds varies, also depending on whether mounds are still “active” or “retired” i.e. with or with few/no living hermatypic corals, respectively (Huvenne et al., 2005; Roberts et al., 2006). Active mounds generally host invertebrate communities associated with living and dead coral reef frameworks (section 5.1.7), whereas both active and retired mounds may host coral rubble and soft-sediment communities with hard-bottom communities present with exposed lithified cements or glacial dropstones and cobbles (Huvenne et al., 2005). Generally, mound habitats contain assemblages compositionally distinct from, and up to three times more speciose than, off-mound habitats, with highest diversity typically in the coral rubble or dead framework communities (Henry and Roberts, 2017). Active CWC mounds may also host demersal fish assemblages distinct from off-mound areas (Ross and Quattrini, 2009). However, sediment deposition, slow dissolution and burial of coral framework, rubble, and other hard substrates on retired mounds make them progressively less diverse over time (Huvenne et al., 2005; Hennige et al., 2020).

In terms of ecosystem services, CWC carbonate mounds provide limited provisioning services (e.g. aggregating some commercial species, occasionally providing precious corals for jewellery), but have strong regulating and supporting services in the form of carbon capture, enhanced carbon/nitrogen cycling, and habitat provisioning, as well as increasing value both intrinsically and especially for education and research (Armstrong et al., 2014; De Clippele et al., 2021).

Carbonate mounds can also refer to those generated by authigenic processes such as hydrothermal venting or methane seeping (Lein et al., 2007). Hydrothermal examples, such as the Lost City Hydrothermal Field on the Atlantis Massif 15 km west of the Mid-Atlantic Ridge (Kelley et al., 2001; Ludwig et al., 2006) are formed by exothermic chemical reactions between sea water and mantle rocks (serpentinization). These are different from the well-known black smoker hydrothermal sites (section 5.1.9), occurring off-axis from mid-ocean ridges, with cooler and more alkaline vent fluids interacting with calcium rich mantle rocks (Kelley et al., 2001). At the Lost City the carbonate structures range from delicate precipitates to flanges and 60-m tall chimneys (Ludwig et al., 2006). Associated life forms include diverse microbial life, along with typical background megafauna, with less indication of obligate megafaunal life linked with the venting environment (Kelley et al., 2001). Such hydrothermal carbonate structures are hypothesised to be relatively common in large parts of the off-axis MAR, but relatively few have been discovered so far. Methane seeps (section 5.1.10) can also generate carbonate slabs, nodules, pavements, and mounds, which again may host background megafauna, but are found to have distinct and diverse microbial communities (Case et al., 2015).

These authigenic carbonate mounds contribute to biogeochemical cycles, create habitats, and may host unique marine genetic resources in their microbial communities, suggesting at a minimum the presence of provisioning, regulating, and supporting ecosystem services.

5.1.7. *Cold-water coral ecosystems*

Biogenic beds refer to raised habitats that clearly differ from surrounding substrate, such as cold-water corals or sponge beds. The occurrence of “cold water” at shallow polar depths as well as in the deep sea complicates any simple definition of cold-water coral habitat. Furthermore, some corals considered “cold water” taxonomically also occur in warm water in some regions of the world (e.g., some Red Sea corals live in 22 °C water at 200 m depth (Roder et al., 2013). A growing consensus of researchers describe cold water corals as “all corals that do not harvest light (azooxanthellate) or are facultatively zooxanthellate (e.g., *Oculina varicosa*), indicating the absence of symbiotic dinoflagellates commonly found in "shallow" (less than 200 m) and "warm" (above 12 °C) water corals” (Liu et al., 2024). This definition covers deep/cold-water corals and excludes the majority of warm-water corals that occur in depths shallower than 30 m.

With the above definition in mind, CWCs form and contribute to multiple habitat types - both on hard and soft substrates. For examples, see Fig. 9. CWC reefs form complex, three-dimensional structures with an abundance of spatial niches and thus associated fauna (Rogers, 1999; Freiwald et al., 2004). Relatively few species comprise the cold-water

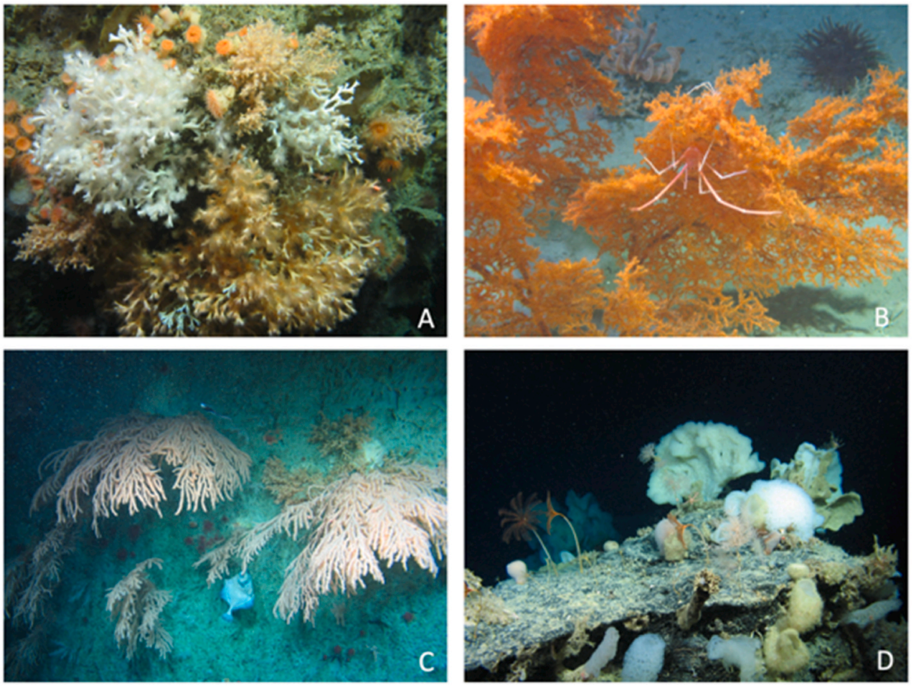


Fig. 9. Examples of benthic habitats – cold-water coral ecosystems and sponge aggregations – of the deep North Atlantic. A) Cold water coral assemblage dominated by two colour morphs of *Desmophyllum pertusum*, 750 m depth, Whittard Canyon, Ireland B) Black coral *Leiopathes* sp. hosting a chirostylid associate, 1052 m depth, Whittard Canyon, Ireland C) Octocoral assemblage on near vertical wall including primnoids and keratoisidids (bamboo corals), 1778 m, Whittard Canyon, Ireland D) Sponge assemblage, 2175 m depth, Porcupine slope, Ireland. All photos taken by ROV Holland I deployed from RV Celtic Explorer, copyright Marine Institute. A, B, expedition CE16009; C, CE23010; D, CE18012.

coral reef habitat across the Northeast Atlantic, primarily *Desmophyllum pertusum* (formerly *Lophelia pertusa*), *Solenosmilia variabilis*, and *Madrepora* sp. These reef structures occur relatively commonly on continental shelves, seamounts, and canyons of the Northeast Atlantic (Freiwald et al., 2004). The CWC reef structures that commonly occur on carbonate mounds (section 5.1.3) are relatively well-studied (e.g. Lo Iacono et al., 2018). CWCs also form major components of other habitats; mainly coral gardens and mixed coral and sponge (see section 5.1.8) garden habitats. Henry and Roberts (2014) separated CWC in UK waters into five habitats: soft-bottom bamboo coral, cup coral, lace coral, black coral, and gorgonian coral gardens; the latter occur on hard, e.g. soft coral gardens off Greenland (Long et al., 2020), and soft sediments, e.g. Canadian *Acanella* fields (Gass and Willison, 2005). In many mixed coral gardens, characterizing species are not identified to species level reflecting not only the difficulty in identifying coral taxa from image data, but also the numerous undescribed species, widespread homoplasy among characters, and the poor quality of early descriptions coupled with lost type material (Pérez et al., 2016). Sea pen fields also occur in the North Atlantic (Baker et al., 2012; Kenchington, 2014) and may be dominated by one of several species (e.g., Morrissey et al., 2023).

In terms of ecosystem services, researchers widely recognize CWC reefs as "ecosystem engineers" that maintain and enhance biodiversity (Roberts and Cairns, 2014). They provide food for many organisms; most famously seastars prey upon CWC (Bo et al., 2019). They provide habitat for 1000s of animal species (Freiwald et al., 2004; Schwentner and Lörz, 2021), including many relevant to fisheries (Costello et al., 2005; Edinger et al., 2007), and a nursery for fish larvae (Baillon et al., 2012). Numerous studies have reported enhanced diversity and abundance of fish around CWC reefs and gardens compared with surrounding areas (Fosså et al., 2002; Henderson et al., 2020) linked to the secondary productivity they create.

The precise role of CWC in carbon sequestration has been hard to define. If the UN delineation for sequestration is followed, with sequestration being the removal of carbon from the cycle for over 100 years, then the many aged CWC (Prouty et al., 2017) hard skeletal taxa clearly play a role; corals lacking hard skeletal parts are likely to be part of microbial recycling at death (Barnes et al., 2021). Models of a species of cold-water octocoral, and the broad diversity of organisms found in these complex habitats, have suggested they contribute towards carbon cycling and carbon sequestration (Alaskan study of the octocoral *Primnoa*; Alexander, 2022). The relatively common nature of CWC across the Northeast Atlantic, especially in waters shallower than 200 m, could indicate a substantial role in carbon sequestration.

Corals are rich in biologically active marine natural products (Rocha et al., 2011; Leal et al., 2012; Soldatou and Baker, 2017; Avalon et al., 2022; Welsch et al., 2022, 2023; Olsen et al., 2024; Afoullouss et al., 2024). Given that most coral diversity occurs in deeper waters (Roberts et al., 2009), this diversity remains an untapped resource in CWC, not only for coral research but also for studying other organisms that inhabit these environments.

Despite ongoing exploration, the field of functional services provided by CWCs remains preliminary with regular new discoveries. For instance, symbiotic nitrogen fixation occurs in CWCs (Middelburg et al., 2016), highlighting their significance. In addition, CWC skeletons provide excellent climate records that have helped understand historical ocean conditions of the north Atlantic (de Carvalho Ferreira et al., 2022).

As with many deep-sea ecosystems, fisheries gears that interact with the seafloor have impacted CWCs. For example, in the Corner Rise seamounts in the NW Atlantic (Waller et al., 2007) no recovery of coral communities occurred over a multi-decadal time scale; a common outcome in studies globally. The longevity of many CWCs likely contributes to prolonged recovery times.

5.1.8. *Sponge aggregations*

Marine sponges form a variety of structurally complex habitats that can cover vast expanses of the deep seafloor. Referred to as sponge grounds, sponge aggregations, sponge gardens or sponge reefs, these habitats are characterized by their richness of structure and community composition, by the variety of geomorphological features on which they are found, and, in the North Atlantic by their spatial extent in terms of latitudinal, longitudinal and bathymetric range (Maldonado et al., 2016; Xavier et al., 2023). For examples, see Figs. 8A and 9D.

Sponge aggregations occur predominantly at upper bathyal depths along continental margins within national jurisdictions, but they also occur deeper on mid-ocean ridges and offshore seamounts in areas beyond national jurisdictions. For instance, multispecific sponge grounds known as "Ostur" (= cheese bottoms) dominated by large-sized tetractinellid sponges (genera *Geodia*, *Stelletta*, *Stryphnus* within class Demospongiae) occur around the Faroe Islands, Norway, Sweden, parts of the western Barents Sea and South of Iceland, extending to the Northwest Atlantic along the Labrador and Newfoundland shelves (including the Grand Banks), and the Davis Strait (Klitgaard and Tendal, 2004; Kutti et al., 2013; Murillo et al., 2018). At lower latitudes, "monospecific" aggregations of hexactinellids occur more commonly. For example, the birds' nest sponge *Pheronema carpenteri* forms dense and extensive aggregrations at 300–2000 m depth along the European and West African margins, from the Porcupine Seabight to the continental slope off Morocco (Rice et al., 1990; Barthel et al., 1996), as well as in the Azores archipelago (Topsent, 1904; Creemers et al., 2018); aggregations of *Poliopogon amadou* are found below 2500 m depth on several Northeast Atlantic seamounts (Xavier et al., 2015; Ramiro-Sánchez et al., 2019; Scepanski et al., 2024); and aggregations of *Vazella pourtalesii*, known as the Russian Hat sponge, occupy a vast area on the Scotian shelf (Eastern Canada) between 75 and 275 m depth (Fuller, 2011; Beazley et al., 2018). Large aggregations of tetractinellid sponges (within the genera *Geodia* and *Stelletta*) have also been reported between 1000 and 2000 m depth on various diapiric structures of the southern Barbados accretionary prism and hypothesised to depend on chemosynthetic production (Jollivet et al., 1990; Olu et al., 1996).

Despite an incomplete understanding of the environmental drivers of sponge species and habitat distribution, studies to date show that factors such as bottom temperature, salinity, and dissolved oxygen, characteristic of particular water masses, are good predictors of models of habitat suitability (Howell et al., 2016; Graves et al., 2022). Some of these factors change under climate change scenarios, raising concerns of potential shifts in (or loss of) the core distributions of these habitats (Beazley et al., 2021; Gregório et al., 2024).

Researchers increasingly recognize the key role of sponge aggregations in the functioning of the deep-sea realm, delivering numerous supporting, regulating, and provisioning goods and services (Table 3). Sponge grounds locally enhance the biodiversity and abundance of epibenthic fauna (Beazley et al., 2015; Hawkes et al., 2019; Lörz et al., 2024), providing habitat and nursery for many demersal fishes including commercial species (e.g. Kenchington et al., 2013; Meyer et al., 2019). Through efficient metabolic pathways, sponges recycle major biogeochemical elements (carbon, nitrogen, silica), and transfer nutrients to higher trophic levels along the food web (Cathalot et al., 2015; Bart et al., 2021; Maldonado et al., 2021). Furthermore, sponges provide prime sources of bioactive compounds, as well as biomaterials (biosilica, collagen) of great potential for human health applications, for instance in the development of new pharmaceuticals (e.g. antibiotics, antivirals; see Calado et al., 2022) as well as tissue engineering solutions (Kaya et al., 2021; Martins et al., 2021).

5.1.9. Hydrothermal vents

The North Atlantic and Caribbean region supports 28 known active and visually confirmed deep-sea (>200 m depth) hydrothermal vent fields (24 sites recorded in version 3.4 of the InterRidge Vents Database, Beaulieu and Szafranski, 2020; one site discovered in 2020, Saskia Brix pers. comm.; three sites discovered in March 2023, Joan Alfaro pers. comm.). Nineteen of those vent fields occur on segments of the Mid-Atlantic Ridge south of the Azores (Boschen-Rose and Colaço, 2021), where they range in depth from 865 m (Menez Gwen, 37.84°N) to 4200 m (Ashadze-1, 12.97°N). Three visually confirmed vent fields occur on the mid-ocean ridge north of the Azores: at Moytirra (45.48°N, 2900 m) on the Mid-Atlantic Ridge; and the IceAGE (60.23°N, 642 m) and Steinaholl (63.10°N, 350 m) sites on the Reykjanes Ridge. The Caribbean region contains three further active deep-sea hydrothermal vent fields confirmed visually; two occur on the Mid-Cayman Spreading Centre (Beebe, 4980 m; and Von Damm, 2300 m) and one on the Kick 'Em Jenny submarine volcano (250 m depth) in the Lesser Antilles Arc (Connelly et al., 2012; Carey et al., 2014, 2016).

North Atlantic vent fields (Fig. 10) occur in a variety of geological settings, including basaltic- and ultramafic-hosted sites in the walls or median valley of the mid-ocean ridge, on ridge-associated seamounts, and in ridge fracture zones. Geological setting may influence the geochemistry of vent fluids, with ultramafic-hosted sites producing fluids richer in H_2 and CH_4 than basaltic-hosted sites (Charlou et al., 2010), and alkaline venting occurring at the off-axis Lost City vent field (Kelley et al., 2001).

Global analyses of species at the genus level presence/absence data at hydrothermal vents recognizes a single North Atlantic biogeographic province for vent-endemic fauna in (e.g. Bachraty et al., 2009; Moalic et al., 2012; Rogers et al., 2012), while at the species level, two biogeographic provinces exist (Ramirez-Llodra et al., 2007). Within the regional species pool of that province, however, occurrences and abundances of taxa recorded at individual vent fields vary. Some abundant species at one vent field, for example, may be rare or absent at other vent fields, and this variation may result from community assembly processes not yet understood at North Atlantic hydrothermal vents. Sites studied over several decades show stability in hydrothermal activity and community composition (e.g. Copley et al., 2007; Cuvelier et al., 2011), but early stages of succession remain unknown for faunal assemblages at hydrothermal vents on the Mid-Atlantic Ridge. Basic biological knowledge remains unknown for most vent species, such as life history (age of first reproduction, growth rate, longevity, fecundity, planktonic larval duration, frequency, and seasonality of reproduction among other aspects) (Van Dover et al., 2001; Colaço, pers. comm.).

In terms of ecosystem services, deep-sea hydrothermal vents provide provisioning, regulating, supporting, and cultural services. They contribute to biogeochemical cycles, some mediated by chemosynthetic microbes, carbon cycling through microbial CO_2 fixation, biomimicry, marine genetic resources, habitat creation, feeding grounds, and productivity source, to name just a few (DOSI, 2023).

5.1.10. Cold seeps

Cold seeps are distributed globally along both active and passive margins (Sibuet and Olu-Le Roy, 2002). They are associated with multiple seafloor structures including mud volcanoes and diapirs, pockmarks, carbonate mounds, chimneys, crusts and plates, brine pools, and oil and gas vents (Ceramicola et al., 2018). Although they can develop in various geological settings, cold seeps primarily thrive as a result of abundant sub-seafloor methane or other hydrocarbons. As methane percolates through sediments, it undergoes anaerobic oxidation by microbial consortia capable of simultaneously reducing sulphate, leading to the creation of hydrogen sulphide (Boetius et al., 2000; Niemann et al., 2006). As well as producing reduced compounds, the microbes release carbonate that precipitates into solid substrates that allow colonization of a wide variety of taxa, including commercially important species (Turner et al., 2020b). As a result, cold seeps exert widespread influence in the deep sea, in that background (non-seep) fauna use them for habitat (e.g. Cordes et al., 2008), food (MacAvoy et al., 2002; Olu et al., 2009; Niemann et al., 2013; Seabrook et al., 2019), or as nursery grounds (Sen et al., 2019).

Ventura-Costa (2022) compiled the known spatial distribution of seeps worldwide and identified 73 structures in the North Atlantic basin, in both the eastern and western margin, distributed in seven geographical areas: Norwegian margin, Hatton-Rockall basin, Gulf of Cádiz, US Atlantic margin, Gulf of Mexico, Caribbean Sea off Grenada,

Fig. 10. Examples of habitats and fauna on hydrothermal vents. A) Hydrothermal chimneys, and B) *Rimicaris hybisae* shrimps and *Maractis* sp. anemones at Beebe Vent Field, depth 4955–4960 m on the Mid-Cayman Spreading Centre, Caribbean Sea (credit: University of Southampton, UK). C) *Bathymodiolus azoricus* mussels at the Lucky Strike hydrothermal vent field, depth 1700 m D) *Rimicaris exoculata* shrimp at the Rainbow hydrothermal vent field, depth 2300 m (credits C and D: Missão Seahma, 2002 (FCT, Portugal *PDCTM*, 1999MAR15281).

and Barbados Accretionary Prism off Trinidad and Tobago, Barbados, and Venezuela, ranging from approximately 300 to 5000 m depth. However, much more widespread seepage likely occurs along continental margins than currently documented (Skarke et al., 2014). Upper abyssal seeps in the SW Gulf of Mexico co-occur with asphalt outflow (vulcanism) and their composition and crystalline structure suggest a temperature and origin of the source fluids with seepage of liquid oil through "supercritical water" (Hovland et al., 2005). Globally, distance between geographic areas does not seem to be the main factor structuring cold seep communities (Ventura-Costa, 2022) and a high level of dissimilarity at the species level characterizes communities from different cold seeps in the North Atlantic. Similar results have been found in regional studies that suggested that seep communities are strongly structured by depth and exhibit horizontal zonation (Olu et al., 2010; Amon et al., 2017; Bourque et al., 2017). Meanwhile, molecular data suggest high potential gene flow between sites (DeLeo et al., 2022). However, and despite the scientific, economic and conservation value of cold seeps, which have been listed as Vulnerable Marine Ecosystems (FAO, 2009), fundamental knowledge on biodiversity and biogeography patterns remains elusive.

5.1.11. *Asphalt volcanoes*

Although methane seepage drives most marine hydrocarbon seeps (Suess, 2014), some studies clearly document seepage of heavier hydrocarbons, particularly crude oil (Kennicutt, 2017). Seepage of viscous heavy hydrocarbons such as tar or asphalt also occurs. Heavy hydrocarbon seeps typically occur as irregular mats and pools of viscous tar and have been described from coastal areas (Hornafius et al., 1999), the continental slope (MacDonald et al., 2003), and associated with oil seeps (MacDonald et al., 2004). However, asphalt seepage can lead to asphalt volcanos and larger formations of solidified asphalt on the seafloor (Jones et al., 2014a).

Although natural seepage introduces an estimated 140,000 tonnes of oil per year in the Gulf of Mexico alone (Kennicutt, 2017), the prevalence of asphalt mounds in the North Atlantic remains unknown. All known North Atlantic asphalt mounds occur in the Gulf of Mexico (France et al., 2019; Hsu et al., 2021), although mounds have been discovered in the South Atlantic off Angola (Jones et al., 2014a) and Brazil (Fujikura et al., 2017). The best-studied asphalt mounds occur at the Campeche Knolls (MacDonald et al., 2004) in the Gulf of Mexico. These mounds consist of extensive lava-like deposits of solidified asphalt that have emerged from near the crest of a salt dome. The asphalt mounds investigated comprise non-chemosynthetic assemblages of epifauna that live either on solidified asphalt or authigenic carbonate that has asphalt inclusions, and sometimes chemosynthetic assemblages, which may include tubeworms (cf. *Lamellibrachia* sp.), mussels (cf. *Bathymodiolus* sp.) and clams (*Solemya* sp.), likely driven by microbial oxidation of hydrocarbons (MacDonald et al., 2004). Lower bathyal and abyssal asphalt seeps apparently do not host an endemic fauna distinct from other chemosynthetic or heterotrophic communities (Jones et al., 2014a; Sahling et al., 2016; Macdonald et al., 2020). At present, the ecosystem services provided by these habitats are unknown, and the ecological importance of these asphalt seeps remains a key knowledge gap. Many other key knowledge gaps include the broad-scale distribution of these features, their role in enhancing biodiversity and community structure, and their long-term dynamics.

5.1.12. *Organic falls*

Organic falls are ephemeral habitats created when nutrient-rich material sinks to the nutrient-poor deep-sea floor. Wood falls and cetacean falls dominate this resource, however, algal falls, fish falls and other food falls, also contribute to this category. Deep-sea whale and wood falls harbour species-rich ecosystems that are partially dependent on hydrogen sulphide (H_2S) from the decay of bones and wood (Kiel, 2011). The fauna hosted by these ecosystems show affinities with other chemosynthetic environments such as hydrothermal vents and cold seeps (Bernardino et al., 2010). These affinities led to the hypothesis that cetacean falls and wood falls provide evolutionary or dispersal 'stepping stones', allowing certain deep-sea species to move between specific, physically unconnected habitats over space and time (e.g. Smith et al., 1989; Lorion et al., 2009; Bernardino et al., 2010; Breusing et al., 2016; Pereira et al., 2022). Nonetheless, the communities that inhabit these habitats often differ from one another with some species specific to a given habitat (e.g., Tunnicliffe, 1991).

Given the limited spatial and temporal extent of these patchy, transient habitats, discovery rates remain low and depend on occasional serendipitous observations based on imagery or recoveries as by-catch in trawls (Romano et al., 2020; Silva et al., 2021). To date, no published studies have documented natural cetacean falls in the North Atlantic, with just one record of a decaying whale bone obtained in a trawl off SW Iceland (Warén, 1996). Shipwrecks and wood transported to the ocean by rivers account for most natural wood falls (Wohl and Iskin, 2021). Similarly, few studies document natural food falls (Higgs et al., 2014). In order to advance scientific knowledge, researchers have deployed parcels of organic material in various shapes and sizes at sites across the North Atlantic Ocean (Turner, 1955, 2002; Tyler et al., 2007; Gaudron et al., 2010, Cunha et al., 2013, Cuvelier et al., 2014, Zeppilli et al., 2015, Amon et al., 2015; Plum et al., 2017, Romano et al., 2020, Alfaro-Lucas et al., 2020), including cetacean carcasses on the Porcupine Abyssal Plain (Jones et al., 1998), off Sweden (Dahlgren et al., 2006), on the MAR, southeast of Faial (Silva et al., 2021), and cow carcasses in the Sétubal Canyon (Hilário et al., 2015a).

5.1.13. Abyssal plains

Abyssal plains occur at depths of 3–6 km (Gage and Tyler, 1991), and comprise the most widespread environment on Earth (~58 % Earth's surface). Abyssal plains in the North Atlantic (including constituent abyssal hills and mountains) cover some 33.7 million km^2 or approximately 75 % of the mapped seabed area (Harris et al., 2014), and include the Porcupine Abyssal Plain west-southwest of Ireland (Hartman et al., 2021), the Madeira Abyssal Plain (Thurston et al., 1998) and the Hatteras Abyssal Plain (Mazzullo et al., 1982). The North Atlantic abyssal province includes all areas north of the equator under the influence of North Atlantic Deep Water (UNESCO, 2009). The biogeographic scheme based on the deep basin(s) in which they occur is modified from Menzies et al. (1973) and Vinogradova (1997) and based on newer data.

Fine sediments dominate these generally flat seafloor environments, interspersed with areas of rock, particularly associated with topographic features, such as knolls (<1000 m high features), seamounts (>1000 m high), fracture zones, and valleys. Given the complete absence of light, abyssal plains rely largely on the flux of organic material from the surface ocean to drive production, but increasing evidence shows that chemosynthesis provides an additional contribution (e.g. Molari et al., 2013), above and beyond the seeps and vents that occur in the abyss (Connelly et al., 2012). Despite this input, the extreme oligotrophy of the abyss and lack of food result in generally low biomass and abundance of benthos (Wei et al., 2010). Paradoxically, abyssal plains support relatively high species richness (Snelgrove and Smith, 2002). Deposit feeders dominate abyssal plain food webs, including megafaunal holothurians (e.g. Durden et al., 2020) and macrofaunal polychaetes (e.g. Laguionie-Marchais et al., 2013). Some evidence suggests generally more cosmopolitan distributions for abyssal species than their shallower counterparts (Glover et al., 2001; Lambshead and Boucher, 2003). Abyssal plains share the same ecosystem functions and services as other deep-ocean environments (e.g. Thurber et al., 2014). Some key knowledge gaps in abyssal plain science include broad-scale spatial and long-term temporal patterns, biodiversity assembly processes, ecosystem dynamics, life-history processes, connectivity, microbial ecology and the effects of anthropogenic impacts.

5.1.14. Hadal trenches

Hadal trenches represent the deepest regions of the ocean, located within the hadal zone, and they cover the deepest 45 % of the global ocean floor (Jamieson et al., 2010). These trenches provide distinct habitats that support unique biological communities, many of which differ significantly from those in the adjacent abyssal zones, and include numerous species new to science (Kaiser et al., 2023). The significant logistical and technological hurdles in studying these deep-sea environments results in the hadal zone remaining one of the least explored and understood areas of marine biodiversity. In the North Atlantic Ocean, a few trenches exist. The only three considered are the Puerto Rico Trench and Cayman Trough, both considered true hadal environments with depths greater than 6000 m, and Kings Trough, a non-hadal feature reaching depths up to 4500 m at its deepest point. Most available data were collected from the only "true trench", the Puerto Rico trench, in contrast to an absence of faunal data for the Caiman and Kings Trough. This contrast underscores real sampling gaps in the deepest areas of the North Atlantic, despite the importance of trenches as significant geomorphological barriers to dispersal and gene flow (e.g. Weston et al., 2022 for Pacific trenches).

The Puerto Rico Trench (PRT), located north of Puerto Rico and the Virgin Islands, marks the northeastern boundary between the Atlantic and Caribbean (Riehl et al., 2020). It is the only subduction zone in the North Atlantic Ocean, formed by the subduction of the North American plate beneath the Caribbean plate (Ten Brink et al., 2004). With depths exceeding 8500 m, the PRT is the deepest part of the Atlantic Ocean (Jamieson, 2015). This trench forms an arc, extending approximately 100 km north of the eastern coast of Hispaniola eastward to about 63°W, and then curving southeast to approximately 17°30′N, 59°30′W (Monroe, 1968; Riehl et al., 2018).

Extensive mapping efforts in the PRT, aimed at understanding tectonic activities for coastal risk assessment, have revealed sediment accumulation within the V-shaped trench (Ten Brink et al., 2004; Jamieson, 2015; Devey et al., 2018). The Vema-TRANSIT expedition aboard RV Sonne provided detailed mapping of the PRT basin, which extends beyond 8000 m north of the Caribbean arc (Devey et al., 2018). Samples collected from the deepest parts of the trench revealed a sedimentary composition dominated by silt and clay (98 %), with a remarkably flat, sediment-covered seafloor (Devey et al., 2018). The nutrient-poor sediments support a low-density benthic fauna in some areas but species richness comparable to adjacent abyssal plains (Tietjen et al., 1989; Richardson et al., 1995). The Vema-TRANSIT expedition significantly expanded knowledge on the PRT's fauna (Brandt et al., 2018a, 2018b). Although the Galathea expedition described species from the PRT in the mid-20th century (Wolff, 1956, 1962), only 38 species of invertebrate macrofauna were known from the PRT until recently (A. Brandt, pers. comm.). Brandt et al. (2018b) identified five major macrofaunal groups (phylum/class), compared to 14 in the neighboring abyssal plains of the Vema-Fracture Zone, with the highest density recorded at 2313 individuals per 1000 square meters. HOV dives and photo lander deployments in 2019 found that the benthic mobile megafauna is dominated by holothurians. Contrary to the report from bathyscaphe dives by Pérès (1965), there was no evidence of endemic snail fishes (Liparidae), usually found in hadal trenches elsewhere in the world (Jamieson et al., 2020).

5.1.15. Mesopelagic

The mesopelagic zone globally comprises c. 20 % of the oceans' volume (Proud et al., 2017), and represents those depths that receive c. 0–1 % of downwelling solar light (i.e., insufficient solar light for photosynthesis but enough for vision; Sutton, 2013). Scientists typically define the mesopelagic zone as the pelagic habitat occurring between 200 and 1000 m, but although we often discuss the mesopelagic (and bathypelagic) zones as discrete entities, these systems connect strongly with deeper waters below and with the epipelagic realm above through numerous physical, chemical, and biological processes. These connections include migratory behaviors, e.g., diel vertical migration (DVM), displayed by myriad oceanic taxa, including large meso- and bathypelagic predators (Braun et al., 2023) and noting the important distinction, between migrant (mostly myctophid fishes, krill, gelatinous and cephalopods) and non-migrant fishes (mostly *Cyclothone* spp.) that create separate deep scattering layers with distinct links to the environment (Peña et al., 2021; Peña and Velez-Belchi, 2023).

Although relatively understudied in comparison to other marine ecosystems (e.g., Webb et al., 2010), a recent study proposed a global biogeography for the mesopelagic realm. Sutton et al. (2017) defined three mesopelagic "ecoregions'' within the North Atlantic (Northwest Atlantic Subarctic, North Atlantic Drift, and Central North Atlantic), based largely on trawl surveys in the basin for micronekton (fishes and crustaceans) (Judkins and Haedrich, 2018). Based on previous studies, they assigned the Mediterranean Sea and Gulf of Mexico (but not the Caribbean Sea) to distinct ecoregions within this scheme, noting distinctive faunas compared to adjacent Atlantic ecoregions (e.g., Bangma and Haedrich, 2008; Judkins and Haedrich, 2018). Across the Atlantic, multiple studies link variation in horizontal and vertical faunal distributions to ambient light levels (Kaartvedt et al., 1996; Frank and Widder, 2002; Olivar et al., 2012; García-Seoane et al., 2020), oxygen concentrations (typically associated with tropical oxygen minimum zones; e.g., Hauss et al., 2016), and water temperatures (Peña et al., 2014; García-Seoane et al., 2023). At finer scales, changes in the biomass and taxonomic composition of mesopelagic fauna underlying mesoscale eddies in surface waters may serve as vectors for faunal transport (e.g., The Ring Group, 1981; Devine et al., 2021).

Mesopelagic ecosystems provide many goods and services (Hoagland et al., 2019), but most recent scientific interest has focused on the roles that mesopelagic species play in the active transport and remineralization of carbon (Sarmiento-Lezcano et al., 2022a, 2022b), and on the potential development of mesopelagic fisheries (Schadeberg et al., 2023). DVM fauna can contribute significantly to the active biological carbon pump (e.g., Saba et al., 2021), but estimates of their contributions remain poorly constrained (Hoagland et al., 2019; Saba et al., 2021). Recent studies suggesting that the biomass of mesopelagic fishes may have been historically underestimated by up to an order of magnitude due to discrepancies between trawl-based and acoustic estimates (Kaartvedt et al., 2012; Irigoien et al., 2014) help drive this interest. Pelagic microcrustaceans (e.g., decapod shrimps) and molluscs (e.g., squids, Vereshchaka et al., 2019; Judkins and Vecchione, 2020) almost certainly reflect historical underestimates, however, large biases from acoustic estimates could derive from species allocation to acoustic echotraces and unknown parameters in acoustic models (Davison et al., 2015).

Despite the public availability of scattered datasets (Olivar et al., 2012; Irigoien et al., 2014; Kunnath and Kloser, 2018; Sarmiento-Lezcano et al., 2023), mesopelagic ecosystems represent one of the largest data gaps within the marine realm (Webb et al., 2010; St John et al., 2016). The wide dispersion of mesopelagic fauna, their sensitivity to sampling gears (Kaartvedt et al., 2012; Irigoien et al., 2014), and the enormous volume of habitable space in the mesopelagic realm make this zone particularly difficult to study in detail, despite increasing anthropogenic threats to the biome ranging from climate change impacts (Levin et al., 2019) to pollution from oil and gas exploitation (Sutton et al., 2022) and microplastics (Lusher et al., 2016).

5.1.16. *Bathypelagic*

The bathypelagic zone globally comprises c. 60 % of the oceans' volume (Wiebe et al., 2010), and encompasses the largest inhabitable living volume on Earth. The bathypelagic zone includes those ocean depths that receive no solar light, typically defined as all waters below 1000 m (Sutton, 2013) and extending to the abyssopelagic zone (>4000 m). Despite its vast size, the bathypelagic zone of the global ocean represents a major knowledge gap in marine biodiversity, characterized by chronic understudy compared to shallower environments (Webb et al., 2010). Bathypelagic fauna comprise a diversity of fishes (e.g., anglerfishes, tubeshoulders, and the ubiquitous and most abundant *Cyclothone* spp.), crustaceans (e.g., Vereschaka et al., 2016), cephalopods (e.g., Vecchione and Pohle, 2002; Vecchione et al., 2010), and other invertebrates (e.g., chaetognaths, polychaetes, pelagic holothuroids). Likely highly diverse, but poorly known, gelatinous zooplankton represent a vital component of food webs at these depths. The few studies conducted on bathypelagic fauna suggest correlations between surface ocean primary productivity and bathypelagic zooplankton biomass (Vereshchaka et al., 2016; Hernández-León et al., 2020), and a larger bathypelagic biomass than expected (Vereshchaka et al., 2016). Although the primary deep scattering layer (DSL) occurs in mesopelagic depths, increasing evidence suggests deeper DSLs occur within the upper bathypelagic zone, although integration apparently depends on species that only migrate seasonally (Van Haren, 2007; Peña et al., 2021). However, regressed swimbladders in these species result in a reduced echo signal (Peña et al., 2023; Sarmiento-Lezcano et al., 2023) that complicates acoustic visualization and transformation of acoustic data into biomass. A broadly distributed fauna of bathypelagic fishes around the Mid-Atlantic ridge contribute to a biomass maximum between 1500 and 2300 m depth, and little biogeographic variation in the region (extending from Azores to Iceland; Sutton et al., 2008). Little-studied ecosystem goods and services likely include important biogeochemical pathways (Hernández-León et al., 2020; Sarmiento-Lezcano et al., 2022b), and substantial undiscovered biodiversity (Sutton et al., 2010; Webb et al., 2010).

5.1.17. *Abyssopelagic*

The abyssopelagic zone spans 4000–6000 m depth, and, by volume, covers around 19 % of the global ocean (Wiebe et al., 2010). This environment fully lacks sunlight, with limiting food availability; high pressure and stable temperatures (2–3 °C) also characterize the abyssopelagic zone. Given the stability of the environment, narrow physiological tolerances likely characterize many species (Robison, 2009). Observations from other oceans show slow metabolisms and low oxygen consumption levels in many abyssopelagic animals related to predator-prey interactions (Robison, 2004). The lack of visual cues in these interactions in a lightless habitat have reduced a need for locomotory capabilities, resulting in low metabolic rates (Childress, 1995; Seibel et al., 1997, 2000). Species living in this zone are often blind or have primitive eyes. Animals in the abyssopelagic zone depend either directly or indirectly (via trophic interactions) on sinking marine snow (food and other particles; Robison, 2009). Few studies have focussed on the abyssopelagic zone in the Atlantic Ocean (Webb et al., 2010). OBIS includes few records for the North Atlantic abyssopelagic zone, covering copepods, a cephalopod, a gastropod, and fishes. Copepods may dominate the zooplankton in abyssopelagic waters, especially at 100 to 15 m above bottom (Christiansen et al., 2010). Within this layer, zooplankton abundance and biomass change little (Christiansen et al., 1999, 2010). Necrophagous amphipods can also occur in this bottom layer or sometimes higher in the water column (e.g., 1200 mab; Thurston, 1990). This lifestyle may reflect an alternative feeding mode from carnivory that depends on food availability (Thurston, 1990). New techniques, including barcoding, can potentially fast-track species discovery in this, and other, pelagic zones, as demonstrated by Bucklin et al. (2010b).

5.1.18. *Hadopelagic*

The hadal zone, which spans 6500–11,000 m depth (Watling et al., 2013), constitutes only 0.21 % of total ocean area and 0.01 % of the ocean volume, while encompassing 45 % of the entire ocean depth range (Wiebe et al., 2010; Jamieson, 2015). This pelagic habitat occurs in trenches and troughs, as detailed in Section 5.1.14 (Trenches). Enclosed trench topography characterizes the hadopelagic zone, reducing the extent of hadopelagic habitats with increasing depth. Challenging conditions, including immense hydrostatic pressure, near-freezing temperatures, geological instability leading to frequent subduction-zone earthquakes, and low food supply make the hadal zone one of the most extreme marine environments (Jamieson, 2015). Du et al. (2021) describe how hydration of the incoming plate, subsequent dehydration of the incoming slab, and hydration of the mantle wedge of the overriding plate profoundly alter sedimentary, geochemical, and biological processes in hadal trenches, mainly described for Mariana's forearc trenches. However, life thrives in these depths, encompassing an array of taxa such as fishes, cephalopods, crustaceans, echinoderms, polychaetes, mollusks, cnidarians, bryozoans, foraminifera, bacteria, and archaea (Gooday et al., 2008; Paterson et al., 2009; Ritchie et al., 2015; Jamieson and Vecchione, 2020; Jamieson et al., 2021; Jamieson and Linley, 2021; Swan et al., 2021). Although the hydrography and environmental aspects of the hadopelagic zone have been relatively well sampled (Johnson, 1998; Jamieson, 2015), technical complexities associated with deep-sea sampling limit knowledge of the fauna inhabiting this realm. In addition, most hadopelagic studies have occurred in the Pacific Ocean, leaving a notable gap in research on ecological structure and functioning of hadal communities, alongside their contributions to global energy and biogeochemical cycles. One study estimated species endemism within the hadopelagic zone at 41 % (Belyaev, 1989), with endemism increasing with depth while overall number of hadal species decreases (Jamieson, 2015). Several reviews have highlighted advances in hadal science (Jamieson, 2015; Jamieson et al., 2018; Liu et al., 2018; Weston and Jamieson, 2022).

5.1.19. *Connectivity among habitats*

Myriad factors affect ocean connectivity. At abyssal depths, the ocean floor of the North Atlantic is considered to be a single geographic province (Watling et al., 2013).The Mid Atlantic Ridge subdivides this province into eastern and western North Atlantic sub-provinces (Watling et al., 2013). At lower bathyal depths (800–3000 m), the North Atlantic biogeographic province encompasses the Atlantic continental slope of North America, the Mid-Atlantic Ridge (MAR), and the Atlantic margin of Europe. On the continental slope and upper bathyal, the oceanography can be complex with benthic environments influenced by a variety of water masses (Section 2). The deep hydrography is dominated by North Atlantic Deep Water. A separate Northern Atlantic Boreal lower bathyal province extends northwards from approximately Cape Hatteras in the west to the Wyville-Thomson Ridge (Watling et al., 2013). Other analyses treat the Mid Atlantic Ridge as a standalone Extended Mid-Atlantic Ridge Lower Bathyal Province (Niedzielski et al., 2013).

The northern MAR significantly influences deep-sea population connectivity. While the ridge itself is a barrier for some megafaunal species (Gebruk et al., 2010; Bell et al., 2013; Alt et al., 2019), fracture zones can provide viable east-west larval dispersal routes across the Atlantic (German et al., 2011). One particular significant feature, the Charlie-Gibbs Fracture Zone (CGFZ), along with the corresponding Sub-Polar Front, acts as a biogeographic boundary for multiple benthic faunal groups (Gebruk et al., 2010). The CGFZ marks the southern distributional extent for some cephalopod species (Vecchione et al., 2010), with fish assemblages differing in composition north and south of the CGFZ (Cousins et al., 2013a,b; Linley et al., 2013). North of the Azores, the MAR provides habitat for bathyal species and consequently supports dispersal and connectivity between continental slopes, seamounts, and plateaus. South of the Azores to the equator, the ridge summit deepens (Priede et al., 2022).

Accumulating research using genetic tools shows species have narrower bathymetric distributions than previously thought, and population structuring along bathymetric gradients. For example, genomic studies showed that the coral genus *Paramuricea* comprises a suite of species that inhabit the slope and canyon habitats on both sides of the North Atlantic, several of which are restricted to relatively narrow temperature and/or depth ranges (Quattrini et al., 2022), whereas DNA sequencing has demonstrated differentiation of populations of the bivalve *Deminucula atacellana* sampled from slope habitats on both sides of the North Atlantic much more by depth than by their east or west location (Zardus et al., 2006). Sometimes a bathymetric distance of even a few 100 m can result in a genetic break (e.g., ophiuroids, Cho and Shank, 2010), showing isolation by adaptation across environmental gradients (summarised in Taylor and Roterman, 2017). Therefore, the often complex topographic and oceanographic habitat heterogeneity of the bathyal zone has likely contributed greatly to evolutionary radiations of deep-sea species (Etter et al., 2005).

In contrast, strong connectivity may characterize *Paramuricea* spp. over 1000s of km of ocean horizontally. Broad distributions characterize at least three species of *Paramuricea* delimited by genomics that extend from Ireland to the Gulf of Mexico (Quattrini et al., 2022). Similarly, RAD-seq data indicate conspecific *Paragorgia arborea* populations from the north Atlantic and South Pacific (Herrera and Shank, 2016). Where broad geographic distributions occur, some genetic structure may be apparent. For example, Florida populations of the deep-sea glass sponge *Vazella pourtalesii* differ genetically from those on the Carolina Shelves and the Scotian Shelf (Patova et al., 2025), with low connectivity estimates across distances of more than 1000 km, but higher connectivity at lesser scales. Slightly different patterns characterize the deep-sea sponge *Phakellia ventilabrum*, with high connectivity from Ireland to Norway, but some differentiation of populations from France and northern Spain (Taboada et al., 2023). On smaller scales, populations often seem highly connected. For example, populations of *Narella versluysi* showed little genetic differentiation over ~360 km among six canyons of the Bay of Biscay (Yesson et al., 2018), with only slightly differentiation of *Bathynomus* sp. populations through the Gulf of Mexico (Timm et al., 2018).

Seamounts present an excellent opportunity to test theories of connectivity among bathyal species, including isolation by distance, although few North Atlantic studies have done so. Studying New England seamount ophiuroids, Cho and Shank (2010) reported that several factors potentially influence gene flow and connectivity, including life history strategies, depth, oceanography, and whether or not the focal species was a coral associate. Lack of data often hinders understanding. For example, increasing data on lithistid sponge assemblages from the Azores suggests wider distributions than initially recorded (Xavier et al., 2021), potentially with connectivity provided by the AzC, as identified previously through particle modelling (Lima et al., 2020). A biophysical dispersal model suggests that populations of the sponge *Pheronema carpenteri* on Azorean seamounts present differential connectivity, with greater isolation in some populations more so than others (Viegas et al., 2024) but noting the absence of any available genetic data on this species.

Cold-water scleractinians comprise some of the best-studied benthic seamount and submarine canyon fauna. In the South Pacific, *Desmophyllum dianthus* and *Solenosmilia mirabilis* were differently connected by seamounts: *S. mirabilis* populations were isolated by asexual reproduction, whereas the seamounts acted as stepping stones for connectivity for *D. dianthus* (Miller and Gunasekera, 2017). Atlantic populations of *D. dianthus* also exhibit extensive connectivity, with populations off Ireland and Northern Spain appearing to play a key role in maintaining connections with populations in the South Atlantic (Addamo et al., 2021). Early work on *Desmophyllum pertusum* (formerly *Lophelia pertusa*), the best-studied cold water coral in the North Atlantic, demonstrated genetic differences between offshore and fjord populations in the North East Atlantic (Le Goff-Vitry et al., 2004); subsequent studies showed populations from the Gulf of Mexico, SE USA, New England seamounts and the NE Atlantic to be genetically distinct (Morrison et al., 2011). Modelling suggested strong larval retention in the Canadian EEZ and Gulf of Mexico, with the Labrador Current providing connectivity southwards, and the Gulf Stream providing connectivity northwards (Guy et al., 2025).

Lower levels of population divergence may characterize abyssal species. For example, low genetic divergence occurs in the bivalve *Ledella ultima*, whose distribution extends from the bathyal onto the abyssal plain among Atlantic basins, although the MAR apparently hinders gene flow (Etter et al., 2011). Similarly genetic differentiation occurs between populations of abyssal macrostylid isopods from east and west of the MAR (Riehl et al., 2018), although the overall geographic extent of species could be extensive; isolation by distance was apparent in those species with the greatest geographic ranges. No bathymetric structuring was apparent in the predominantly abyssal sea cucumber *Psychropotes longicauda*, although some temporal variation was evident in samples spanning 40 years (Gubili et al., 2017).

The limited hadal environments in the North Atlantic (see section 5.1.14) potentially result in high levels of isolation. Extremely limited gene flow among trench populations of the cosmopolitan hadal amphipod *Bathycallisoma schellenbergi* indicates that the abyssal ocean represents a severe barrier to hadal specialists (Weston et al., 2022), with important implications for hadal conservation.

Maintaining connectivity among chemosynthetic habitats potentially presents challenges because of the fragmented distribution of those habitats. Noting various proposed schemes of vent ecoregions (see section 5.1.9), all report a single province in the North Atlantic. *Bathymodiolus* mussels tend to dominate shallow Atlantic vents, in contrast to alvinocaridid shrimps of the genera *Rimicaris* and *Mirocaris* (e.g., Wheeler et al., 2013) that dominate deeper vents (Ramirez-Llodra et al., 2007), .

High dispersal along the MAR occurs in multiple species. A star-like haplotype network produced from COI sequences of *R. exoculata* from five vent systems from the southern MAR at 4°S to Rainbow at 36°N indicates a bottleneck or founder effect followed by rapid demographic expansion, indicative of high dispersal capability (Teixeira et al., 2011). Analysis of microsatellite data confirmed panmixia along these 7000 km of the Mid-Atlantic Ridge (Teixeira et al., 2012). This pattern potentially reflects an extended lecithotrophic stage, deduced from the undeveloped mouthparts and large lipid reserves from the first zoeal stage (Hernández-Ávila et al., 2015). The vent limpet *Divia briandi* also demonstrates high connectivity: sequences of COI demonstrated a panmictic population extending from the shallow Menez at 39 N to the deep Ashazde at 14 N. The presumably planktotrophic larvae of *Divia briandi* migrate to surface waters to feed and disperse (Yahagi et al., 2019). Models of current and effluent flow over Lucky Strike hydrothermal vent show potential trapping of larvae in submesoscale vortices with tidally-induced mixing in areas of variable topography, increasing vertical dispersion and thus enabling longer distance dispersion (Vic et al., 2018a). Similarly, biophysical modelling of connectivity between North Atlantic hydrothermal vent fields indicates a likely influence of pelagic larval duration on faunal distributions and possible regional biogeographic subdivisions with potential importance for managing impacts from human activities (Yearsley et al., 2020). Other taxa demonstrating high dispersal capabilities include dirivultid copepods (Gollner et al., 2016), the holothurian *Chiridota hydrothermica* (Thomas et al., 2022) which also occurs at seeps, and other alvinocaridid shrimps (Teixeira et al., 2013).

Multiple studies demonstrate genetic structure among populations of widely distributed chemosynthetic fauna. Population structuring occurs across the distribution of the vesicomyid clam *Abyssogena southwardae*, which occurs at both vents and seeps, with no COI haplotypes shared among three seep locations extending west to east from the West Florida Escarpment and Barbados Accretionary Prism to the Congo Fan and no shared COI haplotypes present at both vents and seeps (Teixeira et al., 2013); however, gene flow apparently occurs along the MAR, crossing fracture zones, with COI haplotypes shared between Logachev (∼15°N) and Clueless (∼5°S) hydrothermal vents (van der Heijden et al., 2012; Teixeira et al., 2013). Application of coalescent theory to additional COI sequence data detected gene flow between Barbados and the MAR (northern and southern vent samples combined) and between the West Florida Escarpment and the Congo Fan (LaBella et al., 2017), but not among other pairs of sites.

Bathymodiolin mussels are among the best-studied chemosynthetic fauna in terms of connectivity, and their complex patterns of connectivity vary among species. Several species maintain high levels of connectivity among widely distributed seep sites and over a range of depths (Carney et al., 2006; DeLeo et al., 2022; Portanier et al., 2023), yet certain populations appear less well connected (Faure et al., 2015; Portanier et al., 2023). Modelling has again shown that depth of dispersing larvae strongly influences dispersal ability (McVeigh et al., 2017). Four closely related putative species of *Bathymodiolus* occur at hydrothermal vents on the MAR, two north of the Atlantic equatorial belt and two to the south (van der Heijden et al., 2012); the two northernmost species form a hybrid zone where their distributions overlap (O'Mullan et al., 2001). Limited contemporary gene flow between known vent sites (Breusing et al., 2016) suggests *Bathymodiolus* maintain connectivity through as yet undiscovered sites, or alternatively connectivity was enabled by now extinct vents. Modelling indicates potentially high local larval retention (Breusing et al., 2016) which aligns with subtle genetic structure revealed by genomic studies of *Bathymodiolus azoricus* at northern MAR sites (Silva, 2016). Despite increased attention on bathymodiolin mussels, the effects of life history, local topography and oceanography appear to contribute to complex general patterns, which has implications for conservation planning given the challenge of determining source & sink populations without specific studies. Additionally (but with some exceptions e.g., Breusing et al., 2016; Silva, 2016; DeLeo et al., 2022), much of the work to date has relied on single partial gene (usually COI) sequencing.

A few studies have focused on other taxa at vents, seeps, and organic falls, in particular siboglinid worms (Hilário et al., 2010; McMullin et al., 2010; Cowart et al., 2013, 2014; McCowin and Rouse, 2018; Berman et al., 2023), and report varied patterns of connectivity (spatially and temporally) among species, again emphasizing the need for additional studies to allow scientists to fully understand the connectivities between all sites and species.

In the pelagic realm, studies often focus on species of commercial interest. For example, phylogeographic studies using Single Nucleotide Polymorphisms (SNPs) showed genetic discontinuity in stocks of ling (common and blue) between the northern Rockall Trough area and Norway (McGill et al., 2023). The stronger effect in blue ling may reflect aggregations to spawn (common ling does not). Genomic data bring increased power to analyses, a potentially important conservation consideration for species under intense fishing pressure. In orange roughy, SNPs revealed previously unrecognised population structuring with clear relevance for conservation needs (Gonçalves da Silva et al., 2020). Genomic data showed that maturing individuals of the grenadier *Coryphenoides rupestris* move to a habitat best suited to their genotype, leading to vertical population structuring that management measures do not consider (Gaither et al., 2018). Local adaptation, potentially to either depth of dissolved oxygen concentration, could also explain population differentiation of the vampire squid *Vampyroteuthis infernalis* between the Gulf of Mexico and North Atlantic (Timm et al., 2020) although clarification requires more comprehensive genomic data. Even non-commercial deep-sea species may be taken as bycatch, with particularly strong impacts of low fecundity and slow growth rates typical of the deep sea, such that a greater understanding of many pelagic species is required to inform conservation and management strategies.

A meta-analysis of 51 studies of deep-sea connectivity suggested that overall scales of connectivity might resemble those in shallow waters, and emphasized that MPA networks in deep-water environments will need to consider the needs of widely different taxa with varying life histories, and account for regional differences in habitat distributions and fine-scale oceanographic patterns (Baco et al., 2016). Indeed, several relatively small-scale studies have emphasized the need to consider local ocean dynamics (e.g., for sponges; Busch et al., 2021). In studies that report high recruitment, hydrodynamic modelling could potentially indicate locations of source populations (Guy and Metaxas, 2022) meriting particular protection, although this requires knowledge of PLDs, which is often lacking (Hilário et al., 2015b). Evidence that vertical swimming ability of deep-sea larvae can considerably affect the connectivity of populations (Gary et al., 2020), means a comprehensive understanding of species autecology is also essential when considering reserve network design.

5.2. Temporal data

Few time series sites and long-term observatories exist in the deep ocean more widely (Smith et al., 2015), in contrast to several in the North Atlantic (Larkin et al., 2010, Fig. 11). Instruments at these sites enable sustained or periodic observations and/or sampling across physical, chemical, and biological parameters in the pelagic or benthic realms, via long-term moorings, sensors on autonomous vehicles and ship-based equipment. Understanding of long-term change, including changes related to climate, requires such information. As an example, the SIGSBEE long term ecological research site (Gulf of Mexico at 23°N, 92°W with a replicate at 23°N, 94°W) aims to study the changes in the infaunal community (macroinfauna and meiofauna) of abyssal (3800 m depth) soft sediments. Annual sampling of sediment and water column,

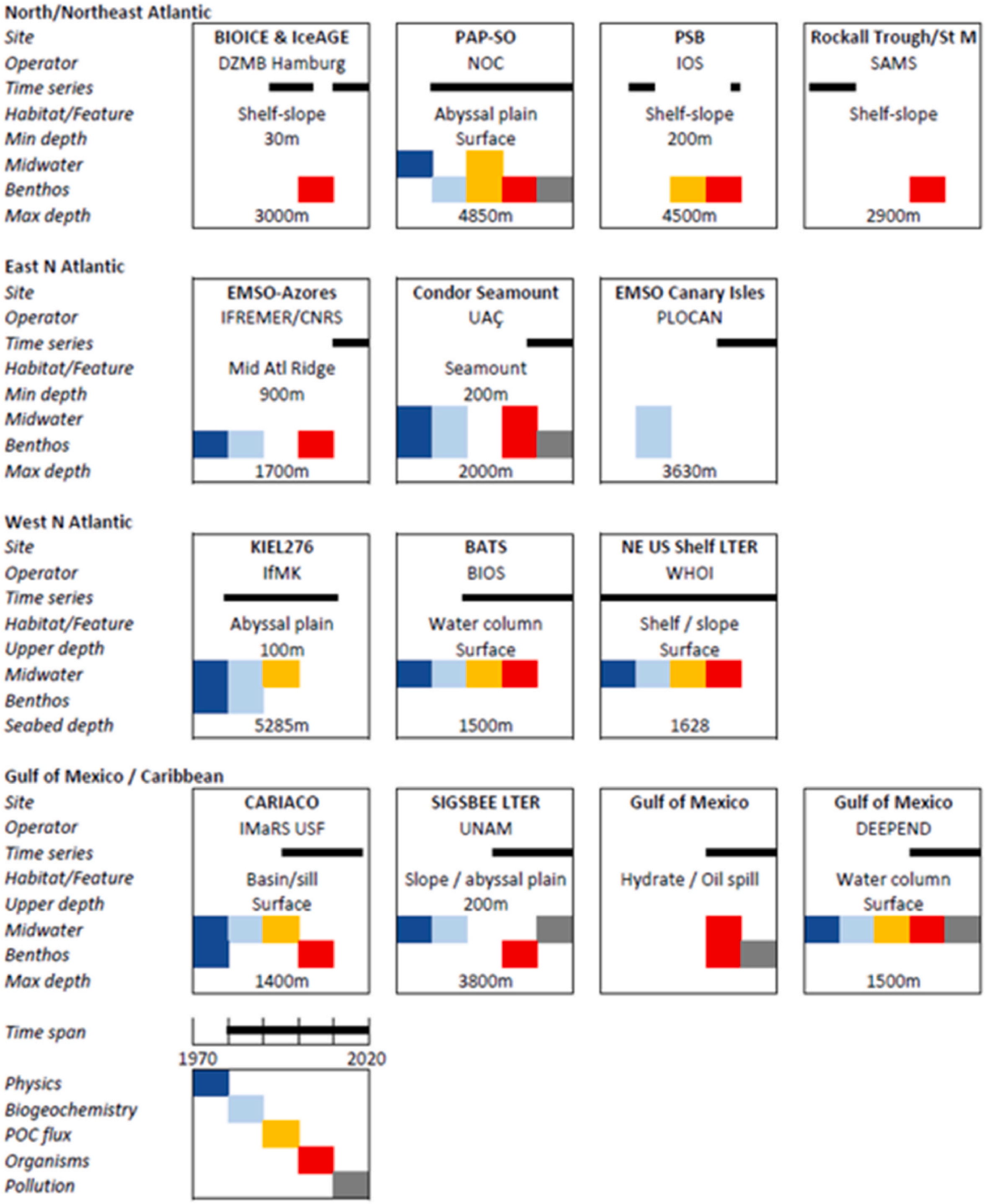


Fig. 11. Key characteristics of major time series sites in the North Atlantic grouped by subregion, indicating duration of observations and key monitoring components (coloured blocks). Parameters or depths that were only monitored infrequently/intermittently are omitted.

supported by UNAM and *R/V Just Sierra*, began in 1997 to investigate the roles of pelagic-benthic coupling, and carbon export and flux. This times series site has a capacity building objective as well as scientific objectives.

Observatory sites frequently contribute to global or regional observing networks such as the Global Ocean Observing System (https://goosocean.org/), Deep Ocean Observing Strategy (deepoceanobserving.org), European Multidisciplinary Seafloor and Water Column Observatory (emso-eu.org), and reveal temporal variability higher than expected (Levin, 2021).

Long-term observations in the deep ocean may also be associated with the study of effects of and recovery from human impacts (e.g. Jones et al., 2012; Huvenne et al., 2016). Information from wider oceanographic observations such as the Argo programme (including Deep Argo and BGC Argo) (Roemmich et al., 2019), long-term ship-based observations and mooring arrays e.g. RAPID (McCarthy et al., 2020) and OSNAP (Desbruyères et al., 2014) and continuous plankton recorder data (McQuatters-Gollop et al., 2015; Batten et al., 2019) provide physical oceanographic, biogeochemical, and ecological information that supports understanding of long-term change in the deep North Atlantic.

Here we focus on the findings of three selected time-series sites, two long-term sites and one shorter, covering contrasting habitats, locations and observation types in the Atlantic that highlight the importance of temporal studies and the major findings they have enabled.

Long-term time series sites reveal variability that studies at a single point in time cannot detect. These observations enable understanding of long-term change in the deep ocean, related to a range of processes and provide important context to variability identified spatially. They not only address today's research questions, but they also provide a resource for understanding phenomena not yet known about in a rapidly changing ocean. The Porcupine Abyssal Plain - Sustained Observatory (PAP-SO)[4] using moorings and annual sampling over >30 years to identify links between biogeochemical processes in surface waters through the water column to the abyssal seabed (Hartman et al., 2021). Much of the present understanding of carbon fluxes to the deep ocean (Lampitt et al., 2010; Giering et al., 2014), temporal variability (Lampitt et al., 2023), and importance to benthic communities (Durden et al., 2020) derives from research at the site. Similarly, the PAP-SO time series revealed variability in abyssal benthic invertebrate communities (Billett et al., 2010) over hours (Durden et al., 2015) to multidecadal timescales (Horton et al., 2020). Spatial studies benefit from co-location of spatial sampling with time-series observations, highlighting the role of habitat heterogeneity (Durden et al., 2015; Stefanoudis et al., 2016). At the EMSO-Azores site[5] on the Mid-Atlantic Ridge, 25 years of monitoring the Eiffel Tower vent edifice has enabled resolution of the fine-scale dynamics of vent communities relating to abiotic factors, and temporal variations of fluid chemistry, hydrothermal edifices, earthquakes, and current flow over the Lucky Strike Vent field (Dusunur et al., 2009; Escartín et al., 2008; Chavagnac et al., 2018; Vic et al., 2018b). Key findings include day-to-day variations in a mussel assemblage (Sarrazin et al., 2014), behavioural interactions between decapod crustaceans (Matabos et al., 2015), determination of the drivers of biological rhythms such as as tidal influences on the transcriptome and physiology of a vent mussel (Mat et al., 2020), and long-term stability and potential low resilience of climax vent communities (Van Audenhaege et al., 2022). The DEEPEND[6] time series verifies the Gulf of Mexico as one of the most speciose pelagic ecoregions of the ocean, particularly among intermediate and higher trophic levels. High spatial connectivity from the surface to bathypelagic depths, and between coastal and oceanic domains characterizes this biodiversity.

6. Summary of human activities

The UN Decade of the Ocean recognizes the need for human activities through its emphasis on sustainable development. Historically, much of the deep sea was inaccessible to humans but this changed throughout the 20th century. Glover and Smith (2003) summarised the (then) past, present, and future impacts on the deep sea. They considered past impacts to be dumping of munitions, radioactive waste, and oil/gas structures, present impacts to be deep-sea fisheries, deep-sea oil and gas drilling, underwater noise, and research/bioprospecting at vents, and future impacts to be carbon dioxide sequestration, climate change, mining and dumping of sewage sludge, albeit with some finer categories within these broad activities. Herein we summarize the current situation under the broad headings of fishing, shipping, mineral extraction, introduction of substances and climate change.

6.1. *Fishing*

The North Atlantic has a long history of deep-water fisheries exploitation dating back to the 1970s, most of which falls under the FAO's Western Central Atlantic Fishery Commission (WECAFC). The international area is managed under two regional fisheries management organizations, the North East Atlantic Fisheries Commission (NEAFC) and Northwest Atlantic Fisheries Organization (NAFO). Deep water fisheries in EEZs are ruled by either national or European legislation. One of the earliest deep-water fisheries was the former Soviet Union roundnose grenadier (*Coryphaenoides rupestris)* fishery. Subsequently, aggregations of alfonsino (*Beryx splendens* and *B. decadactylus*), orange roughy (*Hoplostethus atlanticus*), cardinal fish (*Epigonus telescopus*), tusk (*Brosme brosme*), 'giant' redfish (*Sebastes marinus*) and blue ling (*Molva dypterygia*) were also targeted on multiple seamounts along the MAR (ICES, 2022a). Various nations, including Russia, Iceland, Faroes, Poland, Latvia, Spain and Norway have operated bottom trawl and longline fisheries in the High Seas, but there have been few lasting fisheries, and, in the last decade, there has been a significant decline in fishing activity on the High Seas due to overexploitation (Victorero et al., 2018). Fisheries data in the Caribbean tend to lack detail and consistency, with regulations varying between countries. Despite limited information, the increasing presence of deepwater fisheries presents a significant threat to the marine environment in the region (Talwar et al., 2022).

6.1.1. *Pelagic trawls*

The fishery in the Northeast Atlantic is multinational, involving around 20 nations. Most catch is attributed to Norway, Russia, and Iceland, and is focused primarily on pelagic beaked redfish (*Sebastes mentella*) and blue whiting (*Micromesistius poutassou*). Spain, Germany, Portugal, the Netherlands, Ireland, the Faroe Islands, Latvia, and Lithuania also participate, though their landings are comparatively smaller (ICES, 2022b).

There has been a trend of increasing catch volumes of pelagic species, but with large spikes, in recent years. This pattern has been mostly attributed to shifts in migration patterns and is associated with fishing efforts targeting blue whiting, which is the most abundant species in catches in recent years (ICES, 2022b).

The Northeast Atlantic is home to the largest deep-water fish stock in the world, with blue whiting, which has average annual landings of over 1 million tonnes, accounting for as much as half of the total global deep-sea fish catch in FAO statistics (Priede, 2017). The stock is distributed along the continental shelf edge at depths of 100 to >1000 m from Portugal (36°N) to the North of Norway and Northwest Greenland (71°N) (Post et al., 2019). Large-scale exploitation began in the 1970s mainly by pelagic trawling. Landings reached a peak of 2.4 million tonnes in 2004, declined to 0.1 Mt by 2011 and currently are just above 1 Mt. The main catch is in spawning areas West of the British Isles but the Norwegian Sea is also an important fishery area (ICES, 2023).

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[4] https://projects.noc.ac.uk/pap/pap-front-page.

[5] https://emso.eu/observatories-node/azores-islands/.

[6] https://restore.deependconsortium.org/.

The fishery targeting beaked redfish began in the early 1980s. Throughout the 1980s and 1990s, catches of beaked redfish constituted most of the pelagic catches, with catch volumes showing considerable fluctuations. After this period, catches experienced a marked decline, a trend linked to the depletion of beaked redfish stocks. This decrease in catch was accompanied by a substantial reduction in the number of vessels participating in the fishery (ICES, 2022b).

The main fishery on and near the MAR is the midwater trawl fishery targeting *Sebastes mentella* that operates on the western slope of the Reykjanes Ridge and in the Irminger Sea (ICES, 2022b).

6.1.2. Longlines

Historically there have been two important longline fisheries on the Northeast Atlantic continental slope. Norwegian longliners target ling (*Molva molva*) and tusk (*Brosme brosme*), and to a lesser degree blue ling, on the shelf edge and upper slope (150–450 m), while Spanish and Anglo-Spanish vessels also target hake (*Merluccius merluccius*). This fishery had a bycatch of blue ling and deep-water sharks, and, prior to the EU ban on targeted fishing of deep-water sharks, these were often also targeted.

There is a long standing drifting long-line fishery for black scabbardfish (*Aphanopus carbo*) and intermediate scabbardfish (*Aphanopus intermedius*) off the Madeira archipelago, and, in the 1980s, a new bottom longline fishery for black scabbardfish was established off mainland Portugal. Recent research suggests that catches by the Madeira fleet have been maintained by a progressive spatial expansion of the fishery, and longer gear soak times (Delgado et al., 2018), with concern around overfishing of this species in the wider Northeast Atlantic.

The bottom hook and line fishery, focusing on deep-water and demersal species, is the primary fishery within the Azores EEZ in terms of landed catch value, number of vessels, and employment provided. On average, total landings from these commercial bottom fisheries account for approximately 40 % of the total weight of all catches in the region and about 75 % of the total landed value (ICES, 2022c). The fishing fleet is composed of smaller open-deck boats (under 12 m in length) using handlines, and larger closed-deck boats (over 12 m) using bottom longlines. While these vessels traditionally operated along the island slopes within an intermediate depth range of 200–700 m, there has been a shift towards fishing around seamounts, influenced by fleet modernization and fishing area restrictions (Santos et al., 2019a). This change in fishing zones, coupled with the limited knowledge of these deep-sea habitats and species, has made these environments highly vulnerable to fishing pressures (Santos et al., 2021). Key target species of this fishery include deep-water demersal fish like the blackspot seabream (*Pagellus bogaraveo*) and alfonsinos (*Beryx splendens* and *B. decadactylus*) (Santos et al., 2020). Every stock is categorized as data-deficient, and the fisheries are currently managed using a precautionary approach (ICES, 2022c). The condition of these stocks remains undetermined due to the absence of established reference points.

Recently, Medeiros-Leal et al. (2023) conducted the first status assessment of Azorean priority stocks using length-based methods, and approximately 50 % of the demersal stocks evaluated were considered to be sustainable. While, the three assessment methods implemented demonstrated a strong fit and generally agreed in their conclusions, it is known that these length-based methods are sensitive to life-history parameter values. This sensitivity can lead to inaccuracies in the classification of stock status and thus recommendations for management measures (Hordyk et al., 2015, 2016; Medeiros-Leal et al., 2023). Therefore, recommended practice in length-based assessments is to determine initial life-history values from stock-specific studies (Rudd et al., 2019). Yet, for data-limited small-scale fisheries, such as those in the Azores, such specific studies are often not available. This issue becomes particularly critical for species with complex life histories, such as *P. bogaraveo*. This species is characterized by unique biological features, including hermaphroditism, habitat fragmentation, and ontogenic and spatial movements, all of which are not fully understood in the Azores region (Pinho et al., 2014). Similarly, the alfonsino species also present challenges in terms of understanding and managing their populations in these waters.

In the North Atlantic, two species of *Beryx*, specifically the splendid alfonsino *B. splendens* and the alfonsino *B. decadactylus*, are predominantly harvested by benthic trawls and longlines in mixed fisheries aimed at deep-sea species (FAO, 2016). In many fisheries, alfonsino catches are reported simply as *Beryx* spp. This means that the proportion in the catch, and information on the distribution, reproductive parameters, age, growth, and mortality rates (Santos et al., 2019b) remain ambiguous. Due to limited knowledge about the stock structure of these species, the Working Group on the Biology and Assessment of Deep-Sea Fisheries Resources (WGDEEP) of ICES currently assesses a single stock that includes both species in the North Atlantic (ICES, 2022a). Specific landing data by species are only available for the Azores region (ICES Subarea 10.a.2), where *B. decadactylus* landings constitute an average of 20 % of the total catch of both species (ICES, 2022a).

Over approximately the last two decades, research in the Azores archipelago, augmented by data from the Data Collection Framework, has gathered information on aspects like catch, size, weight, gender, and maturity stage of alfonsinos (Santos et al., 2019b). However, it remains unclear whether the Azorean segment of the alfonsino population should be regarded as a distinct management unit, primarily due to the lack of comprehensive data covering the full spatial distribution of the species in the North Atlantic. This uncertainty is compounded by conflicting genetic findings, limited understanding of migratory patterns, and discrepancies in reproductive data from the Azores (Santos et al., 2019b). As a result, there is no analytical assessment for this resource, leading to the current management of the alfonsinos stock under a 'precautionary approach' (ICES, 2022a).

6.1.3. Benthic trawls

Benthic trawling in the North Atlantic has a long history and has had considerable impact on the biological communities. This has resulted in a number of protected area designations and NEAFC fisheries closures (see section 7). Historically, the Grand Banks off Newfoundland, the North Sea, Celtic Sea, Bay of Biscay, Norwegian Sea and Iceland waters have been heavily trawled with a consequent impact on benthic ecosystems. Some studies have also highlighted benthic trawling activities around the Mid-Atlantic Ridge, though possibly to a lesser extent due to its depth and challenging conditions (Collie et al., 2000; Koslow et al., 2000; Clark et al., 2016).

Benthic trawling has affected depths ranging from continental shelves down to the upper slope and occasionally into the abyssal plains, depending on the fishing practices and target species. Commonly impacted depths range from 200 to 1400 m (Collie et al., 2000; Koslow et al., 2000; Clark et al., 2016). Remote or deeper areas such as seamounts, canyons, and certain regions of the abyssal plains might have experienced less trawling due to the challenges in fishing at extreme depths or because the ecological importance of these areas has been recognised, leading to protective measures. Abyssal benthic trawling is likely confined to occasional research studies, other than at time-series sites e.g. Porcupine Abyssal Plain and Porcupine Seabight, but is also likely to result in impact on the biological communities.

Impacts of trawling may be on target or non-target species. Bailey et al. (2009) showed that two decades of the deep-sea demersal trawl fishery West of Ireland for orange roughy (*Hoplostethus atlanticus*) and Roundnose grenadier (*Coryphaenoides rupestris*) had significantly reduced abundance of fish species at all depths from 800 to 2500 m depth although maximum depth targeted by fishing vessels was ca. 1600 m. Trawling for Greenland halibut (*Reinhardtius hippoglossoides*) on the Greenland slope at 800–1400 m has had a negative impact on sea pen and cup coral abundance (Long et al., 2021b). The anthropogenic impacts of fishing activities on VMEs off Ireland include historical deliberate crushing of coral reefs using trawl chains, doors etc (Grehan et al., 2004), trawl scars at depths of 200–1400 m (see Morrissey et al., 2023 and references cited therein), and reduced densities of sponge aggregations (Vieira et al., 2020). VMEs are, by definition, highly sensitive to fishing activities and efforts have been made to close areas where VMEs are thought to occur to fisheries (e.g., van Denderen et al., 2022). Nonetheless, analyses suggest that 3500 h of bottom fishing occurred within VME-rich areas closed to fishing in the year subsequent to closure, and nearly 20,000 h of fishing took place below 800 m (Victorero et al., 2025) in defiance of the EU Deep-sea Access Regulation (see Section 7.1.3)

6.2. *Shipping*

6.2.1. *Noise*

Anthropogenic noise is increasingly recognised as detrimental to marine animals with the largest body of evidence focused on marine mammals. In the most extreme cases, noise can cause animal strandings. In the North Atlantic, for example, records of whale strandings cross referenced with seismic survey data over a ten-year period suggested that offshore seismic surveys led to increased strandings of long-finned pilot whales (McGeady et al., 2016). Similarly, several stranded giant squid were discovered with damaged statoliths and internal organs following seismic surveys in northern Spain (Guerra et al., 2004), and, while this study was anecdotal, subsequent aquarium-based experiments demonstrated that low frequency sounds caused statocyst damage in multiple species of cephalopod (Solé et al., 2013a). Noise can also have more subtle effects on behaviour and physiology including affecting communication, locomotion and inducing stress (Hatch et al., 2012; Parks et al., 2012; Rolland et al., 2012; Goldbogen et al., 2013).

A recent review of anthropogenic noise in the marine environment (Duarte et al., 2021) summarises sources of sound in the ocean and those animals that are known to be sensitive to it. Anthropogenic noise is generated by vessels, explosives, air guns, dredging, boomers and sparkers, active sonar, chirp sonar, pile driving, wind farm operation and aircraft, while animals that are sensitive to the frequencies that encompass this anthropogenic noise include marine mammals and reptiles, fishes, crustaceans, bivalve molluscs, cephalopods and jellyfish (e.g., Mann et al., 1997; Casper and Mann, 2010; Di Iorio et al., 2012; Martin et al., 2012; Solé et al., 2016, 2017). The increasing activities related to oil, gas, and mineral exploration and exploitation in the deep sea and the consequent increase in noise pollution (Nowacek et al., 2015; Cordes et al., 2016; Lin et al., 2019; Williams et al., 2022; Huang et al., 2023) have the potential to disturb a great number of deep-sea species, and can affect the efficiency of reproduction and migration (Solé et al., 2013b; Peng et al., 2015) by altering the noise landscape.

Noise is pervasive: a hydrophone in the Challenger Deep at 10,830 m depth in the Pacific Ocean recorded anthropogenic sounds from ship propellers, airguns, and active sonar, demonstrating the propagation of sound over significant distances and demonstrating that the deep-sea is not immune to this form of pollution (Dziak et al., 2017). On the other hand, noise is a unique form of pollution that is instantly removed from the ocean when the source is removed (Duarte et al., 2021).

6.2.2. *Introduction of pollutants*

With the increase in maritime traffic the risk of pollution has also increased (Tornero and Hanke, 2016). It is recognised that illegal release of pollutants persists despite the existence of the environmental regulations established with the MARPOL Convention (EMSA, 2012; Tournadre, 2014). Pollutants can be released into the ocean from shipping activities such as accidental spills that may include litter or cargo releases, operational discharges, ballast water, or through antifouling paints (Tornero and Hanke, 2016).

Between 2008 and 2021, on average 1629 containers were lost at sea each year (World Shipping Council, 2022). This highlights not only the risks posed by surface-level incidents but also the real possibility of containers sinking to the deep sea and releasing their contents. The high pressure at such depths can compromise the structural integrity of containers, potentially causing them to rupture. Depending on the nature and toxicity of the released substances, this may have varying effects on marine organisms and ecosystems (Purnell, 2009; Neuparth et al., 2011).

6.3. *Mineral extraction*

6.3.1. *Oil & gas*

Both exploration and exploitation of deepwater oil and gas reserves occur in the North Atlantic. Major deepwater (>200 m) production occurs in UK and Norwegian waters, the Gulf of Mexico, and Trinidad and Tobago (Cordes et al., 2016; Amon et al., 2017). Ultra-deep-water (>1000 m) production occurs in the Gulf of Mexico to 3000 m (Cordes et al., 2016); it is not yet widely developed, but likely to become so. Other countries such as Barbados and The Bahamas have been undertaking oil and gas exploration. Additionally, methane hydrates have been observed in the Gulf of Mexico and off Trinidad and Tobago, although this industry is still considered nascent (Cordes et al., 2016).

Typical operations begin with seismic surveys whereby sound blasts from air guns are used to acoustically image the subseafloor, causing impacts as described in 6.2.1. Typical operations from offshore oil and gas drilling rigs and production platforms result in releases of drill cuttings, production fluids, cooling water, sewage and food waste, exhaust from platforms and support ships, excess sound and light, as well as direct impacts from seafloor installations including anchors and anchor chains, pipelines, and footings. Observations in the Faroe-Shetland channel suggest impacts from released fluids and solid waste are apparent over a few hundred meters in most situations (Jones et al., 2007). Furthermore, these impacts were evident in direct examinations for over 10 years (Jones et al., 2012). Observations in Norwegian waters seldom detected impacts beyond 500 m for platforms but found they could extend over 1–2 km in deeper waters and where there is rapid current flow (Bakke et al., 2013).

The Gulf of Mexico has been subject to the largest subsurface oil spill in history: the Deepwater Horizon oil spill in 2010. In addition to the injection of large volumes of oil and gas into the water column and surface waters, Marine Oil Snow Sedimentation and Flocculent Accumulation (MOSSFA) occurred, which refers to the process of formation, sinking, and seafloor deposition of oil-contaminated marine snow and oil-mineral aggregates (Quigg et al., 2020; Schwing et al., 2020a).

Deep benthic communities including various size-classes and taxonomic groups including microbes, foraminifera, meiofauna, macrofauna, megafauna and corals, experienced changes to community structure, decreases in population density and diversity, and branch loss (Schwing et al., 2020b). Assessment of recovery in many cases was hampered by lack of pre-spill baselines and therefore time-series approaches were necessary to assess trends of response and resilience. The earliest indicators of resilience, such as increases in population density/diversity, and coral branch regrowth ranged from 2 to 10 years depending largely upon the size-class and overall lifespan of each group (Schwing et al., 2020b and references therein). In some cases, where baseline community data were available, it was apparent that despite the density or diversity measures returning to pre-spill levels, the community structure was significantly different (Schwing et al., 2020b and references therein). It has been suggested that impacts are likely to persist for decades to centuries based on the generally long life spans and slow growth rates of deep-sea organisms (Fisher et al., 2014) and modelled recovery rate for corals to return to pre-spill conditions was estimated to be an average of 50 years (Girard et al., 2019). Taking into account oil degradation rates, sedimentation rates and bioturbation depth, it would take 50–100 years for the contaminated sediment layers to become fully buried below the active bioturbated zone (Schwing et al., 2020b and references therein).

There are ongoing long-term research and restoration efforts focused on the deep benthos and mesophotic communities of the Gulf of Mexico, and the temporal baselines and natural variability documented by these efforts will be invaluable in the future, especially considering global energy transition requirements (e.g. wind, solar, wave, tidal, mining) and their potential impacts. Despite the growth of *Desmophyllum* (=*Lophelia*) sp. on oil rigs, no reef has been observed. It takes a long time for a community comparable to a natural one to develop (Gass and Roberts, 2006); however, it has been suggested that communities on anthropogenic structures such as oil rigs could act as stepping stones of connectivity among natural populations (Henry et al., 2018).

6.3.2. Deep-sea mining

Deep-seabed mining for mineral resources is a potential new industry; currently there exist only opportunities for exploratory activities and not for exploitation, but this may change in the next few years. Hydrothermal vents, also referred to as polymetallic sulphides or seafloor massive sulphides, have been targeted for exploration on the northern MAR (nMAR) since 2011. Activities in international areas such as these are regulated by the International Seabed Authority (ISA), which has issued three exploratory licenses (Government of the Russian Federation, Government of France via IFREMER, and Government of the Republic of Poland). Similarly, Norway announced in January 2024 that it will open up its waters for exploratory mining, targeting hydrothermal vents on the Arctic Mid-Ocean Ridge, including Loki's Castle vent field, southwest of Svalbard. Under both governance structures, exploitation activities cannot proceed unless mining contractors demonstrate activities will not result in significant harmful effects to the environment. There are also known mineral resources in other areas of the North Atlantic, even though there are currently no plans to exploit them. For example, there are polymetallic sulphides on the Mid-Cayman Spreading Centre in the Cayman Islands EEZ (Connelly et al., 2012), and polymetallic nodules several hundred miles east of Barbados in ABNJ (Devey, 2015; Riehl et al., 2020).

Impacts from deep-seabed mining include the removal of hard substrate, which will result in habitat loss, fragmentation and modification which can be in the form of changes in sediment composition, mineral composition, topography and chemical conditions, affecting biological communities, and ecosystem structure and functioning (Gollner et al., 2017; Paul et al., 2018; Simon-Lledó et al., 2019; Vonnahme et al., 2020). Additional indirect impacts, which can extend into the water column, can come in the form of noise and light pollution, and sediment plumes which may contain toxic metals adhering to particles (Drazen et al., 2019; Christiansen et al., 2020; Williams et al., 2022). These direct and indirect changes in the living environments of seamounts, nodules and vents can result in increased faunal mortality with consequent species extinctions, changes in food-web interactions, and loss of connectivity (de Jonge et al., 2020). Population and species impacts are likely, although recovery from and resilience to disturbance effects differ between regions (Gollner et al., 2017). Major factors playing a role in recovery potential are species' life history (slow growth, low fecundity), and connectivity and colonization potential, the latter potentially affected by mining operations that will cover a larger spatial and temporal scale than natural disturbance events found on ridges.

The nMAR is one of the most studied regions regarding areas targeted for deep-seabed mining in international waters, and information on biotic and abiotic environmental baselines and resilience is sufficient to inform evidence-based management (Amon et al., 2022c). However, this is not the case for most mining impacts including plume effects, noise and light pollution, and toxicity, and the potential cumulative effects of these impacts (Amon et al., 2022c).

The ISA compiles Regional Environmental Management Plans (REMPs) for licensed areas designed to contain a clear management plan along with tools for its implementation and contractor requirements (International Seabed Authority, 2022a). The ISA's Legal and Technical Commission completed drafting the nMAR REMP in May 2021, but progress has stalled since the Council decided to postpone REMP considerations pending a standardised procedure for the development, review and approval of REMPs. The last available draft nMAR REMP was released for public consultation in 2022 (International Seabed Authority, 2022b). Broadly, the document covers the region-specific goals and objectives (mainly around the Mid Atlantic Ridge) including area-based management measures, categorizing the latter into Areas in Need of Protection (AINPs) and Sites in Need of Protection (SINPs). AINPs are considered large-scale regions of ecological importance, and the three proposed Areas are the Kane Fracture Zone, Vema Fracture Zone, and Romanche Fracture Zone. The 2022 draft nMAR REMP proposes to protect these areas as integrated systems from direct or indirect impacts of mining in the Area. SINPs focus on finer-scale areas where VMEs have been identified; the 2022 draft nMAR REMP identified 11 active vent ecosystems within existing exploration contract areas. It has further identified sites and areas where precaution is warranted, based on inferred location of vents and data from coral and sponge habitat suitability modelling.

6.4. Introduction of substances

6.4.1. Litter

Marine litter/debris is defined by UNEP (2009) as 'any persistent, manufactured or processed solid material discarded, disposed of or abandoned in the marine and coastal environment' and can be broadly categorized in one of five groups: plastic, paper, metal, textile, glass and rubber. Plastic accounts for 50–90 % of marine litter globally (Agamuthu et al., 2019). Marine debris is ubiquitous, found at all depths globally, and even in the most remote regions (Galgani et al., 2015). Ocean currents provide a transport pathway for marine debris, as seen with the accumulation which produced the Great Pacific Garbage Patch (Moore et al., 2001). Highest concentrations observed in the North Atlantic Garbage Patch are estimated at between 4000 and 50,000 pieces per square mile, similar to concentrations in the Pacific (Law et al., 2010).

In the North Atlantic, litter is well documented in deep waters of European Seas (e.g., Mordecai et al., 2011; Pham et al., 2014; Oliveira et al., 2015) and to a lesser extent in the Caribbean Seas (e.g., Debrot et al., 2014; Botero et al., 2020) where global inequalities may limit access to ROV-based research. Marine debris can either enter the marine environment via land-based sources (~80 %) or marine-based sources (~20 %) although these proportions are estimates and have not been verified (NPFMC, 2011; GESAMP, 2021). In the South-Western Caribbean, deep-sea litter was considered to stem more from land-based than ocean-based sources (Botero et al., 2020); in the Leeward Dutch Caribbean, deep-sea litter appeared to be derived from food and beverage containers and this littering pattern may be representative of small populated volcanic islands throughout much of the Caribbean (Debrot et al., 2014).

Marine debris accumulates in several habitats, but canyons act as major sinks of debris due to the topography and hydrodynamics (Galgani et al., 1996; Ramirez-Llodra et al., 2013; Schlining et al., 2013; Pham et al., 2014; Tubau et al., 2015) and the deep-sea becomes the ultimate resting place, with up to 11 million metric tonnes residing on the seafloor (Zhu et al., 2024). Marine debris can damage both the environment and the ecosystem (Gall and Thompson, 2015; Kühn et al., 2015; Kühn and Van Franeker, 2020). Wildlife may become entangled or may ingest plastic (Kühn and Van Franeker, 2020; refer to Kühn et al., 2015 for more details). Suffocation, physical damage of sessile fauna (e.g., corals, sponges, crinoids), and ghost fishing by lost or discarded fishing gear (Ramirez-Llodra et al., 2013; Pham et al., 2014; refer to Bruemmer et al., 2023 for litter-fauna interactions) are commonly reported. See Fig. 12 for example occurrences.

Plastics are manufactured using toxic chemicals which can cause toxicological effects in the marine environment when degraded into microplastics that accumulate in sediments (Thompson et al., 2009). While in its floating phase, litter that eventually reaches the deep sea can adsorb additional toxins (Gall and Thompson, 2015). As they are hydrophobic, microplastics can adsorb additional persistent organic

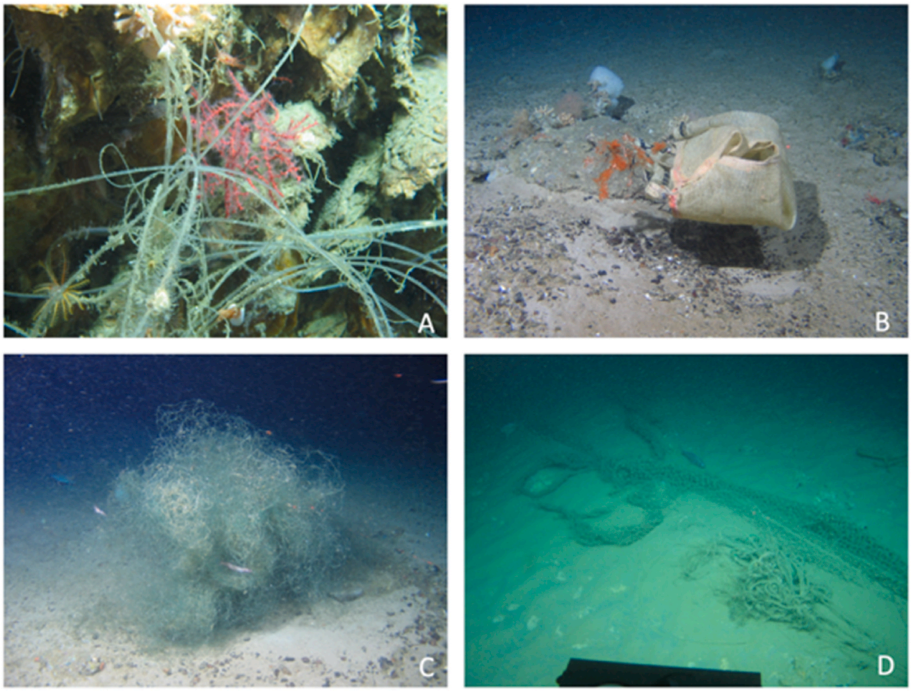

Fig. 12. Evidence of human impacts on deep-sea ecosystems of the North Atlantic. A) Monofilament entangling fauna, 882 m depth, Whittard Canyon, Ireland B) Litter, ~1100 m depth, Porcupine slope, Ireland C) Lost monofilament net, 1394 m depth, Porcupine slope, Ireland; D) Lost trawl gear, 1391 m, Whittard Canyon, Ireland. All photos taken by ROV Holland I deployed from RV Celtic Explorer, copyright Marine Institute. A, expedition CE16009; B, C, CE13008; D, CE23010.

pollutants from seawater. This is exacerbated by a large surface area to volume ratio and they may become up to a million times more contaminated than the ambient seawater (Mato et al., 2001; Hirai et al., 2011; see Rochman, 2015 for more detail of chemicals associated with plastic debris). There are estimated to be 11.6–21.1 Mt of polyethylene, polypropylene and polystyrene microplastics in the Atlantic epipelagic zone (Pabortsava and Lampitt, 2020), whose ultimate fate could be deep ocean sediments. *In situ* measurement of vertical fluxes of microplastics at 50–600 m in the North Atlantic Gyre, show how microplastics can interact with the marine carbon cycle, becoming aggregated into marine snow (Galgani et al., 2022). Once ingested by organisms, as well as causing direct toxicity (e.g., de Oliveira Soares et al., 2020; Ardestani, 2022), there is a potential route for bioaccumulation and biomagnification of microplastics and associated chemical additives (Farrell and Nelson, 2013; see Teuten et al., 2009 review for transfer of persistent organic pollutants to marine organisms via microplastic vectors) through the trophic chain (Wright et al., 2013). Exposure of deep-sea corals to microplastics is not well explored, but exposure to low-density polyethylene particles negatively impacted growth of *Desmophyllum pertusum* (Chapron et al., 2018; Mouchi et al., 2019).

Marine debris may also provide new habitats for microorganisms (Woodall et al., 2018) and even promote the extension range of some benthic species that may settle on debris and be transported to other areas (Song et al., 2021). Nevertheless, the prevalence of marine debris will continue to have detrimental impacts until appropriate action is taken to reduce the input of debris into the marine environment (Agamuthu et al., 2019).

6.4.2. *Deliberate dumping*

6.4.2.1. Historical dumping. The North Atlantic, once assumed to have an almost unlimited assimilation capacity, was historically viewed as an easy solution to waste disposal. It has been the site of sewage disposal, radioactive waste disposal, chemical disposal, and weapons disposal (Tyler, 2003; Ramirez-Llodra et al., 2011). Concern over such activities led to the London Convention on the Prevention of Marine Pollution by Dumping of Wastes and Other Matter (1972), and an update to this, the 1996 London Protocol, which came into force in 2006. The London Protocol, which has been ratified by 53 states including most of the European nations on the eastern margin of the Atlantic, Iceland, Canada but not the US, bans the dumping of all materials at sea without a permit, and allows permits only for eight categories of waste. These include sewage sludge, dredged material, fish processing waste, vessels and offshore platforms, geological material, natural organic material, bulky items where the impact is mostly physical, and carbon dioxide streams (IMO, 2014). In October 2022 at a meeting of the Contracting Parties a proposal was made to remove sewage sludge from the reverse list.

Notable historical dumping activities include sewage disposal at Deep Water Dump Site 106, located 106 miles SE of Ambrose Light New York where seafloor depth is approximately 2500 m (Tiedemann, 1984). Between 1961 and 1992, chemicals, armaments and over 30 million tonnes of sewage sludge were dumped at the surface at this site. Among the largest chemical dump sites was the Puerto Rico Dumpsite over the Puerto Rico Trench, where the seafloor depth is between 6000 and 8000 m. Between 1973 and 1981, 2.5 million tonnes of pharmaceutical waste were dumped here (O'Connor, 1983). Munitions were dumped following World War II with one of the largest dump sites for these being Beaufort Dyke, a submarine depression reaching approximately 300 m depth between Northern Ireland and Scotland, where over 1 million tonnes were deposited. These now act as a potential source of trace metals to other nearby areas (Callaway et al., 2011). Rather more radioactive waste has been disposed of in the North East Atlantic than the North West Atlantic (42.32 PBq versus 2.94 PBq; Feyn, 2001). Radioactive waste has mostly been solid with a low enough radionuclide content that it can be handled normally without shielding, and has been dumped at depths between 1500 and 5000 m (Calmet, 1989; Feyn, 2001). The worst excesses of dumping are now in the past with public awareness playing an active role in policy. In the late 1990s, public outrage at the proposal to sink the Brent Spar oil storage platform in the North East Atlantic effectively prevented that action (Tyler, 2003).

6.4.2.2. Ongoing dumping. The type of materials that are currently still being dumped in the ocean are: uncontaminated sediments resulting from dredged material, vessels, fish waste, etc (US EPA, 2024), but many of these may not be reaching the deep-sea floor. In addition, new materials are now being considered to be dumped in light of climate change mitigation initiatives such as marine carbon dioxide removal (mCDR) and marine solar radiation management (mSRM). mCDR will actively dump material in the ocean at large scales, through ocean alkalinity enhancement, ocean fertilization, or deep ocean biomass sinking. Similarly, mSRM will introduce reflective materials such as engineered particles or reflective bubbles (e.g. GESAMP, 2019). These actions will be at very large scales and may potentially affect the deep sea. The current lack of knowledge of potential impacts calls for a precautionary approach before the application of these marine geoengineered solutions to tackle climate change (Levin et al., 2023).

6.5. Climate change

6.5.1. Ocean acidification

Around one quarter of all anthropogenic CO_2 is absorbed by the ocean (Watson et al., 2020). This process increases the amount of free hydrogen ions in the ocean, thus lowering the pH – a process known as ocean acidification and which has particular impacts on calcifying organisms. Carbonate chemistry is complex, with pH, temperature and pressure among the factors that control the carbonate compensation depth (CCD) – the depth at which the rate of calcium carbonate ($CaCO_3$) dissolution equals the rate of its accumulation. Throughout much of the North Atlantic the CCD is deeper than the depth of the seafloor, but in the western North Atlantic, it rises to around 4500 m (Sulpis et al., 2018). Modelling suggests that the calcite saturation horizon in the North Atlantic has risen in recent decades, leading to calcite dissolution in seafloor sediments. This has potential to have profound effects on benthic calcifiers (Sulpis et al., 2018).

Deep-sea organisms normally use one of two forms of calcium carbonate – either calcite (e.g., foraminera, some molluscs, echinoderms, calcareous sponges, bamboo corals and some other octocorals) or aragonite (e.g., pteropods, bivalves and other molluscs, scleractinian corals, and bryozoans) (Ries et al., 2009; Ries, 2010; Clark et al., 2020). Calcite is the least soluble of the two minerals, and its saturation horizon is normally only slightly shallower than the CCD. Aragonite is more soluble, and the aragonite saturation horizon is shallower; for example, off the Iberian Peninsula, the aragonite saturation horizon is at approximately 2500 m (Fontela et al., 2020). A shoaling of the aragonite saturation horizon could have profound effects for cold water corals. Models (Fontela et al., 2020) predict that Labrador Sea Water (1500–2500 m depth) off the Iberian Peninsula could become unsaturated by 2053 under SSP2-4.5. Under this scenario, Mediterranean Water (500–1500 m, also the depth range of many aragonitic corals) would not become unsaturated, but could become unsaturated by 2070 under SSP3-7.0. Under scenarios in line with the Paris Agreement, neither water body would become unsaturated. Calcifying corals such as *Desmophyllum pertusum* can still build calcium carbonate skeletons in undersaturated conditions although this may require increased energy and feeding and may result in deformed skeletons (see summary in Puerta et al., 2020), but framework reef, on which so much biodiversity is dependant, would begin to dissolve. Researchers have estimated dissolution of framework reef off the Iberian Peninsula could happen in less than hundred years if the Paris Agreement is not met (Fontela et al., 2020). Models have predicted similar scenarios in the Irminger and Iceland Basin (Pérez et al., 2018; García-Ibáñez et al., 2021). Indeed, between 1991 and 2016, the aragonite saturation horizon shoaled by approximately 150 m in the Irminger Sea and models suggest that it could shoal by more than 1000 m if climate change remains unchecked (Pérez et al., 2018).

6.5.2. Temperature/ocean warming

In August 2023, the North Atlantic sea surface temperature (SST) was 1.4 °C warmer than the 1982–2011 average (Kuhlbrodt et al., 2024). The ocean's ability to absorb heat from the atmosphere is crucial in mitigating warming, however increasing SSTs are likely to have detrimental impacts on marine fauna, experienced both directly and indirectly by deep-sea benthos. Warming is predicted to contribute to increased ocean stratification, resulting in weakening ocean currents (e.g., the AMOC, Madan et al., 2023; See 6.5.3 Deep Ocean currents), expanding oxygen minimum zones (6.5.4 Hypoxia), and changes in primary productivity (6.5.5 Potential changes in primary productivity), all of which have individual impacts on deep-sea biodiversity. Temperature in the deep ocean is generally very stable which may encourage the idea that deep-sea biodiversity is unlikely to be influenced directly by warming, however approximately 19 % excess atmospheric heat is absorbed below 2000 m (Talley et al., 2016). While warming may be slower in the deep sea than shallow water, the rate of deep-ocean warming is increasing (Brito-Morales et al., 2020). Some deep-sea species produce planktonic larvae and there is evidence that some larvae migrate to warmer surface waters (Arellano et al., 2014; Yahagi et al., 2017), and thus increasing warmer surface waters may negatively affect these larvae and consequently recruitment in the deep sea.

Ocean warming has the potential to alter the distribution and diversity of deep-sea organisms (Yasuhara and Danovaro, 2016). Evidence of a positive relationship between North Atlantic microfaunal diversity and temperature is present in Paleoecological research (Yasuhara et al., 2009), but present-day deep-sea fishes show contrasting patterns (Emblemsvåg et al., 2020) with northern range expansions and reduced suitable habitats (Morato et al., 2020). Deep-ocean temperatures are not expected to exceed the thermal tolerance of the important CWC *Desmophyllum pertusum* (Brooke et al., 2013)*,* however they could be fatal to corals living closer to their physiological tolerance. Despite this, combined climate change impacts may reduce the suitable habitats of scleractinian corals in the North Atlantic by more than 50 % (Morato et al., 2020). Additionally, marine heatwaves may put shallower CWCs – such as those in the Northeast Atlantic or on seamounts – at risk of extreme temperatures (Puerta et al., 2020). Since thermal tolerance varies between taxonomic groups, further research should encompass a wider range North Atlantic diversity – particularly benthic organisms below 1500 m – to allow a better understanding of physiological and ecological responses to a warmer environment, and thus the impacts on biodiversity.

6.5.3. Deep ocean currents

Stommel (1957) first described the deep-water circulation belt that connects all oceans on earth. In the Atlantic, this is characterized by warmer northward flowing waters and deep colder waters flowing southward. Anthropogenic activities can change physical properties of the ocean, for example through heat balance, leading to variation in density gradients and therefore ocean currents. Because of the heat transport facilitated by the AMOC (see Section 2.1), this circulation is key in understanding the impacts of a changing climate on the oceans. Recent improvements in hindcast models (VIKING20X; Biastoch et al., 2021) have led to realistic simulations of Atlantic circulation including the decline of the subpolar AMOC as measured by a drop in Deep Western Boundary Current transport in the Labrador Sea at 53°N.

Currents are crucial for mixing internal ocean waters via breaking of internal waves and turbulence (Moum, 2021). Globally, mixing determines the distribution of water masses on the largest spatial scales. For example, intermediate waters in the north Atlantic are crossed by the Mediterranean outflow, which creates salinity gradients and 'salt fingers', vertical columns of turbulence that enhance ocean mixing and nutrient replenishment at oligotrophic depths (Kawase and Sarmiento, 1986; Oschlies et al., 2003). Although several studies highlight the potential involvement of large aggregations of organisms in the creation of biomixing, their role is not yet totally understood (Kunze, 2019, and references therein; Fernández-Castro et al., 2022). Oceanic currents also play a major role in the transport and dispersion of pollutants, including plastics, at the global scale.

Ocean circulation also plays a key role in weather patterns and climate, affecting all areas of life on Earth (Siedler et al., 2001; Poloczanska et al., 2013). For example, changes in ocean physical characteristics and ocean currents displace the less mobile species (i.e. the base of food webs), ultimately affecting larger animals (i.e. apex predators) with a northward migration of many fisheries stocks (Kubelka et al., 2022). Most of the world's commercial species are concentrated close to the continental coasts, particularly areas where deep currents (i.e. upwelling, eddies) drag deep nutrients to the surface (Kämpf and Chapman, 2016; Peña et al., 2015, 2018). However, the open ocean is inhabited by the most abundant invertebrates in the world, the meso- and bathypelagic species, playing as little climate pawns in the 'carbon pump' through active transport of carbon from the surface and its remineralization at depth (Sarmiento-Lezcano et al., 2022a,b). These oligotrophic areas are poorer in nutrient content, but temporal enhancement of nutrients occurs by means of mesoscale currents such as eddies or slope currents that create nepheloid layers dragging biogenic material from the coast (Peliz et al., 2009; Palomino et al., 2016).

Global efforts to collect large databases on the ocean's physical and biogeochemical properties are allowing less studied or accessible areas such as ice-covered zones (Johnson et al., 2022) to be evaluated, but datasets are still in general limited to the first thousand meters of the water column. Additionally, vertical resolution of physical data is often restricted to 1 m, preventing the detection of microstructures and associated phenomena. Technological challenges to study life in deeper waters are being overcome (Peña and Hernandez-Leon, 2023) but oceanographic data with the same level of resolution are not yet available, precluding the combined study of deep ocean currents and marine life.

6.5.4. *Hypoxia*

Oxygen depletion in marine systems can be continuous, seasonal or incidental. In the Atlantic region, shallow water and coastal hypoxia occur in enclosed seas (the Black Sea, Baltic Sea, and parts of the Mediterranean), in Norwegian fjords and in the Gulf of Mexico. The largest continuous hypoxia, also known as mesopelagic oxygen minimum zones (OMZs), are oceanic and occur in association with upwelling regions. They result from biochemical oxygen consumption, with circulation affecting their distribution and position within the water column (Wyrtki, 1962). The Atlantic has relatively few oxygen minimum zones (Karstensen et al., 2008) and North Atlantic OMZs have relatively high oxygen minimum values of about 35–40 μmol kg^{-1}. OMZs in the Atlantic include one in the Benguela Upwelling System off Namibia. This OMZ intercepts with the continental slope resulting in altered benthic communities (Levin, 2003). Another permanent midwater oxygen minimum zone occurs in the eastern tropical Atlantic where it ranges from 300 to 600 m (Karstensen et al., 2008; Gilly et al., 2013). Since ocean life depends on oxygen, OMZs may structure pelagic community distribution. For example, *Beroe* ctenophores avoid depths with reduced oxygen levels, while *Lilyopsis* siphonophores occur specifically at the depths of the Eastern Tropical Atlantic OMZ (Hoving et al., 2020). Some gelatinous fauna are well adapted to OMZs due to their ability to store oxygen in the mesoglea (Thuesen et al., 2005). Oxygen minimum zones in the open ocean are expanding as a result of warming, reduced mixing and ventilation, and increased stratification (Stramma et al., 2008), with varying implications for ocean life (Gilly et al., 2013). Expansion of Atlantic OMZs has reduced the habitat volume and made billfishes increasingly vulnerable to fisheries (Stramma et al., 2012). Mesoscale eddies in the eastern tropical Atlantic that originate from off West Africa and propagate westwards may have extremely low oxygen levels when encountering the Cape Verde islands (Karstensen et al., 2015). The conditions inside these deadzone eddies may prevent pelagic fauna from migrating and select for gelatinous taxa with tolerance for hypoxia (Hauss et al., 2016).

6.5.5. *Potential changes in productivity*

Primary productivity in the North-Atlantic surface ocean is expected to decrease due to the impacts of climate change, altering deep-sea communities. Climate-induced increases in sea surface temperature (see 6.5.2) and ocean acidification (see 6.5.3), precipitation and ice sheet meltwater can intensify stratification (Bopp et al., 2013), weaken ocean circulation and reduce nutrient upwelling (Kwiatkowski et al., 2019), all leading to reduced surface primary production. Productivity in the North-Atlantic ocean is expected to decline the most (up to −40 % primary productivity) globally, due to weakening of the Atlantic meridional overturning circulation (Steinacher et al., 2010). The majority of deep-sea ecosystems rely on particulate organic carbon (POC) from the surface ocean as the base of their food web, therefore changes in surface primary productivity directly impact these ecosystems (Glover et al., 2010). Primary productivity declines are predicted to have notably detrimental effects on the already food-limited bathyal and abyssal ecosystems (Jones et al., 2014b; Larkin et al., 2010; Sweetman et al., 2017). This is likely to reduce deep-sea biomass – specifically of macrofauna (Yool et al., 2017), and at coral gardens and seamounts (Jones et al., 2014b). Climate-linked fluctuations in POC to the deep North-Atlantic have been documented and have been impacting deep-sea communities since the early 2000s (Ramirez-Llodra et al., 2004; Ruhl and Smith, 2004). Furthermore, they have been consistently documented to impact biomass and community structure, particularly in the Northeast Atlantic (Brun et al., 2019; Horton et al., 2020; Osman et al., 2019). Ultimately, changes to deep-sea ecosystems will likely be detrimental to the functions they provide (Thurber et al., 2014), resulting in lower carbon sequestration and fewer habitat provisions (Sweetman et al., 2017), which have potential for negative feedback effects on the physical environment (Hilmi et al., 2023).

However, there are still major uncertainties in primary productivity projections, specifically when considering physical and biogeochemical factors (Tagliabue et al., 2021), with potential for primary productivity to increase locally, up to certain threshold levels for certain species, and the combined effects on deep-sea biodiversity. Ruhl et al. (2023) outline practices that could be followed and applied to improve forecasts of biomass under various future climate change-induced impacts. The state of many deep-sea ecological processes (e.g. microbial action, food-web structure, bentho-pelagic coupling) in reduced primary productivity scenarios are largely unknown; hence, research into these processes could further scientific understanding of deep-sea biodiversity in a future of climate change and provide insight into how the deep-sea can help mitigate climate challenges.

6.5.6. *IPCC models*

Although past climate changes are evident in the deep-sea observational record, these observations are sparse in both space and time. Thus, ocean models are a key tool to create spatially continuous three-dimensional projections of climatic variables necessary for effective spatial management plans for the deep ocean under climate change. Principal among these models are a suite of earth system model outputs developed by the Coupled Model Intercomparison Project (CMIP) and used by the Intergovernmental Panel on Climate Change (IPCC) and others to represent changes in physical and biogeochemical variables (e.g. the variables covered in sections 6.5 of this review) throughout the 21st century in a range of IPCC climate change scenarios (Bindoff et al., 2019). These models show that deep-ocean biodiversity faces an inevitable acceleration in climate velocities, most significantly in the mesopelagic (200–1000 m), compared with shallow waters (Brito-Morales et al., 2020) and reveal notable heterogeneity in projected impacts in areas associated with other anthropogenic impacts such as fishing, oil and gas, and deep-sea mining (Sweetman et al., 2017; Levin et al., 2020; Amon et al., 2023). CMIP model outputs have also been used to project distributions and connectivity of key deep-sea taxa and habitats with climate change (e.g. Levin et al., 2020; Morato et al., 2020), portending large reductions in seafloor biomass in a worst-case scenario (Jones et al., 2014b). Despite their utility, these models have notable biases in representing deep ocean circulation and do not resolve important mesoscale oceanographic features such as eddies (Heuzé, 2021; Liu et al., 2022; Gong et al., 2022) and large observational gaps must be filled in order to parameterize these biases (Levin et al., 2019). Statistical downscaling techniques and increases in model resolution arising from increases in computational accessibility and power may drastically reduce these biases in future model iterations (Haine et al., 2021), potentially revealing additional climate impacts or refugia for deep ocean systems.

7. Existing conservation measures

7.1. *International agreements, spatial mechanisms, and cooperation*

7.1.1. *Cartagena Convention*

The Convention for the Protection and Development of the Marine Environment of the Wider Caribbean Region came into force in 1986. This regional legal agreement is also known as the Cartagena Convention and its goal is to protect the marine ecosystems in the Gulf of Mexico, the Caribbean Sea and the adjacent Atlantic south of 30° N within 200 nautical miles (nm). Three technical protocols support the Cartagena Convention in the Wider Caribbean Region: Co-operation in Combating Oil Spills (1986), Specially Protected Areas and Wildlife (SPAW 2000), and Pollution from Land Based Sources and Activities (2010). The SPAW Protocol has among its aims reaching the global Aichi Target 11 of the Convention on Biological Diversity that is seeking to conserve at least 10 % of coastal and marine areas, and the new regional target of the Caribbean Challenge Initiative to protect 20 % of coastal habitats by 2020. SPAW requires Marine Protected Areas (MPAs) to be designated to protect rare and fragile habitats and ecosystems where endangered and threatened species exist. Among the major threats recognised to the deep sea in the Wider Caribbean Region are the direct overexploitation of resources, which includes fishery and oil and gas drilling activities. Oil spills from extraction and from shipping can also be a threat if deep sea and ultra-deep water oil extraction expands; such an expansion, if done carefully, could provide valuable information from deep-sea ecosystems (UNEP-CEP, 2020). After the Deepwater Horizon oil spill response, it was recommended that national contingency plans should include offshore areas and an organization scheme, such as the Incident Command System (Sagrera, 2014). Co-operation through regional preparedness and response capacity and assistance could be an important tool in combating oil spills. As of August 2021, the SPAW protocol has been ratified by 18 states: The Bahamas, Barbados, Belize, Colombia, Cuba, Dominican Republic, France, Grenada, Guyana, Honduras, Netherlands, Nicaragua, Panama, Saint Lucia, St. Vincent and the Grenadines, Trinidad and Tobago, USA, and Venezuela. The number of MPAs in the insular Caribbean has significantly increased in the last 20 years with the French and Dutch territories and the Dominican Republic leading and having almost 14 % coverage of oceanic and deep-sea MPAs. The insular Caribbean has MPA coverage in oceanic areas and at depths >200 m of almost 7 % (Knowles et al., 2015).

The Regional Seas Programme, focused on deep ocean issues in its early stages, tried to reduce the sea's degradation through cooperative efforts and is considered the background of the Pollution from Land Based Sources and Activities protocol (Powers and VanderZwaag, 2008).

7.1.1.1. Cartagena protocol on biosafety to the Convention on Biological Diversity. The Cartagena Protocol is an international legal instrument combining health, safety, and environment that into force in 2003 complementing the Convention of Biodiversity and regulating biotechnology. It has been suggested that, due to its approach to biotechnology, it could serve as a model of a regulatory framework for ocean fertilization (Hubbard, 2016).

7.1.2. *The Oslo-Paris convention (OSPAR)*

OSPAR is a regional seas convention and is the mechanism by which 15 Governments and the EU cooperate to protect the marine environment of the Northeast Atlantic. Originally focused on marine pollution, the OSPAR convention evolved to also consider protection of 'threatened and declining species and habitats' listed under Annex V of the convention. At the Ministerial Meeting in Sintra in 1998, OSPAR Ministers agreed to promote the establishment of a network of marine protected areas for the protection of Annex V species and habitats and, following a period of preparatory work, the 2003 OSPAR Ministerial Meeting in Bremen adopted Recommendation 2003/3 on a network of marine protected areas with the purpose of establishing an ecologically coherent network of Marine Protected Areas in the Northeast Atlantic that is well managed by 2016, later updated to 2020. The OSPAR network of MPAs (see Fig. 13) aims to protect, conserve and restore species, habitats and ecological processes which have been adversely affected by human activities; to prevent degradation of, and damage to, species, habitats and ecological processes, following the precautionary principle; and to protect and conserve areas that best represent the range of species, habitats and ecological processes in the maritime area. Within nations EEZs, OSPAR MPAs are identified by national governments, and the majority of OPSAR MPAs are designated within territorial waters (overall coverage of 21.2 %). Outside of EEZs, OSPAR MPAs can be proposed by the OSPAR secretariat, national Governments, scientists, non-governmental organizations and wider civil society. In 2010, acknowledging the ecological value of Charlie Gibbs Fracture Zone (CGFZ) and aiming to protect it, the Charlie-Gibbs South High Seas MPA was declared (OSPAR, 2010/053). In 2013, a second MPA was established to protect the north of the CGFZ, but it only covers the water column. According to the 2023 OSPAR Quality Status Report,[7] 19.5 % of the OSPAR region that encompasses High Seas or Extended Continental Shelf areas is protected by OPSAR MPAs. Recent designations include the 600,000 km^2 North Atlantic Current and Evlanov Sea (NACES) MPA, first designated in 2021 for seabirds (protecting the water column) and extended in 2023 to include the seabed with additional protection for coral gardens and deep-sea sharks among others.

7.1.3. *Europe*

Conservation measures in European countries are fostered by European directives such as the Habitats and Birds Directives. The EU Habitats Directive requires member states to identify Special Areas for Conservation (SACs) for the projection of habitats or species listed on Annex I and II of the Directive respectively. The Birds Directive requires member states to identify Special Protection Areas (SPAs) for the conservation of birds. Collectively SACs and SPAs are known as Sites of Community Importance and form a network of protected sites across Europe known as the Natura 2000 network. Several 'deep-sea' SACs have been notified for the protection of reef habitat, most often *Desmophyllum pertusum* reef but also geogenic reef hosting coral gardens. Fisheries are managed at European scale through the EU Common Fisheries Policy. In addition to national advice, ICES coordinates the provision of scientific expertise and advice to the European Commission on measures relating to sustainable management of European Fisheries. In 2016, the EU adopted the Deep-sea Access Regulation, which contained two measures for the preservation of deep-sea ecosystems. The first was a bottom trawling ban at depths below 800 m, which was implemented as early as 2017. The second was a ban on bottom-fishing gears at depths below 400 m where Vulnerable Marine Ecosystems are known or likely to occur. This last measure was implemented for the first time in 2022 (Commission Implementing Regulation (EU) 2022/1614). Following ICES recommendations (van Denderen et al., 2022), 87 areas

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[7] https://oap.ospar.org/en/ospar-assessments/committee-assessments/biodiversity-committee/status-ospar-network-marine-protected-areas/assessment-sheets-mpa/mpa-status-2023/.

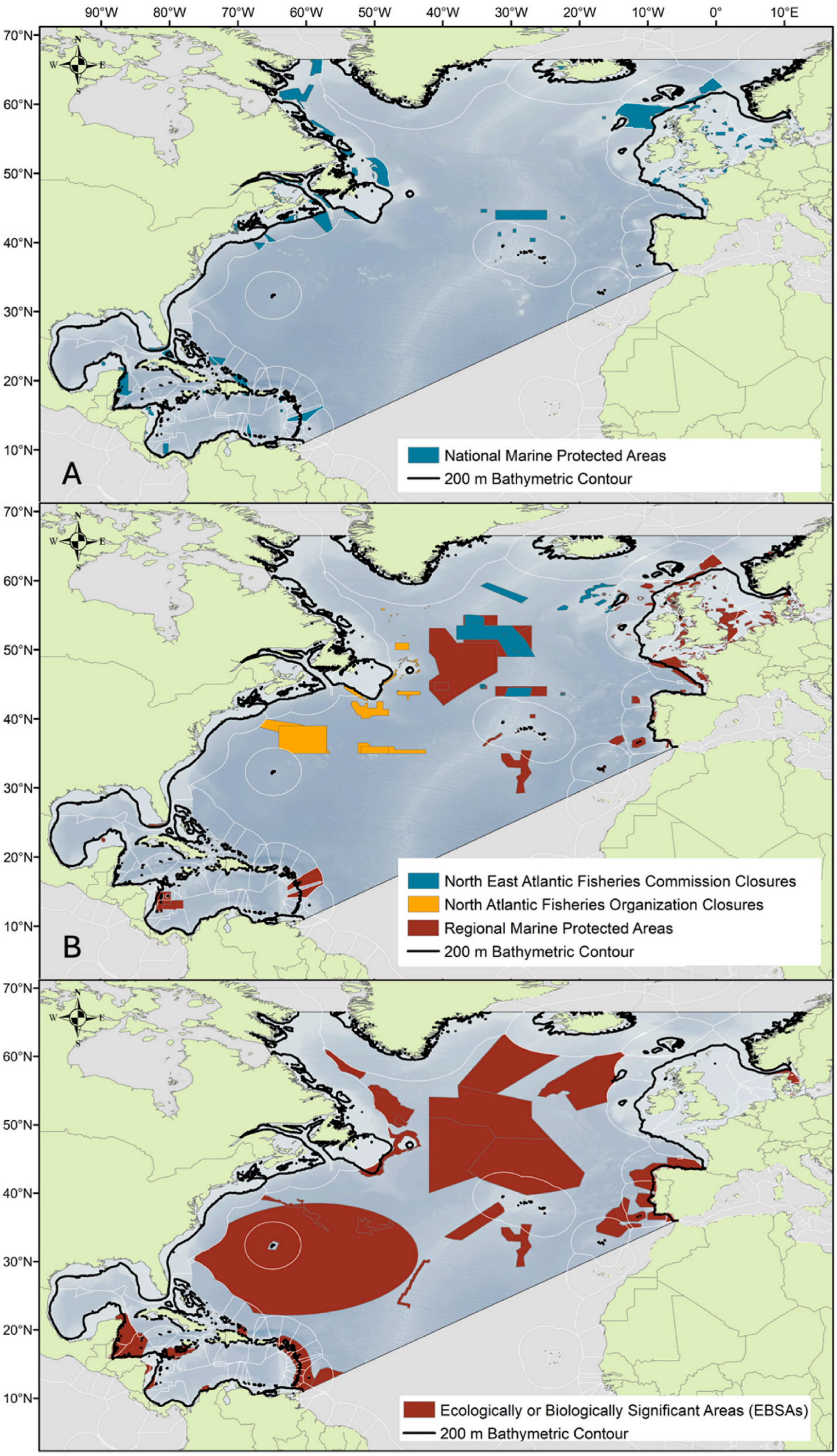

Fig. 13. North Atlantic Areas based conservation tools A, National Marine Protected Areas; B, Fisheries closures and regionally agreed Marine Protected Areas (including areas outside EEZs); C, Ecologically or Biologically Significant Areas.

totalling 16,419 km^2 were closed to bottom fishing in Atlantic EU waters, over an area extending from northern Norway to the Gulf of Cádiz.

7.1.4. Regional fisheries management organizations (RFMOs)

RFMOs are international organizations established under the UN FAO. They establish binding measures for sustainable management of fisheries in ABNJ and conservation of biodiversity. In the North Atlantic there are two RFMOs, the North-East Atlantic Fisheries Commission (NEAFC) and the North Atlantic Fisheries Organization (NAFO) who manage the north-east and north-west regions of ABNJ respectively. In addition, the Western Central Atlantic Fisheries Commission (WECAFC) is an advisory regional fisheries body formed to promote the effective conservation, management, and development of the living marine resources in the Wider Caribbean.

RFMOs are mandated to put in place measures for the conservation of Vulnerable Marine Ecosystems via UN General Assembly Resolution 61/105. This resolution "calls upon States to take action immediately, individually and through regional fisheries management organizations and arrangements, and consistent with the precautionary approach and ecosystem approaches, to sustainably manage fish stocks and protect vulnerable marine ecosystems, including seamounts, hydrothermal vents and cold water corals, from destructive fishing practices, recognizing the immense importance and value of deep sea ecosystems and the biodiversity they contain"; There are three principle means by which action is achieved: areas may be closed to damaging fishing practices where VMEs are known or likely to occur; new fishing areas require an environmental impact assessment prior to opening; and, where fishers encounter VME beyond set by-catch weight thresholds, they must cease fishing and move a set distance away from the VME encounter location (the so called implementation of the move-on-rule). Both NEAFC and NAFO have been proactive in identifying areas of VME and closing such areas to bottom trawl fishing activities, although NEAFC has been subject to criticism as it currently does not use models to identify where VMEs are likely to occur. There are several VME bottom trawl closures in North Atlantic ABNJ (Fig. 13).

In addition, the International Commission for the Conservation of Atlantic Tunas, ICCAT, is an intergovernmental fishery organization responsible for the conservation of tunas and tuna-like species in the Atlantic Ocean and its adjacent seas. There are no current spatial management actions in place under ICCAT.

7.1.5. Convention on Biological Diversity (CBD)

The CBD is an international treaty that was adopted in 1992 at the Earth Summit in Rio de Janeiro. It entered into force on December 29, 1993, has 196 Parties and 168 signatories. Notably the United States of America and the Holy See are the only two nations who are not parties to the CBD. Its provisions include the conservation of biological diversity, the sustainable use of its components, and the fair and equitable sharing of benefits arising from the use of genetic resources. In 2008 the CBD formally adopted the idea to identify and protect particularly important marine areas in the world's oceans based on a set of scientific criteria. These areas are known as ecologically or biologically significant marine areas or EBSAs. The CBD scientific criteria for identifying EBSAs (annex I, decision IX/20) are 1. Uniqueness or rarity; 2. Special importance for life history stages of species; 3. Importance for threatened, endangered or declining species and/or habitats; 4. Vulnerability, fragility, sensitivity or slow recovery; 5. Biological productivity; 6.Biological diversity; 7. Naturalness. Between 2011 and 2019, 338 areas meeting the EBSA criteria were described, 34 of which are in the North Atlantic and Caribbean. Identification of a site as an EBSA does not trigger any management actions, however it does allow other agencies to use their own tools to enhance conservation in a particular area already identified as important for conservation. The EBSA process includes areas within national jurisdiction and areas beyond national jurisdiction.

7.1.6. The International Seabed Authority (ISA)

Within the North Atlantic region the ISA have issued exploration licenses for polymetallic sulphides to the Government of Poland, the Government of the Russian Federation and Government of France via IFREMER. The licensed area lies south of the Azores on the Mid Atlantic Ridge and is known to the ISA as the Northern Mid Atlantic Ridge. As part of their strategy to ensure protection of the marine environment, the ISA are in the process of developing a Regional Environmental Management Plan (REMP) for this area. One element of the REMP is the identification of Areas of Particular Environmental Interest (APEIs); these are non-mining zones that form a network designed to represent the full range of biodiversity and habitats in the region. ISA workshops held in Portugal in 2019, and on-line in 2020, identified a series of Sites in need of protection (SINPs), Areas in need of protection (AINPs) and Sites/Areas in need of increased precaution as part of the development of a REMP for the Northern Mid-Atlantic Ridge (see section 6.3.2 Deep-sea mining). SINPs are fine-scale sites, where there is observation or evidence of vulnerable or sensitive species/ecosystems. They were described on an individual basis, using, within the context of ISA, the Food and Agriculture Organization's criteria for vulnerable marine ecosystems (VMEs). Areas in need of protection (AINPs) are large-scale areas of ecological importance due to their uniqueness and/or biodiversity. They were described using the scientific criteria of the CBD for EBSAs. Sites/Areas in need of increased precaution are either fine-scale sites or large-scale areas that have been predicted to have features that may give the site/area conservation value (International Seabed Authority, 2020). As yet, no formal APEIs have been proposed but this is likely to develop in the near future. While it was agreed that connectivity was an important consideration for determining suitable networks of representative areas, ISA workshops did not include detailed scientific discussion on connectivity.

7.2. National achievements

Many countries, but not all, in the North Atlantic have designated or implemented conservation measures, including spatial mechanisms, that include deep-water ecosystems.

The Portuguese EEZ covers 1,700,000 km^2 across three regional subzone components separated by international waters: the mainland (western and southern Iberian margin and shelf), the Azores archipelago, and the Madeira archipelago (including the Selvagens archipelago). The three, however, are united, in terms of national jurisdiction for the protection and the exploration of resources of the seabed and subsoil, and by the Portuguese proposal for the Extension of the Continental Shelf submitted to the UN Commission on the Limits of the Continental Shelf, which results in a contiguous area of around 4,000,000 km^2. Currently, the protected area below 200 m depth corresponds to approximately 10 % of this area, 3 % protected under the OSPAR network of MPAs and 7 % under the EU Marine Strategy Framework Directive and Natura 2000 Network, covering seamounts, hydrothermal vents and other ridge habitats. In 2017, the Portuguese government convened a multidisciplinary task-force to provide advice on how to extend the existing set of MPAs in the mainland and Portuguese Macaronesian regions to include new MPAs in order to form a coherent network across 14 % of the marine space of Portugal by 2020. For example, the Azores Marine Park in the Azores region and part of the extended continental shelf includes Condor, Altair, Anti Altair, and the Meteor Complex seamounts, hydrothermal vents of the Azores triple junction and the corresponding part of the ridge, and a large area north of the Azores (the Marine Protected Area of MARNA), that encompasses abyssal, and bathyal ecosystems, and is between the Altair and Anti-Altair seamounts. In this context, four proposals to extend the protected area by a further 4 % are under evaluation and include fracture zones, cold seeps (mud volcanoes), coral mounds and seamounts. Other conservation measures that exist are fisheries closures and a bottom trawling ban. EU fisheries ministers have agreed to ban trawling on the sea bed around Madeira, the Azores and Canary Islands to save their unique coral reefs from destruction (Council Regulation (EC) No 2287/2003).[8] In October 2024, the Azores government approved legislation to establish 287,000 km^2 of marine protected area — the largest MPA network in the North Atlantic. Thirty percent of Azorean waters are now protected with 15 % designated as fully protected and 15 % as highly protected, which means that fishing and other extractive activities will

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[8] https://eur-lex.europa.eu/legal-content/EN/TXT/HTML/?uri=CELEX:32003R2287.

either be restricted or banned in these areas.

The total marine area of Spain extends to 1,008,165 km^2, including the western Mediterranean area, Gulf of Cádiz, the Cantabrian, Galician coasts and the Canary Islands. Several large MPAs protect Spain's deep waters. In the Mediterranean, the largest include the Mediterranean migration corridor for the protection of cetaceans and the Fuerteventura-Lanzarote area which cover 4.6 % and 1.4 % of the total area respectively. El Cachucho (0.3 %), the Avilés Submarine Canyon System (0.3 %), and the Galician Bank (0.1 %) MPAs protect coral-habitats off northwest Spain; the recently designated (2024) Southwest Canary Islands Seamounts (4.5 %) and Northeast Canary Islands Seamounts (3 %) protect similarly vulnerable deep-sea habitats further south in the Atlantic. The Mud Volcanos of the Gulf of Cádiz (0.3 %) are protected off southwest Spain.

In France, a network of Natura 2000 sites has been designed for the conservation of reef habitats (Habitat 1180 of the EU Habitat Directive) along the continental slope of the Bay of Biscay. The network includes seven sites of community importance encompassing in total 4547 km^2, with each site ranging from 200 m to 2000 m depth. The sites are spread along the margin, from the Brenot Spur to the Cap-Ferret Canyon, and include the range of upper-bathyal reef habitats known to occur in canyons of the northern Bay of Biscay (Van den Beld et al., 2017).

The United Kingdom has implemented a network of marine protected areas within its EEZ and wider Continental Shelf Limit, notified under various different policy measures. Here we limit consideration to UK offshore waters, defined as the area outside the territorial seas limit (12 nm from shore). The former Natura 2000 network of sites (stemming from when the UK was a member of the EU), includes both SACs and SPAs. There are currently 25 SACs that fall partly or wholly within UK offshore waters, and eight SPAs. SACs and SPAs are managed for the protection of Annex I habitats and/or Annex II species for which they are designated in the case of SACs, and the protection of vulnerable bird species in the case of SPAs. In addition England, Wales and Northern Ireland have designated Marine Conservation Zones (MCZs), which are areas that protect a range of nationally important, rare or threatened habitats and species. There are currently 89 MCZs designated in England and a further two in Northern Ireland offshore waters. In Scotland, Nature Conservation (NC) MPAs perform a similar role, and there are 13 NC-MPAs in Scottish offshore waters. MCZ and NC-MPAs have various different levels of protection in the form of specific management measures; only three in offshore waters have been identified for highly protected status, where extractive, destructive and depositional activities will be prohibited. However, management measures are not yet in place. In addition, there are various other effective area-based conservation measures (OECMs) implemented (largely spatial fisheries management measures), for example the Haddock Box on Rockall Bank.

Ireland's 2020 Programme for Government includes a commitment to expand Ireland's network of MPAs to 30 % of its maritime area by 2030, in line with the recently published EU Biodiversity Strategy. Protected sites in Ireland are, to date, primarily protected and managed under the Natura 2000 framework. Recent designations of two large deep-water SACs off the Atlantic coast of Ireland and two large SPAs in the Irish and Celtic Seas for the protection of birds, together encompassing more than 30,000 km^2, have expanded the size of Ireland's MPA network to almost 10 % of total sea area. There are currently eight deep-water SACs, seven on the continental margin and one on the slope of the Rockall Bank, and legislation is currently being developed to facilitate MPA designation for features not encompassed in the Habitat or Bird Directives.

Norway has a number of small protected areas focused on cold water coral reefs within 12 nm, but is still working on developing statutory instruments for protections further offshore or for other deep-water habitats. However, as a member of the EEA, Norway adheres to the EU > 800m trawling ban and leans on this as an OECM to give some level of protection to deep-water habitats.

The marine area of Iceland's EEZ is 758,000 km^2. Most of the fishing activities are within 500 m depth (226,000 km^2) on the shelf and slopes. There are currently extensive area-based fisheries restrictions established as Fisheries Restricted Areas (FRAs) regulated by the Act on Fishing in Iceland's Exclusive Fishing Zone. These are actively used to regulate fishing and ensure responsible and sustainable utilization of the fish stocks. The primary management goal of these areas is recovery of overharvested stocks by protecting undersized fish by prohibiting bottom-contacting fishing gear. While many of the regulations are enacted temporarily (e.g. real-time and seasonal closures), several have persisted for a long time, some over 30 years. Under the same Act, a regulation aiming for protective measures for sensitive marine areas and benthic ecosystems has been implemented. This regulation includes slightly impacted areas, cold-water coral areas, and areas of distinctive bottom ecosystems, including hydrothermal vents, coral and sponge gardens, and seamounts. Fishing with bottom-contacting gear is prohibited in these areas, protecting them from the main current destructive impact. The total area of these closures is 12,431 km^2, which is just under 2 % of the Icelandic EEZ. The Nature Conservation Act has been utilized to protect specific marine features like hydrothermal vents, areas of world heritage and nature reserve, comprising less than 0.03 % of the EEZ. Iceland has committed to the biodiversity conservation target of protecting 30 % of the ocean by 2030 and has initiated work on management plans to fulfill its objectives. FRAs, where restrictions are for bottom-contacting gears, have received interest as candidate areas for OECMs.

Greenland is currently in the process of setting up a seabed management plan and has committed to protect its biological biodiversity including marine biodiversity as part of their biodiversity strategy 2030 (Government of Greenland, 2021). Currently few areas of the Greenlandic offshore seabed are actively protected by conservation measures. In order to comply with Marine Stewardship Council regulations, the Greenlandic halibut fishery in west Greenland has voluntarily closed the area of the Greenlandic EEZ between 64°30'–68°N and has limited the majority of its demersal trawling to a defined area between 64°30' and 63°N (MFHA, 2021). Recent work has recommended a set of Greenland shelf areas to be included in conservation efforts based on identity and richness of present megafauna (Zwerschke et al., 2025).

Canada has committed to meeting the conservation target of protecting 25 % of their oceans by 2025 and 30 % by 2030. To achieve this, a number of OECMs and MPAs have already been established and legislated with a few more currently undergoing consultation, which all together will form a network of MPAs. In the Northwest Atlantic, there are currently three MPAs in deep water, the Laurentian Channel, St Ann's Bank, and the Gully. The Laurentian Channel MPA, a deep submarine valley (depth: 100–500 m) is the largest at 11,580 km^2 (0.20 % of overall conservation target) and the youngest, established in 2019, with various objectives such as protecting significant aggregations of sea pens, along with black dogfish, smooth skate and porbeagle sharks and promote the survival and recovery of northern wolffish and leatherback sea turtles. St Ann's Bank is 4364 km^2, includes a wide diversity of habitats, and was established in 2017 to protect benthic, demersal and pelagic biodiversity and productivity. The Gully, a deep submarine canyon, is the smallest (2363 km^2) and oldest of the three (established in 2007) with the goal of minimizing harm to cetaceans and deep-water corals. Canada has also established 16 marine refuges as other effective conservation measures in the Northwest Atlantic.[9] Most of these are fisheries closures or restriction zones with conservation objectives for the protection of deep water corals and sponges.

The US EEZ in the North Atlantic extends over 1,900,000 km^2 and encompasses six ecoregions in the cold, warm and tropical Northwest Atlantic Biogeographic Provinces (Spalding et al., 2007). It includes varied deep-sea habitats, including temperate and tropical shelves,

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[9] https://www.dfo-mpo.gc.ca/oceans/oecm-amcepz/refuges/index-eng.html.

slopes, canyons, ridges and seamounts, along with the deepest Atlantic trench (Puerto Rico Trench). New deep-sea exploration and research of the US EEZ in the 1990s and early 2000s increased awareness of the extent and importance of deep-sea biogenic habitats and their vulnerability to human impacts. The most widespread and serious manageable anthropogenic threats to benthic biogenic habitats are bottom-contact fishing and oil and gas development (currently limited to the Northern Gulf of Mexico) (Lumsden et al., 2007; Cordes et al., 2016; Hourigan et al., 2017). Efforts to address fishing threats led to extensive area-based closures to bottom trawling and most other bottom-contact gears covering over 263,000 km^2, most established since 2010. The largest closures were precautionary measures to prevent expansion of bottom-trawling into areas that might contain deep-sea corals and other vulnerable biogenic habitats, complemented by more targeted protections to known vulnerable habitats on the continental shelf and upper slope (NOAA, 2010; Hourigan, 2015; Hourigan et al., 2017). The management of impacts from oil and gas development on vulnerable ecosystems is principally conducted through general regulations and Notices to Lessees, including distance of avoidance from sensitive deep-water biological communities, including coral and chemosynthetic communities (Boland et al., 2017). In December 2023, the US released the scientific studies underpinning its claim to areas of the extended continental shelf beyond the EEZ. In the North Atlantic, these areas include several additional New England Seamounts, the Blake Ridge, and areas within the Gulf of Mexico (United States Department of State, 2023).

Countries in central America have taken various steps to begin to protect deep-sea ecosystems. Several MPAs designated by Mexico encompass some deep water areas (particularly where reef drop off is steep). Of major importance though is the Mexican Caribbean Biosphere Reserve, designated in 2016, which encompasses 57,000 km^2 of the Caribbean Sea and aims to protect a variety of deep-sea habitats including deep reef ecosystems, escarpments, submarine canyons and sand falls, and regions with pelagic upwelling important to turtles and whale sharks.

In 2019, the Belize government approved a plan to create “Fisheries Replenishment Zones” – essentially expansions of existing MPAs – to protect waters ranging from 200 to 3000 m depth. In 2020, the government enacted the first part of this expansion at the Sapodilla Cayes Marine Reserve, extending the reserve’s total area to 1300 km^2 and including a strictly protected area covering nearly 1000 km^2 of deep sea.

The marine area of Costa Rica is almost 12 times its terrestrial area, but most of it is in the Pacific. There, Costa Rica’s Isla del Coco National Park encompasses 54,844 km^2 and is a no take area, open only for research and tourism. It contains vast deep-sea habitats, and the 2024–2034 management plan incorporated pelagic environments, seamounts, and other focal conservation elements (SINAC, 2024). Additionally, a further marine management area—the Área Marina de Manejo del Bicentenario—was designated in 2021, covering 106,286 km^2, and its general management plan is currently under development (La Gaceta, 2022). Together, these areas form the Área de Conservación Marina Coco (ACMC), which encompasses around 30 % of Costa Rica’s Exclusive Economic Zone, making it the largest conservation area in the country (Singh et al., 2021). The exploration of Costa Rica’s Caribbean coast deep environments is more limited (Cortés, 2016; Quezada-Perez et al., 2023).

Currently, Panama protects 54 % of its marine area. In the Caribbean, the expansion of the Banco Volcán Managed Resource Area (’Área de Recursos Manejados Banco Volcán’), established in 2015, increased its coverage to 93,390.9 km^2 in 2023 (Republic of Panama, 2023). This expansion helps safeguard deep-sea environments down to 4205 m, with a mean depth of 3051 m. The total area of Bajo Volcán has been zonified, at least fifty percent (50 %) of the total protected area is designated as a zone of absolute protection. In the other 50 %, controlled fishing is allowed. Industrial fishing is prohibited in the entire area.

Colombia surpassed the goal of 30 % of marine protected areas by 2022 through joint work with the institutions that are part of the National Environmental System (SINA) and academic and scientific actors. New protected areas were declared and existing ones were expanded. Colombia thus went from having 13.41 % of marine areas under protection to more than 37 % of the country’s marine territory. In the Caribbean, the recently created Natural Reserve of Cordillera Submarina Beata (Category Ia; IUCN) spans depths from 1500 m to 4400 m (Republic of Colombia, 2022). This reserve presents both research opportunities and management challenges in the deep sea; it borders to the north with the territorial waters of the Dominican Republic and to the east with Venezuela’s platform. Activities other than conservation, research, and education are prohibited within the Natural Reserve. Since Beata Ridge is a shared space, Colombia and Dominican Republic signed an agreement in 2022 to protect it and to collaborate jointly (Beata-Taino Corridor). Additionally, the Seaflower Marine Protected Area, which is a part of the Seaflower Biosphere Reserve designated by UNESCO in 2000, protects various shallow environments as well as deep waters. This MPA is zoned for *in situ* conservation and sustainable use.

Two protected areas in Venezuela have deep water components although neither was implemented primarily for deep-sea protection. La Isla de Aves wildlife refuge protects the island of the same name west of Dominica and surrounding waters (circa ~1500 km^2 in total). Here protection is primarily in regard to sea birds and turtles, but fishing in the waters is prohibited which likely affords some protection to other habitats. Los Roques Archipelago national park protects an area of 800 km^2. Primarily designated for coastal ecosystems, the park encompasses areas where depth reaches 1700 m, although there are no specific measures in place to protect deep-sea habitats.

The territorial waters of Bonaire (Dutch ABC Islands), St. Eustatius and Saba (Netherlands Lesser Antilles) were legally established as a 25,000 km^2 nature park in 2023 with a core objective of protecting megafauna. Fisheries regulations ban purse seine nets, drift longlines, gill nets larger than 20 m x 2.5, and bottom and drop longlines with more than 20 hooks.

Many Caribbean island nations, despite being 70–99 % deep ocean by area, are yet to designate any deep-ocean marine protected areas or area-based management tools. However, several, such as Trinidad and Tobago, Dominica, St. Lucia and Barbados are moving in the right direction by undertaking marine spatial planning exercises or proposing/committing to the establishment of protected areas (FAO, 2018). However, not only are these protected areas yet to be legally established, but scientific knowledge of the habitats, communities within, as well as the functions and services they provide, remains nearly non-existent. Additional baseline research is critically needed.

France has designated a large (138,000 km^2) Specially Protected Area (Sanctuaire Agoa) under the Cartagena Convention that encompasses the territorial waters of Guadeloupe, Martinique, Saint Barthélémy and Saint-Martin, and which includes extensive areas of slope and abyssal plain. The main objective is to provide protection for marine mammals, particularly with respect to migration corridors, and breeding and nursery areas. Limited management measures are in place to date.

The Dominican Republic is actively pursuing the objective of achieving 30 % coverage of its territory with protected marine areas for 2024. In the Greater Antilles, protection in deep waters remains minimal or non-existent primarily due to a lack of scientific understanding and technical capacities for effective management. As of February 2024, extensive oceanic research is underway in the Beata Ridge, aimed at potentially designating this area as an oceanic Marine Protected Area. This initiative seeks to enhance conservation efforts, particularly for seamounts and deep waters, and contribute towards reaching a total of 24 % coverage of marine protected territory. Furthermore, in the Atlantic region, deep water studies are anticipated to conclude this year, with plans to expand the existing Marine Mammals Sanctuary Bancos de La Plata and Navidad resulting in a coverage increase to 30 % of marine protected areas by end of year.

By the end of 2022, Cuba had designated 15,435 km^2 as marine protected areas (MPAs), covering 5.5 % of its total marine jurisdiction, including internal waters, territorial sea, and exclusive economic zone (EEZ). According to its National Biodiversity Strategy and Action Plan (NBSAP), Cuba aims to conserve and manage at least 13 % of its national territory and jurisdictional areas by 2030, reflecting a 6 % increase from the 2022 baseline. This goal will be achieved through the National System of Protected Areas and other Effective Area-Based Conservation Measures (OECMs), supported by integrated and participatory spatial planning to prevent the loss of natural ecosystems. For the marine environment, the target is proportionally lower, aiming for 11.8 % coverage, with the largest expansion expected through the designation of new OECMs. Analyses are currently underway, with support from the Caribbean Biological Corridor, to identify priority conservation areas in offshore and deep-sea zones where conservation efforts are currently minimal. These areas hold significant potential for expanding marine conservation coverage, contributing further to Cuba's biodiversity protection and sustainable ocean management goals.

In the Bahamas, both the Cay Sal Marine Managed Area (16,500 km^2) and the Southeast Bahamas Marine Managed Area (25,000 km^2) encompass some deep-water habitat. However, no entity is responsible for their management. Some National Parks managed by the Bahamas National Trust expand into deeper waters and include the Exuma Cays Land and Sea Park and Conception Island National Park. Several other sites with deep areas have been designated but are unassigned to management authorities, such as Hogsty Reef Protected Area of Inagua, Southwest Bahamas Marine Managed Area, Cross Harbour Marine Protected Areas of Abaco, Southern Exuma Cays MPA, Orange Creek MPA of Little San Salvador Island and Cat Island, East Coast Cat Island, Columbus Point MPA of Cat Island, Hawk's Nest and Cutlass Creeks MPA of Cat Island, Lighthouse Point MPA of Eleuthera, West Schooner Cays MPA of Eleuthera, Flamingo Cay Spaggs of Ragged Island, Cay Verde MPA of Ragged Island, Columbus Bank MPA of Andros, Little Inagua MPA, Inagua MPA, South Inagua MPA, Southeastern Bahamas Marine Managed Area of Mayaguana, Crooked Island and Acklins, and Cay Sal Protected Area.[10],[11]

8. Research priorities to support high-level management

The deep ocean is increasingly recognised as indispensable for addressing the multiple challenges that the planet faces in decades to come (Levin, 2019). In the North Atlantic, deep-sea ecosystems are already under stress from multiple human activities (section 6). Consequently, the twin environmental crises of climate change and marine biodiversity loss are gathering momentum. Effective evidence-based decision making is required if the ocean is to prosper in the face of these crises. For this, it is essential to close persistent knowledge gaps highlighted in this review, in particular on i) distribution of species and habitats, ii) population and habitat connectivity, and iii) processes leading to ecosystem services. But, to close these gaps and ensure effective evidence-based decision making across the entire North Atlantic, including those areas where our analyses show persistent data gaps, the decolonisation of deep-ocean science must occur. The deep-sea community requires i) equitable access to ocean science infrastructures, ii) capacity sharing, and iii) for differential investment in ocean science to be addressed.

8.1. Key scientific gaps requiring further research

8.1.1. Distribution of species and habitats

Knowledge of the distribution of key species and habitats is essential to inform spatial management, including in relation to impacts in the deep ocean from human activities, area-based management tools (ABMTs), and other conservation measures, including MPAs. It is also critical to support further scientific research by identifying priority locations in which to study species, communities, and ecosystems.

At a basin scale, knowledge of the distribution of marine life is best achieved through advanced predictive modelling techniques that require unbiased and comparable/standardised datasets incorporating data from traditionally poorly sampled regions, using recently developed low-cost technological solutions, coupled with rapidly evolving artificial intelligence. This will need to be supported by substantial increases in deep-sea scientific exploration at a local scale, particularly in the EEZs of many Caribbean nations, Areas Beyond National Jurisdiction, and all EEZs below 500 m depth, as highlighted by our results (Section 4). While this should still include physical sampling, the use of autonomous underwater vehicles with mapping and imaging capabilities may help to increase the effectiveness.

The potential of big data and computer vision tools to map biodiversity calls for expanding collaborations with computer scientists to transfer the needed knowledge of these methods and facilitate their appropriation by ecologists (Goodwin et al., 2022). With the current enthusiasm surrounding artificial intelligence tools, there is a risk that its expanded use could lead to "producing more and understanding less" (Messeri and Crockett, 2024). Thus, integrating this technology into deep-sea research requires careful consideration and assessment of its appropriate and reliable applications. In this context, broad awareness of its benefits and drawbacks - achieved through experimentation, training, and thorough supervision - must accompany its development and implementation.

The most cost-effective tools for monitoring and assessing subsequent changes to biodiversity may be molecular. DNA barcoding continues to highlight undescribed deep-sea diversity (e.g., Varela et al., 2021; Morrissey et al., 2022; Taite et al., 2023) while eDNA and metabarcoding could be implemented at scale in the deep sea (e.g., Le et al., 2022; Stefanni et al., 2022) and build on recent developments such as the use of deep-sea sponges as eDNA samplers (Gallego et al., 2024).

8.1.2. Population and habitat connectivity

Connectivity is an important element in the design of effective networks of MPAs. This consideration is especially important in the context of the multiple pressures that the deep ocean is facing, as connectivity enhances resilience to and recovery from perturbations. However, data needed to assess present-day ecological connectivity are lacking for most deep-sea species. Further, climate change is expected to impact ecological connectivity in many ways, and consideration of this needs to be integrated in future-proofing conservation efforts.

To evaluate realized connectivity, large-scale sampling for genetic structure is required. Such studies can elucidate source-sink dynamics and identify areas of particular importance to conservation (e.g., DeLeo et al., 2022; Xu et al., 2024). Few studies have investigated the genetic connectivity of deep-sea invertebrates outside of chemosynthetic habitats (see review by Taylor and Roterman, 2017 and section 5.1.19 herein) and expansion of this research across multiple taxa at all spatial scales across the entire Atlantic is fundamental to expanding our understanding of conservation requirements and to delivering an ecologically coherent network of MPAs.

Alternatively, to evaluate potential connectivity (structural or demographic), knowledge is needed of current and projected future distributions of deep-sea species, particularly those most vulnerable to pressures and ecosystem engineers. For species with limited motility, potential connections across populations can be estimated from the dominant ocean currents and information on early life history, such as

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[10] https://marineplanning.org/wp-content/uploads/2019/07/Bahamas-Protected_MPA-Management-Guidance_Final-Report_rev.March2019.pdf.

[11] https://laws.bahamas.gov.bs/cms/images/LEGISLATION/GAZETTES/2021/2021-0028/2021-0028.pdf.

fecundity, timing of spawning, planktonic larval duration and larval swimming behaviour. At present, ocean circulation models at the ocean basin scale are of coarse resolution and lack accuracy in areas with high topographic complexity, such as canyons and seamounts. Additionally, validation is often incomplete, particularly near the seabed at great depths. Data on life history are sorely lacking and logistically difficult to obtain and much more effort needs to be directed towards at least bounding some of the parameters to allow for scenario analysis. Expected changes in suitable habitat, ocean circulation and some life history parameters, such as larval duration, due to ocean warming and acidification need to be described to ensure realistic projections of potential connectivity into the future.

8.1.3. *Delivery of ecosystem services*

While deep-sea ecosystems have intrinsic value, the functions and processes of the deep sea and its inhabitants are critical to human wellbeing and prosperity as well as planetary resilience (Thurber et al., 2014). Increasing our understanding will better equip us to set up effective plans for management and conservation to maintain and enhance these services. Given increasing human activities, and associated impacts, in the deep sea, as well as globally, it is imperative that humankind ensure that further development does not compromise the maintenance of ecosystem services, especially at the detriment of future generations.

While a framework to integrate deep-sea ecosystem services into management, conservation and policy is available via ecosystem service-functional groups matrices (La Bianca et al., 2023), in the North Atlantic this is not yet possible given the poor existing knowledge (Table 3). Many questions remain on the mechanisms underpinning the role of deep-sea functional groups in service delivery, particularly “supporting” services that are fundamental for the supply of other ecosystem services. Answering these questions requires new observations and standardised measures of rates of service provision enabling quantification based on habitat condition and type.

Demonstrating how ecosystem services support human well-being has been instrumental in setting policy and management objectives for sustainable resource use in terrestrial and coastal marine ecosystems. Thus, it is critical to link deep-sea ecosystem services to the benefits delivered to human society. This can be done through end-to-end logic chains as proposed by System of Environmental-Economic Accounting, Ecosystem Accounting (SEEA EA), a spatially based, integrated statistical framework for organizing biophysical information about ecosystems, measurement of ecosystem condition, capacity and rates of provision of ecosystem services in monetary and non-monetary terms (United Nations et al., 2021). SEEA EA can be applied to any geographical territory, such as environmentally defined areas within a country, or areas of policy or analytical interest such as protected areas within or beyond national jurisdiction. However, SEEA EA is poorly developed for deep-sea areas, mainly because of difficulties associated with data collection and the paucity of available data in repositories (Cummins et al., 2023). Further, because the highly cross-cutting and spatial nature of ecosystem accounting, implementation will require the active participation of representatives of many different agencies and disciplines, including geography, ecology, economics and statistics. Such highly collaborative approaches between natural and socio-economical scientists are still in their infancy in deep-sea research (Popova et al., 2023) and are of increased complexity when dealing with regional or international conservation and management actions.

8.2. *Decolonise deep-ocean science*

8.2.1. *Ocean science infrastructures*

Advances in ocean science and consequent effective ecosystem management and conservation partly depend on our capacity to acquire accurate information about biodiversity patterns and processes leading to ecosystem services. Multiple tools, from the “primary” research vessel to new platforms integrating a variety of sensors *in situ*, allow us to measure essential variables in all compartments of the deep ocean (Danovaro et al., 2020). However, the cost to access adequate research infrastructure is prohibitive to many nations, including the majority of those bordering the North Atlantic Ocean, which has led to a bias in biodiversity records towards countries with more developed economies (Fig. 5; Amon et al., 2022a; Bell et al., 2022, 2023). Despite recent efforts to develop cost-effective tools (e.g. Giddens et al., 2021; Dominguez-Carrió et al., 2021; Novy et al., 2022), access to data collection is still one of the major challenges in deep-sea science. Unsurprisingly, a global assessment of the technical capacity for deep-sea exploration and research showed that, whereas Central America and the Caribbean, like Western Africa, have limited access to marine infrastructure and deep-sea technology, North America and Northern Europe have the greatest access (Bell et al., 2022, 2023). Nonetheless, over 30 % of the respondents from North America and Europe identify access to research vessels and deep-submergence vehicles as two of the most important challenges in deep-sea research.

A first critical step to reverse the observed inequities is to address systemic barriers that are perpetuated in international ocean science governance so that underrepresented countries and regions can set objectives and prioritize ocean science and data collection relevant to their own needs (Singh et al., 2021; Ota et al., 2024). Additionally, there is a need for transnational programmes of cooperation and collaboration to better utilise the existing infrastructures and improve sharing of knowledge for mutual benefits. The consecutive phases of the European programme Eurofleets (https://www.eurofleets.eu), now Aquarius (https://aquarius-ri.eu), that granted European and international scientists access to research vessels and deep-submergence vehicles, are an example of such transnational cooperation. More science utilising shared assets should be led by researchers from underrepresented countries, and should focus on local or regional impact rather than academic metrics such as number of publications (Harden-Davies et al., 2022b; Spalding et al., 2023). This was emphasized by respondents of the Global Deep-Sea Capacity Assessment underscoring that the presence of in-country individuals with deep-sea expertise exceeds the availability of deep-sea tools (Bell et al., 2022, 2023). More access to vessels, deep submergence vehicles, sensors, and data tools would activate available expertise to conduct locally-led deep-sea exploration and research.

While the increasing capabilities of the sampling sensors and platforms to acquire more data may be helpful, it may also lead to bottlenecks in the analysis pipeline preventing data from rapidly translating into a better understanding of the North Atlantic Ocean. However, the development of large dataset analysis (big data) as well as automated image annotation (Computer Vision) methods in other scientific and commercial sectors offers the possibility to bypass this bottleneck (MacLeod et al., 2010; Schoening et al., 2016). For these new tools to effectively accelerate understanding and stewardship in the North Atlantic Ocean, the democratization of data through in-country training on its collection, analysis, and use for the marine research community must occur (Howell et al., 2019; Crosby et al., 2023; Villon et al., 2022; Spalding et al., 2023).

8.2.2. *Capacity sharing*

Capacity development is a major priority in the United Nations Decade of Ocean Science for Sustainable Development (Ocean Decade) (Polejack et al., 2025). Capacity development implies not only the provision of training to students, scientists, technical staff and policy makers, but more importantly, long-term strategies to ensure that the skills and knowledge acquired are applied to the development of marine science (Miloslavich et al., 2018; Arbic et al., 2024). There have, however, been issues raised around this framing, with the need to move away from the transactional and unidirectional notion of ‘capacity building or development’ with the integrated and bidirectional perspective of ‘capacity sharing’ (Harden-Davies et al., 2022b; Spalding et al., 2023).

As in access to infrastructure, there is a large bias in human capacity to undertake deep-sea research in nations surrounding the North Atlantic. European countries have the highest ratio of researchers as a proportion of the total population (IOC-UNESCO, 2020a), but even here the lack of financial support to attract, retain and sustain local talent in the long-term has been identified as a challenge in deep-ocean research (Bell et al., 2022). An example of this systemic issue is the authorship of this review. Despite accelerating efforts to increase global deep-sea research capacity, an authorship policy that was open to anyone who felt they had a contribution to make, and wide dissemination of the call for authors through established regional distribution lists, almost two thirds of the authorship are from the UK, USA, Germany and Portugal. Further, only 11 % of coauthors are from the under-resourced Caribbean region, the north coast of South America, and the east coast of Central America (30+ countries).

Capacity issues have been further compounded by a high rate of parachute science (de Vos, 2020, 2022; Stefanoudis et al., 2021) which has perpetuated and widened inequalities, provided little to no tangible benefit to researchers from under-resourced countries, and undermined local expertise, ultimately hindering the potential for conservation success (de Vos, 2020, 2022; Stefanoudis et al., 2021; Bennett et al., 2021; de Vos et al., 2023). International collaborations are the norm given the expensive and complex nature of deep-sea operations and it is paramount that local researchers are equal partners in such collaborations and not just facilitators of national access.

Given the imminent blue economy applications, the implementation of global ocean agreements, and the need to prevent social harms, it is urgent to make deep-ocean science more equitable and fair (Harden-Davies et al., 2022a,b). For this, a paradigm shift is needed where the scope of who leads, who participates, and who benefits is broadened by developing protocols to ensure deep-sea research programs integrate local capacity and centre local self-determined needs and priorities in order to develop solutions, especially for those who are most ocean dependent (Singh et al., 2021; Harden-Davies et al., 2022a, b; Spalding et al., 2023). Other key actions include the building of equitable partnerships and opportunities, respecting indigenous and local knowledge, guaranteeing inclusive authorship, the creation of safe working practices and spaces, establishing access agreements to peer-reviewed literature; and ensuring inclusivity by translating and inviting participation from non-English speakers (Amon et al., 2022a,b; de Vos, 2022; Harden-Davies et al., 2022a,b; Spalding et al., 2023; de Vos et al., 2023). Further, including social sciences, humanities, and co-production involving multiple disciplines will assist in addressing the complexities of issues of the geographically diverse North Atlantic (Spalding et al., 2023). Finally, integral to all of this will be acknowledgement of racist and colonial histories and reflection on one’s own positionality, privileges and power, as well as the involvement of the research community, institutions, funding agencies and publishers (de Vos et al., 2023).

8.2.3. *Differential investment in ocean sciences*

The most recent version of the Global Ocean Science Report (IOC-UNESCO, 2020a), despite underrepresentation of economically developing nations, has shown that investment in ocean sciences in nations surrounding the North Atlantic Ocean represents less than 5.5 % of the of gross domestic expenditure on research and development. Ireland (5.3 %) is the leading country in this respect, followed by Norway (4.4 %) and Portugal (3.5 %). Considering the importance of the ocean to human well-being (Thurber et al., 2014), the average 1 % of national research budgets to support ocean science is remarkably low when compared to the contribution of the ocean to the global economy. For example, in 2018, the direct and indirect impact of the ocean economy on the Portuguese economy has been translated into 5.1 % of the Gross Domestic Product (GDP) (Statistics Portugal, 2020) whereas the investment in ocean science was 0.048 % of the GDP. Realising the full potential of our ocean demands a durable balance between ocean use and ecosystem integrity, in which science and technology play a key role. As such, investment in equitable ocean science and innovation should become a priority (OECD, 2019). To achieve the ambitions of the Ocean Decade, national funding for ocean science needs to increase, and other sources must be mobilized.

Currently, public/national research and innovation funds are the major source of financing deep-ocean science (IOC-UNESCO, 2020a). Financing is generally project-based and short-term, often resulting in unsustainable outcomes once funding ends (National Research Council, 2008). Ultimately, this lack of support undermines the ability of ocean science to support ocean management and conservation. Philanthropic funding sources are becoming more common, particularly through the operation of state-of-art research vessels and deep-submergence vehicles. Private organizations, but also all funders, can play an essential in catalysing collaborative and equitable efforts and initiatives, such as data sharing, education, outreach, and building a long-term impact (IOC-UNESCO, 2020b; de Vos et al., 2023; Haugan et al., 2024).

Established and emerging ocean-based industries and activities in the deep ocean, such as offshore extraction of oil and gas, renewable energy generation, deep-seabed mining, biotechnology, and marine climate interventions, can be characterized by the application of cutting-edge science and technology in their operations (OECD, 2016). Strengthening the connection between science “producers” and science “users”, such as governments, administrative authorities, regulators, and industry could increase awareness of the pertinence of deep-ocean science, providing immediate benefits to the “users”, while potentially opening new funding channels for both applied and fundamental research. However, it must be underscored that the independence of scientific research is pivotal in understanding and monitoring the potential impacts of human activities as well as in designing conservation and restoration actions.

9. Conclusion

Despite more than 150 years of exploration of North Atlantic deep seas, many knowledge gaps persist, with considerable spatial biases in the distribution of data. There are large spatial gaps in benthic megafauna data west of the MAR in the North American and Newfoundland Basins, and in benthic macrofauna in the sub ocean basins both sides of the MAR. There are orders of magnitude fewer data from the EEZs of many nations within and bordering the Caribbean Sea as compared with EEZs of other North Atlantic nations. Pelagic data records are less numerous but have wider spatial coverage albeit with similar data gaps in the Caribbean Sea and lower efforts along the MAR and south of Greenland. The density of both benthic and pelagic records declines with depth. It has previously been suggested that the density of biodiversity data collected and published in biodiversity databases such as OBIS and GBIF could be used to track progress on Ocean Decade challenges (Muller-Karger et al., 2024). The data presented here will allow progress to be tracked for the North Atlantic over the coming years.

The areas most densely studied have contributed hugely to our knowledge of deep-sea ecosystems, but gaps in this knowledge are also many. In particular, fundamental knowledge such as distribution of the habitat (e.g., sponge aggregations) or fauna within the habitat (e.g., abyssal plains) is not well known for many ecosystems. In many cases, biogeographic patterns and connectivity are poorly understood (e.g., for seamounts, ridges, hydrothermal vents, cold seeps, abyssal plains). And while we now appreciate that deep-sea habitats contribute to key ecosystem services, knowledge of the functioning and specific processes involved is near non-existent for multiple habitats (e.g., asphalt volcanoes) and in its infancy for many better studied ones (e.g., cold-water coral ecosystems).

Thus we recommend key priorities to ensure that we have the knowledge to support the effective stewardship of deeper waters into the future and beyond the UN Decade of the Ocean. We advocate prioritizing scientific research that leads to 1) increased knowledge of the distribution of key species and habitats; 2) increased knowledge of connectivity of species and habitats; and 3) better understanding of the processes leading to the delivery of ecosystems services. However, to gain this knowledge and understanding across the breadth of the North Atlantic will require equitable access to ocean infrastructures, investment in capacity sharing, and substantial investment in equitable ocean science by governments, industry, philanthropy and private investors. Although our focus has been driven by data from the North Atlantic, our conclusions broadly align with those of studies where the focus has been wider (e.g., Roberts et al., 2023; European Marine Board, 2024).

While nations across the North Atlantic have generally improved their commitment to marine management and conservation, efforts to date mostly fall short of agreed international targets. Multiple nations have some deep-water protected areas that do have management plans, while others have identified deep-water protected areas but management plans are not in place. Several nations have committed to protecting 30 % by 2030, but much progress is required over the next five years to reach that target. Other nations have made commitments to, but not yet delivered, specific deep-water protected areas. Twenty years ago, then current pressures on deep-sea habitats were identified as deep-sea fisheries, deep-sea oil and gas drilling, underwater noise, and bioprospecting at vents (Glover and Smith, 2003). Then future pressures were thought likely to stem from climate change, CO_2 sequestration, deep-sea mining, and the dumping of sewage sludge. The pressures experienced 20 years ago continue, and some of the predicted new pressures are indeed now being exerted. In the face of increasing human pressures on the deep ocean, the research priorities that we identify, if fulfilled, could transform States' abilities to successfully deliver the science and conservation actions required to meet international commitments, and ensure development is sustainable.

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Data availability

Data are from accessible databases; links to datasets are provided in Table 1.

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