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REVIEW OF THE CENTRAL AND SOUTH ATLANTIC SHELF AND DEEP-SEA BENTHOS: SCIENCE, POLICY, AND MANAGEMENT

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Abstract The Central and South Atlantic represents a vast ocean area and is home to a diverse range of ecosystems and species. Nevertheless, and similar to the rest of the global south, the area is comparatively understudied yet exposed to increasing levels of multisectoral pressures. To counteract this, the level of scientific exploration in the Central and South Atlantic has increased in recent years and will likely continue to do so within the context of the United Nations (UN) Decade of Ocean Science for Sustainable Development. Here, we compile the literature to investigate the distribution of previous scientific exploration of offshore (30 m+) ecosystems in the Central and South Atlantic, both within and beyond national jurisdiction, allowing us to synthesise overall patterns of biodiversity. Furthermore, through the lens of sustainable management, we have reviewed the existing anthropogenic activities and associated management measures relevant to the region. Through this exercise, we have identified key knowledge gaps and undersampled regions that represent priority areas for future research and commented on how these may be best incorporated into, or enhanced through, future management measures such as those in discussion at the UN Biodiversity Beyond National Jurisdiction negotiations. This review represents a comprehensive summary for scientists and managers alike looking to understand the key topographical, biological, and legislative features of the Central and South Atlantic.

Keywords: Atlantic deep sea; Benthic ecology; Marine spatial planning; Biodiversity patterns; Gap analysis; Area-based management

Introduction

The Central and South Atlantic Ocean is a large ocean area between Africa and South America, providing a variable environmental setting and supporting abundant and diverse life. Owing to the prevalence of developing nations bordering this region, studies on the biology of deep-sea environments both within and beyond nations' Exclusive Economic Zones (EEZs) lag behind other ocean basins and parachute science is rife. Meanwhile, globally expanding human activities are increasing pressure on undiscovered and undescribed deep-sea species and communities. In an effort to consolidate research efforts and gain a better understanding of what we do and do not know about the region, we present here a review of the science, policy, and management of the deep Central and South Atlantic benthos.

The aims of this review are to (1) collate the available information on deep-sea (>30 m) epibenthic and demersal macro- and megafaunal biodiversity of the Central and South Atlantic; (2) identify knowledge gaps (both within the literature and spatially); and (3) summarise information on key human activities in the region, together with existing policies and relevant area-based management measures. The collection and synthesis of information was facilitated through the Central and South Atlantic Regional Scientific Research Working Group of the UN-endorsed Challenger 150 Ocean Decade Programme. The aim of the Programme is to bring together scientists from bordering nations to develop our understanding of vast deep-sea areas to inform future deep-sea research activity under the UN Ocean Decade. The deep sea is commonly defined as those areas deeper than 200 m, however, the challenges associated with collecting data deeper than standard SCUBA depths are similar, and therefore, for the purposes of this review, we include information below 30 m. Additionally, many nations in the region are in early stages of deep-sea exploration, and thus, do not participate in strictly deep-sea research, as per the aforementioned definition.

Geographic setting

The Central and South Atlantic Ocean is confined by Africa to the east and Central and South America to the west. Latitudinally, it extends from 36°N to 60°S but does not bound this entire region (Figure 1). The southern boundary is defined by the northern boundary of the Convention for the Conservation of Antarctic Marine Living Resources (CCAMLR), which comprises a line at 50°S between 22°E and

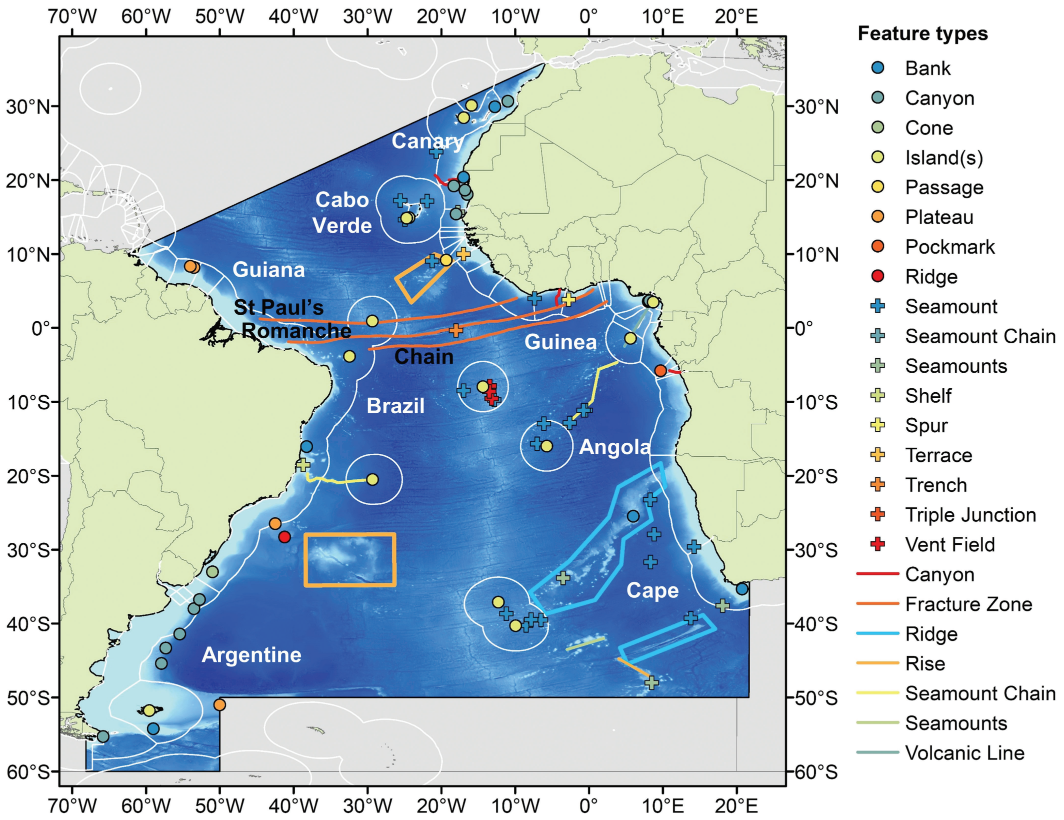

Figure 1 The major topographic features of the Central and South Atlantic region. The northern boundary is defined so as to include the full extent of the west coast of Africa and the near full extent of the east coast of South America excluding the Caribbean region; the southern boundary is defined by the Convention for the Conservation of Antarctic Marine Living Resources. White lines depict the Exclusive Economic Zones of bordering nations. Basins are labelled with white text and the equatorial fracture zones with black text. The locations of major topographic features are identified here and labelled in Figure 2. Bathymetry provided by GEBCO 2020 Grid. Map drawn in WGS84.

50°W and a line at 60°S between 50°W and 70°W. For the purpose of this paper, the northern boundary is defined so as to include the full extent of the west coast of Africa and the near full extent of the eastern coast of South America excluding the Caribbean region. The area defined above covers 49 million km^2 of the world's ocean, is topographically diverse (Figure 2), and has an average depth of 3845 m and a maximum depth of 7770 m (GEBCO Compilation Group 2020).

In 1982, the 200 nautical mile (nm) EEZ was formally adopted as part of the United Nations Convention on the Law of the Sea (UNCLOS; UN 1982). This dictates that coastal states can exercise sovereign rights for the purposes of exploring, exploiting, conserving, and managing natural resources over the 200 nm of water column and seabed adjacent to their coastline. Areas Beyond National Jurisdiction (ABNJ) represent the majority of the ocean, where no single state has authority, and constitute the 'High Seas' and 'the Area' (UN 1982). The former refers to the water column in ABNJ, and the latter to the seabed and subsoil. For the purposes of geographically separating areas within and beyond national jurisdiction in this review, areas claimed through Commission on the Limits of the Continental Shelf submissions are *not* considered within EEZs. Additionally, below we list the bordering states of the Central and South Atlantic. We accept there are many disputed territories in the world, some of which border this region. This manuscript follows the

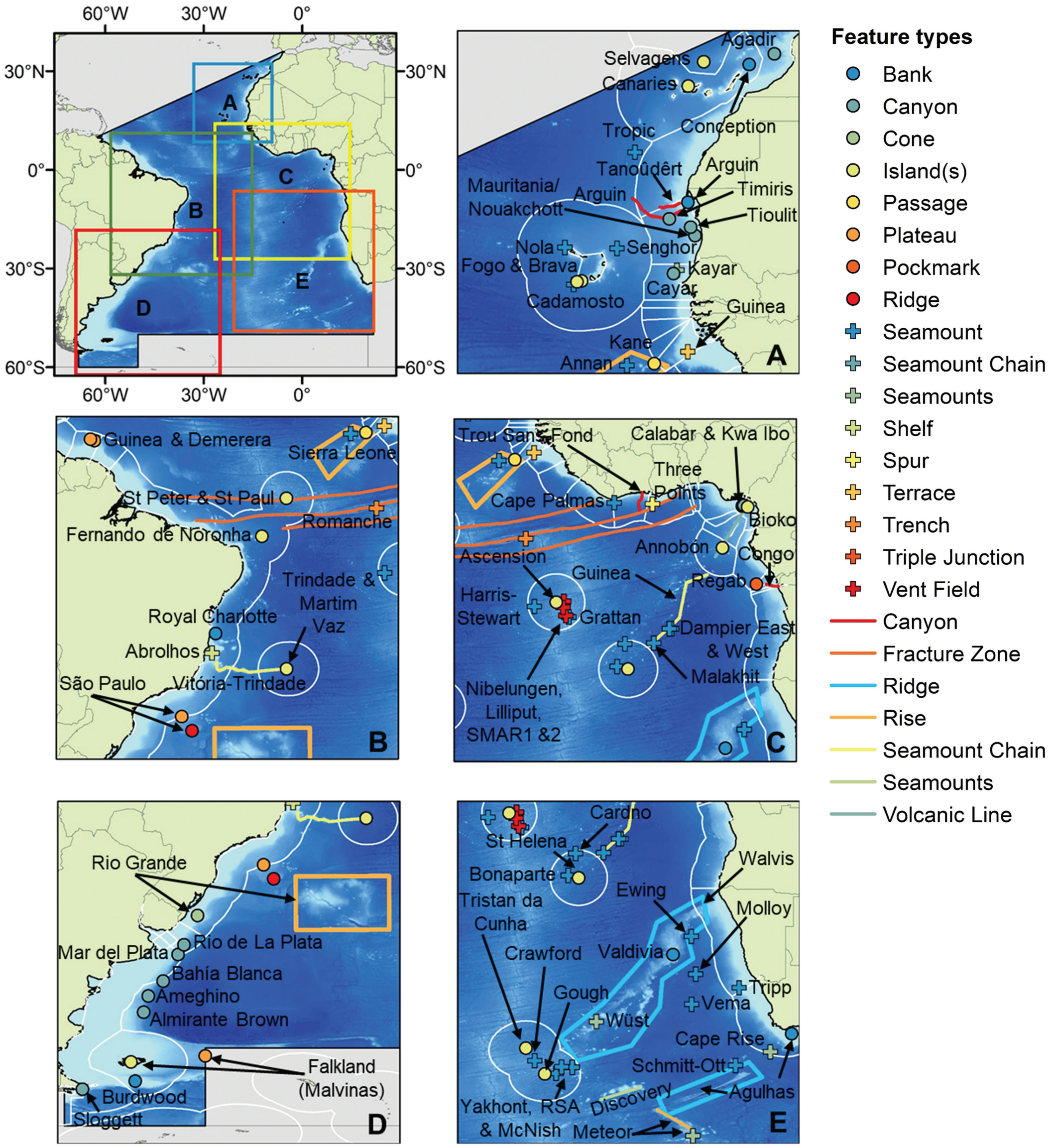

Figure 2 The major topographic features of the Central and South Atlantic region. Where some features are cut-off, refer to Figure 1 for full extent. White lines depict the Exclusive Economic Zones of bordering nations. Bathymetry provided by GEBCO 2020 Grid. Map drawn in WGS84.

naming-convention found in United Nations (UN) documentation referring to non-self-governing territories. The names used in no way reflect the personal views of any of the authors nor their affiliate institutions. To refer to the 200 nm miles of ocean around the Falkland Islands (Malvinas), the term Falklands Maritime Zone is used.

States that border the Central and South Atlantic include: Venezuela, Guyana, Suriname, French Guiana, Brazil, Uruguay, and Argentina to the west; Morocco, Mauritania, Senegal, The Gambia, Guinea-Bissau, Guinea, Sierra Leone, Liberia, Côte d'Ivoire, Ghana, Togo, Benin, Nigeria, Cameroon, Equatorial Guinea, Gabon, Congo Republic, Democratic Republic of the Congo, Angola, Namibia and South Africa to the east. The UN also identifies the disputed region of Western Sahara. In addition, there are several large ocean states and territories, including the Selvagens Islands (Portugal), Canary Islands (Spain), Cabo Verde, São Tomé and Principe, Annobón Island (Equatorial Guinea), St. Peter and St. Paul Archipelago (Brazil), Fernando de Noronha Island (Brazil) and Trindade and Martim Vaz archipelago (Brazil) and the United Kingdom Overseas Territories (UKOTs) of the Falkland Islands (Malvinas) and Ascension, Saint Helena, and Tristan da Cunha, the latter of which is formed of four separate oceanic islands (Figure 1). Although we recognise the review focus area includes sections of the Chilean EEZ and Chilean Antarctic Territory in the South Atlantic, these are not discussed in this review due to the small areas in question.

Topography and oceanography

The Mid-Atlantic Ridge

The Mid-Atlantic Ridge (MAR) is the centre of the Atlantic seafloor spreading system that runs the length of the entire region down to the Bouvet Triple Junction (approximately 55°S), separating oceanic basins lying to the east and west. In the Central Atlantic, between West Africa and north-eastern Brazil, the Romanche Fracture Zone system is present; it was formed at the junction of North and South Atlantic spreading centres nearly 60 M years ago. This system comprises three parallel fracture zones (FZs), St. Paul's, Romanche, and Chain, as well as the Romanche trench found at depths between 6330 and 7600 m. The Romanche FZ (Figure 1) is the central feature that offsets the MAR by 900 km from the Guinea Basin (16°W) in the east to the Brazil Basin (20°W) in the west and from 2°N to 2°S. It comprises an 850 km long, 20–60 km wide, and 5000–7800 m deep central valley, flanked by northern and southern transverse ridges (Searle et al. 1994). These ridges peak at a depth of 1000–2000 m, except at the western extreme where they emerge and form the St. Peter and St. Paul's Archipelago, within the Brazilian EEZ. Along with St. Paul's and Chain, the Romanche FZ forms conduits for the west to east flow of the densest water masses of the Atlantic: Antarctic Bottom Water (AABW; >4000 m) flowing from the south to North Atlantic and North Atlantic Deep Water (NADW; 1500–4000 m) flowing from the north to the South Atlantic (Mercier et al. 1994; Mercier & Speer 1998). Further south, the MAR emerges to the surface at Ascension Island (8°S).

The region is influenced by intensified Particulate Organic Carbon (POC) flux originating from seasonal blooms that take place in the eastern equatorial Atlantic, derived from north–south oscillations of the trade wind regime. This wind regime is intensified during the boreal summer, which causes the shoaling of the thermocline in the eastern equatorial Atlantic and the upward transport of inorganic nutrients to the photic zone, thus enhancing primary production and consequent POC flux-to-depth into ridge and trench areas (Pérez et al. 2005, Lutz et al. 2007).

Central Atlantic

The Central Atlantic comprises mostly deep ocean with few areas shallower than 2000 m (FAO, 2020). Large topographic features in the Central Atlantic include the Sierra Leone Rise, the Cameroon Line, and the adjacent Guinea Seamount Chain, the latter two forming a chain of seamounts from the Gulf of Guinea towards Saint Helena. The major basins in the Central Atlantic include the Canary, Cabo Verde, and Guinea basins in the east and the Guiana Basin in the west (Figure 1).

The Selvagens Islands (two islands and a cluster of smaller islets), Canary Islands (eight islands and numerous islets), and Cabo Verde (ten islands and eight islets) form three offshore island archipelagos in the Central Atlantic off the north-west African coast and are, together with Madeira and the Azores, part of the biogeographical region known as Macaronesia (Figure 1; Castro et al. 2022). Here, surface currents typically flow southwards from the Azores to the Canary Islands via Madeira (Morton et al. 1998, Santos et al. 1995). This area is also heavily impacted by the Canary Current. The oceanography around Cabo Verde is somewhat more complex owing to its location at the boundary between the North Atlantic subtropical Gyre and the North Atlantic Tropical Gyre

(Pelegrí & Peña-Izquierdo 2015). In addition to the oceanic islands themselves, these archipelago EEZs are also home to numerous seamounts and other topographic features, often providing a diversity of substrates including rock, steep slopes, boulders, and sand (Santos et al. 2019). For example, Concepcion Bank, the largest of 16 prominent seamounts in the Canary Islands Seamount Province, is located 75 km north-east of the islands of Lanzarote on the Canary Ridge (Rivera et al. 2016). This seamount rises from 2687 to 158 m and represents a productivity hotspot due to its interaction with currents, thus forming eddies (Rivera et al. 2016). Further south in the Cabo Verde EEZ, seamounts include Cadamosto, Nola, and Senghor, the latter rising from approximately 3500 to 100 m (Christiansen et al. 2011). Seamounts are also present between the archipelagos in ABNJ including Tropic Seamount, a four-armed, star-shaped guyot rising from 4200 m, culminating in a flat summit at 1000 m (Yeo et al. 2019).

The north-west African region falls within the Canary Current Large Marine Ecosystem (CCLME) that extends from the Strait of Gibraltar (36°N) as far south as Guinea-Bissau (11°N) and occupies approximately 97,653 km^2 of shelf area (Valdés & Déniz-González 2015). This region contains one of the world's four major eastern boundary upwelling ecosystems (EBUEs), where deep, cold, and nutrient-rich waters rise to the surface sustaining high primary production reaching >300 g C/m^2/y. About 8% of the world's primary production derives from the north-west African EBUE (Heileman & Tandstad 2009).

The continental shelf off Morocco and south towards Mauritania is 40–50 km wide on average and narrows to 20 km north of Agadir. The shelf edge is located between 100 m depth in the north and approximately 150 m in the south. The many mud volcanoes, cone-shaped edifices up to 2500 m in diameter and 150–300 m thick (León et al. 2006), in the Gulf of Cadiz that extend into the Moroccan EEZ (Foubert et al. 2008), are a geological peculiarity. Further south between Cape Spartel and Rabat, sections of the shelf are accentuated by a ridge running parallel to the coast between 70 and 120 m (Maurin, 1968). The continental slope is traversed by numerous channels and escarpments, with major features including the 460 km long Agadir Canyon from 600 to 1500 m water depth (Wynn et al. 2000) and the large headwall of the Sahara Slide, a giant submarine landslide off the western Sahara region (Georgiopoulou et al. 2010).

Further south and separated by a sharp oceanic frontal system, the waters off Mauritania and Senegal exhibit different environmental conditions to those further north. Here in the Cabo Verde Frontal Zone (CVFZ), both the southward-flowing Canary Current and the northward-flowing Mauritanian Current are deflected seaward. The resulting upwelling waters derive mainly from North Atlantic Central Water (NACW) north of the front and South Atlantic Central Water (SACW) south of it. Along the continental slope, the poleward undercurrent passes northward underneath the CVFZ with variable seasonal intensity. This undercurrent may reach the Canary Islands and possibly the Iberian Peninsula (Pastor et al. 2008, Peña-Izquierdo et al. 2012).

The continental shelf off Mauritania has an average width of 30–50 km, but it widens to approximately 140 km off the Gulf d'Arguin, with the shelf break located at 150 m (Ramos et al. 2017a). The continental slope opposite the Gulf d'Arguin is dissected by 64 submarine canyons, with the Arguin and Timiris Canyon systems being the largest (Sanz et al. 2017). In the Senegalese EEZ, the two active canyons are the Cayar and Mauritania/Nouakchott systems, both draining onto the Gambia Abyssal Plain (Ruffman et al. 2015). Also present are the Kayar seamounts, a complex of three features 100 km north-west of Dakar, named Kayar, Petit Kayar, and Petit Medina, with the former being the largest and rising to a summit depth of 184 m (Valdés & Déniz-González, 2015). South of Dakar, submarine canyons become less abundant but are still present. The continental margin shows a series of giant submarine landslides that induced substantial backstepping erosional features (Krastel et al. 2019). The headwall of the largest submarine slide, the Mauritanian Slide Complex located between approximately 16°N and 19°N, is considered to be stabilised by parts of a cold-water coral mound barrier (Antobreh & Krastel 2007, De Mol et al. 2009).

The continental shelf widens further off the coast of Guinea-Bissau and Guinea, extending to approximately 300 km width in an area known as the Guinea Terrace. The slope then steepens, becoming the Kane passage, which separates the Guinea Terrace from the Sierra Leone Rise seamount chain. This area is home to around 10 seamounts including Annan Seamount, a shallow feature with a summit depth of 200 m. The northern section of the Sierra Leone continental margin is approximately 120 km in width but decreases to around 30 km in the south (Jones et al. 1998). There are few reported geomorphological features of note within the Sierra Leone EEZ, and similarly, the continental shelf of Liberia to the south-east is also flat with few features (Schlee et al. 1973). Noteworthy are the complex slump features and two submarine valleys on the north-western shelf in the Liberian EEZ, as well as other slump-like features in the south-east (Schlee et al. 1973).

Moving eastwards into the northern Gulf of Guinea region, the shelf break is initially located at 130 m off Côte d'Ivoire, getting marginally shallower with eastward movement towards Ghana, Togo, and Benin where it is between 85 and 110 m (Martin, 1970). In this region, canyons are present along the continental shelf and slope descending to depths below 2000 m, including Trou Sans Fond canyon on the Côte d'Ivoire continental shelf, a radial system formed of eight canyons on the mid-continental slope of Ghana (Nibbelink and Huggard, 2002), and four submarine canyons in the Nigerian EEZ (Jimoh et al. 2018). Despite these, the continental shelf region between Côte d'Ivoire and Nigeria is described as generally smooth and featureless, although a number of banks shallower than 200 m are present (Martin, 1970). This is likely due to the large sediment load of the Niger-Benue Rivers burying irregular topography (Emery et al. 1975). Further offshore, Cape Palmas Seamount occurs approximately 40 km off Côte d'Ivoire rising ~1000 m to a summit depth of 790 m, and Three Points Spur off the Ghanaian coast (GEBCO Compilation Group, 2020).

Similarly, the eastern Gulf of Guinea region extending down to the Democratic Republic of Congo is also home to canyon systems, notably Kwa Ibo and Calabar that extend down to depths of 2800 m in the EEZ of Equatorial Guinea (Houbolt, 1974). These canyons run adjacent to the Cameroon Line, a series of two seamounts and four island groups (Annobón, São Tomé, Príncipe and Bioko) that extend off mainland Cameroon, terminating at Annobón Island, a province of Equatorial Guinea. Adjacent to the EEZ of Annobón Island is the Guinea Seamount Chain, a long series of seamounts extending approximately 1600 km in a south-westerly direction, terminating at the island of Saint Helena.

The eastern Gulf of Guinea is also home to two large deep-sea fans. The Ogooué deep-sea fan is present just south of São Tomé and Príncipe, extending 550 km westwards from the Gabonese shelf to the Cameroon Line. This well-developed deep-sea fan displays additional features such as tributary canyons and lobe elements and is fed by the Ogooué River (Mignard et al. 2019). The Congo deep-sea fan extends up to 750 km from the west African coast and reaches depths of 5000 m, thus constituting one of the major depocenters of the south-eastern Central Atlantic. The Congo River feeds the Congo Canyon on the continental shelf and upper slope. This is then followed by submarine valleys (e.g., the Congo channel) on the lower continental slope that end in several distal lobes on abyssal plains (Savoye et al. 2009). The Congo River is one of the most voluminous rivers in the world, and therefore, it supplies a large volume of particulate and dissolved organic matter to the marine environment off West Africa. This is evident both within surface waters and at the seabed, with hydrodynamic regimes within the Congo Canyon playing an important role in flux of organic matter to depth in the eastern Central Atlantic (Sibuet & Vangriesheim 2009).

On the western side of the Guiana Basin, Venezuela, Guyana, Suriname, French Guiana, and northern Brazil border the Central Atlantic, with their continental shelf widths ranging between 80 and 150 km. This region is severely understudied, with few reports on the geomorphological features observed. Of note, the Demerara and Guiana Plateaus are located within the Suriname and French Guiana EEZs, adjacent to the Demerara Abyssal Plain in ABNJ. The Demerara Plateau stretches 380 km wide and straddles the EEZs of Suriname and French Guiana. It is characterised by a steep seaward flank, but a more shallow-sloping north-western descent from 700 m to approximately 3000 to 4000 m (CLCS, 2008). Cabo Branco in north-east Brazil is the most easterly point of the South American continent, above which we consider the Central Atlantic. Here, prominent topographic features include seamounts, banks, and ridges that largely track the 1200 m isobath (dos Santos et al. 2022). Key oceanographic features in this region include the Deep Western Boundary Current (DWBC) that is important for heat exchange between the northern and southern hemispheres (Rhein et al. 1996). This flows south-east along the South American continental margin between 1200 and 4000 m, interacting with the northward-flowing Antarctic Intermediate Water (AAIW) above it and the AABW below it (Rhein et al. 1996).

South-east Atlantic

Angola, Namibia, and South Africa share the Benguela Current Large Marine Ecosystem (BCLME), another of the world's four major EBUEs (Shannon, 1985). To the south, the BCLME is bounded by the warm Agulhas Current that travels south-west from the eastern coast of Africa, turning back on itself and heading east at Cape Agulhas; to the north, it is bounded by the Angola Front. The characteristic intense upwelling in the region gives rise to some of the world's most productive fishing grounds (Crawford et al. 1987).

The Angolan EEZ is characterised by a narrow continental shelf, particularly in the south, of approximately 200 m depth, covered by the warm southward-flowing Angola Current until the Angola-Benguela Front in the south (Kirkman & Nsingi 2019). The north of the EEZ is influenced by the Congo River which has a high nutrient load triggering intermediate productivity. Like many west African countries, submarine channels are found within the Angolan EEZ (Gee et al. 2007). Also present are asphalt mounds, large solid structures formed from seepage of hydrocarbons associated with subsurface salt structures (Jones et al. 2014).

The dominant topographic feature of the Namibian EEZ is the start of the Walvis Ridge at approximately 20°S, although the majority of this feature falls within ABNJ. North of this, the Namibian shelf is rather narrow, but it widens to the south of the Walvis Ridge up to ~90 km off Walvis Bay (Sakko 1998). A mud belt stretching along the inner shelf composed of organic matter-rich sediments reflects the strong upwelling in the region (Bremner 1981). Located off the dry Namib Desert, the Namibian shelf only receives continuous freshwater input in the very north through the Kunene River and in the very south through the Orange River, which may explain the obvious lack of any canyon systems. Close to the South African border, Tripp Seamount reaches a shallow summit depth of around 150 m (Kensley 1980).

The passive western margin of South Africa is characterised by a wide and flat shelf with a deep (300–600 m) shelf break, terraced in places (de Wet & Compton 2021), and mantled by glauconite and foraminiferal sandy sediments with a mud belt on the mid-shelf (Birch et al. 1986, Dingle et al. 1987). Several submarine canyons incise the shelf, and although the Orange Basin is gas-rich with thousands of pockmarks (Palan et al. 2020), seep-associated taxa have not yet been detected (Sink et al. 2019). Cape Rise comprises a group of seamounts that include Protea and Argentina seamounts rising to approximately 700 and 1400 m, respectively (GEBCO Compilation Group 2020). To the east off Cape Agulhas lies the Agulhas Bank, a large, triangular feature of the continental shelf extending up to 250 km off the coast (Sink et al. 2019). There are four oceanic current systems that circulate along the western margin of South Africa. The deepest of these is the AABW system which influences the abyss and lower slope (Weigelt & Uenzelmann-Neben 2004). NADW encompasses a net south-easterly flow in the 1500–4000 m depth range (Berger & Wefer 2002), whereas AAIW has a north-westerly flow above this in the 500–1500 m depth range (Weigelt & Uenzelmann-Neben 2004). The Benguela Coastal Current is the shallowest current flowing in depths of up to 500 m (Shannon 1985) and comprises a general equatorward flow of cool water on the eastern limb of the South Atlantic Gyre, with dynamic wind-driven upwelling on the shelf, enhanced at particular locations by local bathymetry (Shannon 1985, Shillington 1998, Verheye et al. 2016).

Adjacent to the BCLME lie the Angola and Cape basins, the two major basins in the south-east Atlantic, separated by the Walvis Ridge (Pérez-Díaz & Eagles 2017). The Angola Basin is almost 5500 m deep, situated north of the Walvis Ridge. The water column here is strongly stratified due to interactions between different water masses. From the surface to 200 m depth, waters comprise South Atlantic Subtropical Surface Water (STSW), at which point SACW dominates down to 1400 m, along with AAIW and Upper Circumpolar Deep Water (UCDW). Below 1400 m, the Angola Basin is filled with NADW which is modified by injections of AABW through deep gaps in the MAR system (Reid 1989, Shannon & Chapman 1991, Larqué et al. 1997) as well as by the Namib Cold Current (Speer et al. 1995). In the north of the basin, the influence of the Congo River plume can be detected in the water column up to 800 km from the coast (van Bennekom & Berger 1984, Larqué et al. 1997); thus, this area is highly influenced from both northern and southern deep-sea basins (Kröncke & Türkay 2003). The Cape Basin is oceanographically dominated by waters from the South Atlantic Gyre travelling in an easterly direction towards the coast (Sink et al. 2019). Here, the waters of the Indian and Atlantic Oceans interact through Agulhas rings or eddies that are shed by the retroflection of the Agulhas Current coming from the east (Sink et al. 2019).

The Walvis Ridge that separates the Angola and Cape basins is a long feature running north-east to south-west, interspersed with an extensive chain of seamounts; it extends westward from the African continental margin to the southern MAR before terminating at the archipelago of Tristan da Cunha. While many areas of the ridge remain poorly mapped and unsampled, certain areas have been described, typically those associated with historic or present fisheries. Ewing is an irregularly shaped seamount on the north-eastern section of the Walvis Ridge, with a summit depth of 780 m that rises from 3000 m (Bergstad et al. 2019, López Abellán et al. 2011). The Valdivia Bank is also found in the north-eastern part of the Walvis Ridge. This complex is home to four large seamounts, commonly referred to as Valdivia North, Valdivia Middle/Central, Valdivia West, and Valdivia Central/South (Bergstad et al. 2019, López Abellán et al. 2011). The four seamounts rise from between 2700 and 1700 m and have summit depths between 200 and 550 m (López Abellán et al. 2011). Finally, Wüst is a large seamount complex located on the south-western part of the Walvis Ridge, just north-east of the Tristan da Cunha EEZ. This complex remains largely unmapped, but the shallowest summit depths recorded are 600 and 1000 m (Bergstad et al. 2019). Alongside seamounts, the Walvis Ridge also encompasses other structures including canyons and submarine slides (Hoernle et al. 2014).

Tristan da Cunha is one of three oceanic islands/archipelagos in the South Atlantic that form a UKOT, along with Ascension Island and Saint Helena. While Tristan is in temperate waters, Ascension and Saint Helena occur in the tropical Central/south-east Atlantic at approximately 7 and 14°S, respectively. All three islands/archipelagos host seamounts within their EEZs. At Tristan da Cunha, two island groups are separated by approximately 410 km of ocean. Between the main island group in the north and Gough Island in the south is the Subtropical Convergence Zone (STCZ), a frontal system that shifts throughout the seasons (Smythe-Wright et al. 1998). Several seamounts are also found between the islands, including Yakhont, Crawford, RSA, and McNish, with reasonably shallow summit depths between 160 and 320 m (Barnes et al. 2013, 2021, Morley et al. 2018, Whomersley et al. 2019). In the tropical UKOT EEZs, notable seamounts include Harris-Stewart and Grattan at Ascension with summit depths of 280 and 115 m, respectively (Barnes et al. 2015, 2019), and Bonaparte and Cardno at Saint Helena with summit depths of 115 and 110 m, respectively (Morley et al. 2018, Whomersley et al. 2019). Ascension Island EEZ is also home to hydrothermal vent fields owing to its location on the MAR. Across the four fields, Nibelungen (Melchert et al. 2008), SMAR1 and 2 (Devey et al. 2005), and Lilliput (Haase et al. 2009), there are black smokers, extinct chimneys, and diffuse vent sites. Of particular note is the Nibelungen field as, due to its location outside of the axial valley of the MAR, it represents a new form of hydrothermal system (Melchert et al. 2008).

In the region east of Tristan da Cunha and south of the Walvis Ridge, there are numerous seamounts and seamount complexes in ABNJ. Vema Seamount is a conical feature located approximately 500 km away from the northern South African EEZ. A flat, 11 km wide summit extends into depths shallower than 100 m, with the shallowest point recorded well into the photic zone at 22 m (Bergstad et al. 2019). Further south lies Schmitt-Ott Seamount, approximately 300 km from the South African EEZ boundary, rising to a summit of 920 m (Bergstad et al. 2019). Below this seamount lies the Agulhas Ridge, a prominent ridge system with its most north-easterly feature, a 1500 m deep plateau, 390 km from the South African EEZ, and its most westerly point just north of the Meteor Rise seamount complex. This area is largely unsampled with no high-resolution bathymetry maps available; however, there are reports that several seamounts rise from depths of approximately 3000 m to summits at 1000 m (le Roex et al. 2010). West of here and just south of Tristan da Cunha in sub-Antarctic waters are the Discovery Seamounts, a chain of seven features including Herdman, Shannon, Discovery, Tablemount, and Schwabenland seamounts (Buhl-Mortensen et al. 2019).

South-west Atlantic

The south-west Atlantic is characterised by a more passive continental margin than other parts of the Central and South Atlantic and is home to one of the largest continental slope regions on the planet, the Patagonian Shelf (considered here as the continental shelf south of approximately 35°S). The south-west Atlantic hosts a great variety of topographic features including submarine canyons (Bernardino et al. 2019), abyssal plains and hills, seamounts, sills, escarpments, ridges, and trenches (Hernández-Molina et al. 2009, COPLA 2017, Alberoni et al. 2019, Sumida et al. 2020). The major basins in the south-west Atlantic are the Brazilian and Argentine basins split by the Rio Grande Rise, although Brazil has identified a further 12 smaller sedimentary basins within its EEZ that are referred to throughout (Alberoni et al. 2019, Sumida et al. 2020). Continental margins of the south-west Atlantic are characterised by reasonably complex water mass structure which is known to influence the distribution of benthic taxa associated with varying substrates (Saeedi et al. 2019, Shimabukuro et al. 2019, Shimabukuro & Sumida, 2019, Souza et al. 2021). Key water masses present along the eastern South American continental shelf are the Superficial Tropical Water (STW) between 250 and 300 m, SACW between 300 and 550 m, AAIW between 550 and 1200 m, NADW between 1200 and 3500 m, and AABW below 3500 m (Durrieu de Madron & Weatherly 1994).

Below Cabo Branco, the Brazilian continental shelf becomes thin, descending steeply to 3000 m. Further south, the continental shelf widens at the Royal Charlotte Bank and Abrolhos Shelf to approximately 200 km. At 20°S, the Vitória-Trindade Seamount Chain extends 950 km east off the Brazilian coast, formed as a result of volcanic activity in the Cenozoic, 40–60 million years ago. It comprises over 30 aligned seamounts that act as important barriers for the circulation of intermediate and deep waters along the South American continental margin (Motoki et al. 2012, Silveira et al. 2020). The chain terminates in the east at Trindade and Martim Vaz Islands. The Brazilian continental margin is also home to 161 submarine canyons (De Leo et al. 2020), but few have been studied in detail.

Further south, the Rio Grande Rise, a prominent geological feature covering nearly 480,000 km^2 (Pérez-Díaz & Eagles 2017), extends from ~28 to 32°S. In the western sector lies the largest plateau area known as Alpha (140,000 km^2 above the 4000 m isobath), with a 580–700 m deep flat summit and a 300 km long, 40 km wide, and 1200 m deep trough crossing the structure's surface in a north-west to south-east direction (Gamboa & Rabinowitz, 1984, Mohriak et al. 2010, Montserrat et al. 2019). Alpha is flanked to the west by the 5000 m deep Vema Channel through which over 70% of AABW flows northward into the Brazil Basin (Morozov et al. 2010). The São Paulo Ridge extends linearly to the west of the Rio Grande Rise for 350 km, delimiting the southern boundary of the São Paulo Plateau (Bassetto et al. 2000). The São Paulo Ridge disrupts the southward flow of the NADW and the northward flow of the AABW, the boundary between which lies at 3400 m over the ridge escarpment (Perez et al. 2020b). The São Paulo Plateau extends over 400,000 km^2 between ~21 and 29°S connecting the slope of the Brazilian meridional margin to the Brazil Basin at depths of 2500–4500 m (Alberoni et al. 2019) and contains some of the largest hydrocarbon deposits of the world (Perez et al. 2020a).

Despite its small size compared to neighbouring countries, the Uruguayan EEZ is considered one of the most productive areas of the southern hemisphere (Burone et al. 2021) owing to regional oceanic circulation patterns and interactions with the Río de La Plata freshwater discharge. Offshore at the Brazil-Falkland Confluence Zone, the southward-flowing subtropical Brazil Current meets the northward-flowing Falkland Current, displacing Antarctic water masses. The Uruguayan EEZ presents a wide continental shelf, with its outer portion dominated by sandy and/or muddy bottoms with scarce rocky outcrops. Straddling the continental margins of Uruguay and Argentina, the Río de La Plata submarine canyon system is present between 35 and 38°S (Lonardi & Ewing 1971) and is comprised of six canyons on the middle and upper slope, including a mega slide canyon (Franco-Fraguas et al. 2014, Hernández-Molina et al. 2016). The continental slope and rise regions extend from 180 to 4500 m and give rise to several types of geomorphological features including terraces, channels and drifts, seamounts, chimneys, and oil seeps. The lower slope and abyssal plain are dominated by mud deposits (Burone et al. 2021).

The continental margin of Argentina comprises continental shelf, a slope descending from 200 to ~3500 m, continental rise, and abyssal plain, with the latter characterised by large muddy sedimentary wave fields of up to 40 m high mud volcanoes and erosional scars (COPLA, 2017). The shelf is dominated by sediment ridges approximately 15 m high, while the continental slope below supports large submarine canyons (especially in the north), gullies, pockmarks, and iceberg plough marks (Portela et al. 2012). In the Argentine EEZ, there are around 70 submarine canyons grouped from north to south in the systems called Río de La Plata, Mar del Plata, Bahía Blanca, Ameghino, and Almirante Brown (Hernández-Molina et al. 2009, COPLA, 2017, Bozzano et al. 2017, see Figure 2D). Other features include a series of terraces and escarpments, submarine valleys, trenches, contour channels, contourite and turbidite deposits, drifts, and abyssal plain deposits (COPLA, 2017). At the southern limit of the Argentine EEZ are a series of banks, the largest of which is Burdwood Bank. This undersea plateau covers 34,000 km^2 with depths ranging from 50 to 200 m on the plateau and slopes descending from 1100 to more than 3000 m (Schejter et al. 2016). Burdwood Bank straddles the EEZ of Argentina in the west and the Falklands Maritime Zone in the east.

Summary of benthic biodiversity research

Although understudied in comparison to the global north, scientific exploration of offshore ecosystems in the Central and South Atlantic dates back to the fifteenth century. While important national and international collaborative initiatives have provided significant data and knowledge, there are two notable initiatives that have contributed significantly to the regional knowledge base. These are the HMS Challenger Expedition (1872 to 1876) and the EAF-Nansen Programme (1981 to present).

The HMS CHALLENGER Expedition represents the first dedicated deep exploration of many areas in the Central and South Atlantic (Murray, 1895). During this expedition, many features within the region were sampled on the outward and returning journeys. Legs of the route covering areas in the Central and South Atlantic include Bermuda to Cabo Verde (stations 58 to 94), Cabo Verde to Fernando de Noronha (Brazil, stations 95 to 113A), Fernando de Noronha to the Cape of Good Hope (stations 113B to 140), Magellan Strait (Chile) to Ascension Island (Stations 313 to 343), and finally the return from Ascension Island to Portsmouth (stations 344 to 354). The HMS Challenger Expedition dataset still represents an important reference for this region.

More recently since 1981, the EAF-Nansen Programme, initiated by the Government of Norway and the Food and Agriculture Organisation (FAO) in 1974, expanded research efforts along the west African margin, carrying out detailed mapping of resources within the EEZs of nations (Bianchi et al. 2016). In 1993, the programme began a new phase escalating research efforts in south-west Africa with an aim to develop capacity in fishery research and management (Bianchi et al. 2016). During these early years, the EAF-Nansen Programme played a role in establishing the Benguela Environment Fisheries Interaction and Training Programme (BENEFIT), which later developed into the Benguela Current Commission (BCC), providing a platform for collaborative research on transboundary resources (Bianchi et al. 2016). More recently, the EAF-Nansen Programme has surveyed ABNJ in both the Central and south-east Atlantic with the RV Dr. Fridtjof Nansen. Since 1990, more than 50 surveys have been carried out by the EAF-Nansen Programme in the south-east Atlantic (EEZs and ABNJ), collecting invaluable data on fish stocks and the marine environment (Bianchi et al. 2016).

Here, we summarise the current benthic biological knowledge base for ABNJ followed by areas within EEZs. The HMS Challenger Expedition and EAF-Nansen Programme are referred to throughout.

Areas beyond national jurisdiction

While early exploration of ABNJ in the Central and South Atlantic was driven by scientific curiosity, much of the more recent scientific exploration has focused on the identification and mapping of Vulnerable Marine Ecosystems (VMEs) and their associated taxa (e.g., Bergstad et al. 2019, German et al. 2002, Koschinsky, 2006). VME is a term adopted by the United Nations General Assembly (UNGA) to refer to areas where the biology may be vulnerable to damage from bottom fishing and are thus protected under various UNGA resolutions requiring managers to prevent significant adverse impacts (SAIs) and protect the marine biodiversity that these ecosystems contain (FAO, 2009). VME-related research is largely focused on mapping the distribution of corals and sponges, and this is reflected in the available literature.

The Mid-Atlantic Ridge

Biodiversity of the southern MAR was first sampled during the HMS Challenger Expedition. Sampling effort was concentrated during the return trip to England between Tristan da Cunha and Ascension Island, producing records of over 80 taxa captured by dredge tows between 2200 and 3600 m. More recent exploration of the southern MAR provided description of chemosynthetic communities in hydrothermal vents at 5 and 9°S, although the latter site falls within the Ascension Island EEZ. Both sites include vent fauna similar to that found in the northern MAR, including *Bathymodiolus* spp., alvinocarid *Rimicaris* shrimps, and the vesicomyid clam *Abyssogena southwardae* (Haase et al. 2007, German et al. 2008, Teixeira et al. 2012, van der Heijden et al. 2012). Interestingly, while there are inferred vents, there are no other confirmed hydrothermal vent fields south of approximately 15°S until the Scotia Ridge and South Sandwich Volcanic Arc that both fall outside the review focal area (Beaulieu & Szafranski 2020).

In 2009, non-vent benthic and deep pelagic fauna were sampled during the South Atlantic MAR-ECO Expedition (Perez et al. 2012). Results included deep pelagic fish assemblage composition and genetic structure associated with the MAR and Walvis Ridge (Kobyliansky et al. 2010, Gordeeva 2011) and taxonomic studies of hermit crabs (Family Parapaguridae), shrimps (Family Caridae), amphipods (Family Stilipedidae), acorn worms (Class Enteropneusta), and glass squids (Family Cranchiidae; Cardoso & Fransen 2012, Cardoso & Lemaitre 2012, Holland et al. 2013, Serejo 2014, Bolstad et al. 2014).

Biological and ecological data on the deep habitats of the Romanche FZ system are scarce. The Romanche trench was sampled during large-scale French and Russian expeditions from the 1950s to the 1970s, starting in 1956 when the RV Calypso took the first photographs of benthic habitats and fauna in the area (Heezen et al. 1964). Records of fauna collected with trawls and grabs in the region and general ecological information were reviewed by Beliaev & Brueggeman (1989) and more recently by Jamieson (2015). In 2009, benthic trawls conducted at the northern transverse ridge and valley of the Romanche FZ, during a survey along the South Atlantic MAR under the Census of Marine Life Project, provided preliminary evidence for high benthic diversity (Perez et al. 2012) and the addition of new deep fauna records (Holland et al. 2013).

A trans-Atlantic expedition in 2013 aboard the RRS James Cook (JC094 TROPICS; Robinson 2013) sampled features on and either side of the MAR with a focus on the biogeochemistry of deep-sea corals resulting in knowledge about historical oceanic turnover in this region (Bradtmiller et al. 2014, Wilson et al. 2014). Subsequently, the broader biological investigations have highlighted the utility of bamboo (Farmer et al. 2011) and stylasterid corals (Samperiz et al. 2020) as climate records, helped initiate the Bristol Sponge Microbiome Collection (Williams et al. 2020), led to publication about sponge silicon isotopes (Cassarino et al. 2018), resulted in new species discoveries (Maxwell et al. 2022), and contributed to the first recording of microplastic ingestion by deep-sea animals (Taylor et al. 2016).

Central Atlantic

ABNJ in the Central Atlantic have been poorly studied, with sparse examples of biological surveys in the literature. The Sierra Leone Rise represents a major feature in this region and was the subject of an experimental fishing survey, Palguinea-2001, carried out by the Instituto Español de Oceanografía (IEO) in 2001 to assess the *Beryx splendens* stock (Salmerón et al. 2015), but there was no investigation into the benthic invertebrate taxa during this survey. However, more than 20 years later in early 2022, the EAF-Nansen Programme surveyed five seamounts (Annan, Falsos, Perdido, La Meseta, and Rompetodo) on the Rise with the RV Dr. Fridjtof Nansen. The survey focused on characterising and mapping benthic habitats using multibeam swathe, benthic trawls, and video imagery (FAO 2022a). Preliminary results reported by the FAO describe observations of mixed coral and sponge gardens harbouring large antipatharian corals between 400 and 1500 m (FAO 2022a).

The JC094 TROPICS survey utilised the remotely operated vehicle (ROV) *Isis* to survey five seamounts across the equatorial Atlantic, with diverse coral gardens comprising *Corallium* spp. and *Enallopsammia* spp., vampire squid, and echinoid breeding events all recorded. Eighty-seven hours of video footage from depths between 200 and 2730 m on Annan Seamount, alongside high-resolution multibeam bathymetry data, were used to assess the diversity and distribution of multiple habitats on the seamount flanks (Victorero et al. 2018). Findings suggest that the seamount harbours a diverse range of benthic assemblages and taxa, with high rates of species turnover with depth. Summit communities were characterised by ophiuroids, holothurians, and echinoids. This changed to a community dominated by the pencil urchin *Cidaris cidaris* to approximately 650 m. Deeper than 1000 m, extensive multispecies coral gardens, a VME habitat type, were observed down to 2000 m, at which point soft-substrate habitats dominated (Victorero et al. 2018).

Tropic Seamount, located between the Canary Islands and Cabo Verde, was the primary focus of another cruise aboard the RRS James Cook (JC142; Murton 2016) in 2016 that set out to map the cobalt-rich ferromanganese crusts on the seamount due to their commercial value. Data collected include high-resolution multibeam swath bathymetry of the whole seamount, CTD data, and imagery. The latter was collected using the ROV *Isis* over 28 dives between depths of 2600 and 3600 m (Murton 2016). Analysis of the footage by Ramiro-Sánchez et al. (2019) suggests that Tropic Seamount hosts a high diversity of VME-indicator taxa including 15 cold-water coral species (scleractinians, antipatharians, and gorgonians) whose identities varied with depth, several sponge species forming sponge grounds, and xenophyophore and crinoid fields. The seamount was also identified as a potential spawning ground for squid (Ramiro-Sánchez et al. 2019). Physical specimens of ferromanganese crusts were collected and found to host abundant corals and bivalves (Kfouri et al. 2021).

In addition to the numerous French-led cruises along the equatorial African margin that straddled ABNJ and EEZs (see the Gulf of Guinea section below), a French national programme called

CONGOLOBE (ANR) surveyed ABNJ in the Gulf of Guinea region between 2011 and 2014. The programme involved two cruises (2011 and 2012), each equipped with the ROV *Victor 6000*, a high-resolution multibeam echo-sounder, and a long-range black and white camera. The objectives were to study the biology and biogeochemistry of the terminal lobes (or lobe complex) of the Congo channel. Six sites were surveyed, ranging in depth from 4700 to 5100 m, located between 750 and 800 km offshore. Four sites were selected along the active channel from the lobe complex entrance to the outer rim of the sediment deposition zone, and two sites positioned cross-axis and at increasing distance from the active channel (Rabouille et al. 2017). The large input of organic matter from the Congo River to the lobe area is thought to contribute towards sulphide production by anaerobic decomposition, consequent sulphate reduction, and anaerobic oxidation of methane, thus promoting reducing habitats such as chemosynthesis-based cold seep-like ecosystems (Rabouille et al. 2017). Imagery and multibeam data were collected at four of the six sites revealing the presence of two vesicomyid clam species and ampharetid polychaete tubes (Krylova & Cosel 2011, Rabouille et al. 2017, Sen et al. 2017). Near to the vesicomyid field, giant foraminifera (*Bathysiphon* spp.) aggregations were detected via high-resolution imagery and multibeam, owing to their large size and extensive coverage (Sen et al. 2017). Sessile and mobile species were also recorded such as anemones, zoarcid fish, shrimp, squat lobsters (*Munidopsis crassa*), and holothurians (Sen et al. 2017).

South-east Atlantic

Deep-sea benthic communities in ABNJ in the south-east Atlantic appear somewhat better studied than central areas. They are diverse, often comprising many suspension-feeding VME-indicator taxa such as scleractinian, stylasterid, and gorgonian corals (Bax & Cairns 2014, Durán-Muñoz et al. 2014, Bergstad et al. 2019, Buhl-Mortensen et al. 2019, 2021). This said, deep-sea assemblages from the extensive number of seamounts in the south-east Atlantic remain largely unsampled, and therefore, ecological processes and species biogeography are still elusive (Clark et al. 2020).

The role of the Walvis Ridge as a barrier to the distribution of abyssal and bathyal meio- and macrofauna has been the focus of multiple cruises across varying institutions. L'Institut Français de Recherche pour l'Exploitation de la Mer (IFREMER) conducted cruises focused on and around the Walvis Ridge in the 1970s aboard the RV Jean Charcot. WALDA-001 CH18 (Pautot 1971) and WALDA-002 CH19 (Reyss 1971) were cruises undertaken in 1971. While their main focus was the geological study of the African continental margin, a biological study using epibenthic dredge samples was carried out in parallel. The WALVIS I Expedition (Sibuet 1978) took place later in 1978 and had a more biological focus but maintained the same aim, this time using a beam trawl and an epibenthic dredge to collect physical samples. While, to our knowledge, the results of the biological aspects of the IFREMER cruises do not appear in the published literature, datasets are available from the Campagnes Océanographiques Françaises website. Much later in 2014, sampling campaign SO-233 WALVIS II, led by GEOMAR Helmholtz Centre for Ocean Research Kiel, took place aboard the RV Sonne. One of the aims of this expedition was to understand connectivity in the region and the role of the Walvis Ridge, alongside describing the biological communities found. Samples were collected using a TV-multicorer, a TV-grab, sediment traps on geological dredges and by harvesting invertebrates from the hard rocks collected via dredging. Preliminary results yielded low numbers of taxa mainly comprising brachiopods (*Eucalathis* spp.), sponges, octocorals, hexacorals, molluscs, polychaetes, bryozoans, cirripeds, isopods, and amphipods. During the complementary German DIVA 1 and ANDEEP III Expeditions, on board of RV Meteor and RV Polarstern, respectively, samples were obtained from each side of Walvis Ridge (DIVA: Latitudinal Gradients of Deep-Sea Biodiversity in the Atlantic Ocean; ANDEEP: Antarctic benthic deep-sea biodiversity: colonisation history and recent community patterns). Based on these samples, it appears that the Walvis Ridge is not an absolute distributional barrier as demonstrated for a range of macrofaunal taxa (Fiege et al. 2010, Broekeland 2010, Brix et al. 2011).

The DIVA 1 and 2 Expeditions with RV Meteor took place in 2000 and 2005, respectively, and sampled abyssal macro- and megafaunal communities in the Cape, Angola, and Guinea basins at depths between 5047 and 5657 m using a box corer, epibenthic sledge, and modified Agassiz trawl (Kröncke & Türkay 2003, Kröncke et al. 2013, Kaiser et al. 2022a,b). Polychaetes, peracarids, and bivalves were found to dominate the macrofauna, whereas ophiuroids, bivalves, and actiniarians were prevalent in the megafauna. Abundance and community structure of both macro- and megafauna were strongly shaped by food availability (Kröncke et al. 2013, Kaiser et al. 2022a,b). Macrofaunal peracarid fauna was represented by 241 species of which most belonged to the Isopoda, followed by Tanaidacea, Cumacea, Amphipoda, and Mysidacea (Brandt et al. 2005). A wealth of new species was collected during these cruises, including realised descriptions of a new genus and 20 new species of asellote isopods (see, for example, Brandt 2004, Brenke et al. 2005, Brix 2007, Kaiser & Brix 2007, Broekeland 2010, Brix et al. 2011, 2015) as well as three new species of carnivorous deep-sea sponge (Cristobo et al. 2005).

More recently, Spanish and Namibian scientists collaborated on the RAP-Sur project, one of four Atlantic projects with aims to map the seabed, identify VMEs, study the interaction with bottom fisheries, and select suitable areas to preserve VMEs (Durán-Muñoz et al. 2014). The RAP-Sur project ran three multidisciplinary cruises on the Walvis Ridge during 2008 and 2010 focused on Ewing Seamount and Valdivia Bank, surveying depths between 218 and 3000 m with bottom trawls, rock dredges, and box cores. The benthic fauna associated with VMEs consisted mainly of antipatharians and colonial scleractinians that formed coral gardens. The larger, reef-forming corals provided substrate for solitary scleractinians, octocorals, and small sessile organisms, thus drastically increasing the biodiversity within the area. Of the samples collected, a large proportion of the scleractinians were found dead, although *Enallopsammia rostrata* retained live polyps (Durán-Muñoz et al. 2012).

In 2015, the EAF-Nansen Programme led a research cruise in the South East Atlantic Fisheries Organisation (SEAFO) Convention Area aboard the RV Dr Fridtjof Nansen, focusing on several seamounts and prominent features including Ewing Seamount, Valdivia Bank, Vema Seamount, and Wüst seamount complex (FAO 2016, Bergstad et al. 2019). Similarly to the RAP-Sur project, the cruise devoted time to multibeam mapping, benthic video mapping of VME-indicator taxa, hydrographic sampling using CTDs, and physical sample collection using a variety of grabs and trawls (FAO 2016). Physical specimens were preserved and later identified by taxonomic experts; Arthropoda and Cnidaria were found to be the two most speciose phyla, respectively, and reef-building corals were collected, with *E. rostrata* identified (Ramil 2015). Gil and Ramil (2021) reported 27 hydroid species collected during this cruise including a new species (*Monotheca bergstadi* sp. nov.). FAO (2016) details the individual seamount data, with some video dives recording large amounts of dead scleractinian coral rubble, suggesting past extensive densities of reef-building corals and VMEs; live coral was relatively patchy on the surveyed locations (FAO 2016, Bergstad et al. 2019). Coral-dominated communities comprising scleractinians and gorgonians were abundant across most seamounts, with Valdivia Bank harbouring the highest scleractinian colony density (Bergstad et al. 2019). Bergstad et al. (2019) also reported an area where sea pens were 'quite abundant' on soft ground on Valdivia Central, possibly indicating the presence of a sea pen field (a VME habitat type).

In January 2019, a second EAF-Nansen Programme cruise complemented the 2015 cruise and sampled Discovery Seamounts further south (Buhl-Mortensen et al. 2019). The specific aims of the cruise were to investigate VMEs, fisheries resources, and biodiversity of selected seamounts both within and outside of fisheries closures, with wider aims including further development of databases and collections to benefit regional science and enhance understanding of the area. Benthic video mapping was undertaken at 14 locations between 400 and 1800 m with analysis leading to the identification of over 200 taxa. VME-indicator taxa were present at all locations, suggesting widespread occurrence of several cold-water coral groups and sponges (Buhl-Mortensen et al. 2019).

Tablemount and Discovery Seamount hosted the highest densities, with octocorals particularly prevalent. Reef-building scleractinian species were not observed at any locations, and many of the observed octocorals were dead. A total of 366 fish and 13 cephalopods were recorded in nine different habitats described on these seamounts. Fish were classified into 32 morphotypes, included in 8 orders and 12 families. Macrouridae was the most diverse family, while Moridae the most abundant, including two dominant species: *Laemonema* sp. and *Guttigadus* sp. The explored region was found to contain a mixture of tropical, subtropical, and sub-Antarctic faunas of the Atlantic (Perez et al. 2022). With similar aims to that of the 2019 cruise, the EAF-Nansen Programme returned to ABNJ in the south-east Atlantic in 2022, this time undertaking benthic habitat mapping of four seamounts (Dampier East, Dampier West, Malakhit, and an unnamed feature) at the south-westerly extent of the Guinea Seamount Chain. Data collected included video, grabs, and beam trawls alongside environmental samples. Live coral gardens were recorded on all seamounts characterised by *E. rostrata* and primnoid corals; extensive areas of dead *Solenosmilia variabilis* reef and dead octocoral gardens were also observed (FAO 2022b).

South-west Atlantic

Deep basins and topographic features of the south-west Atlantic remain poorly explored in relation to other regions of the Atlantic (Perez et al. 2012). Despite this, of the studies that are available, data suggest that the south-west Atlantic hosts a diverse range of benthic assemblages including coral gardens (Durán-Muñoz et al. 2012, Portela et al. 2012) and deep-sea sponge aggregations (Portela et al. 2012, Durán-Muñoz et al. 2014, Hajdu et al. 2017).

The Rio Grande Rise represents one of the best-studied topographic features in the south-west Atlantic, with the first images of benthic habitats and megafauna from Alpha plateau coming from surveys aboard the RV Vema and RV Conrad between 1962 and 1974. These early biological explorations were often carried out in tandem with geological and fishing exploratory surveys. For example, Russian fishing explorations during the 1960s–1980s provided significant contributions to data available on demersal and benthopelagic megafauna in the region (reviewed by both Clark et al. (2007) and Perez et al. (2012)). Several taxonomic studies followed these expeditions, notably resulting in a report of 65 species of demersal, benthopelagic, and bathypelagic fish, nearly half of them within the families Macrouridae, Alepocephalidae, Synaphobranchidae, and Chlorophthalmidae (Parin et al. 1995). Additionally, concentrations of commercially valuable fish on the Rio Grande Rise including *Beryx splendens*, *Pentaceros richardsoni*, and *Epigonus telecopus* were reported (Kakora, 2005; Vinnichenko & Kakora 2008).

Significant advances in the description of habitats, diversity, and ecology of major topographic features around the Rio Grande Rise have been made in recent years, in some cases in response to the potential development of seafloor mining initiatives (Perez et al. 2020a). A major scientific contribution to the ecology of the region can be derived from the global expedition, Quelle 2013 – QUest for the Limits of LifE, led by the Japan Agency for Marine-Earth Science and Technology (JAMSTEC), which searched for extreme deep-sea environments with the RV Yokosuka and the manned submersible *Shinkai 6500* (Kitazato et al. 2017). During the first leg of the Iatá-Piuna Expedition in the south-west Atlantic, selected areas of the Alpha plateau were explored revealing a hexactinellid sponge garden formed by dense concentrations of *Sarostegia oculata*, a branched sponge associated with symbiotic zoanthids, which is thought to mimic the 3-dimensional skeletal framework of coral gardens (Hajdu et al. 2017). In the same area, 36 species of fish and eight crustaceans were reported, the former divided into 11 orders and 17 families, with most records within the Macrouridae, Synaphobranchidae, and Chaunacidae families. Distinctive fish assemblages were identified and associated with depth and habitat diversity (Perez et al. 2018). Of the crustacean fauna, notable finds included *Nematocarcinus parvus* (not previously known to occur in the Atlantic), *Chaceon sanctaehelenae* (previously thought to only occur in the east Atlantic), and *Projasus parkeri* (a rare species of lobster, Cardoso et al. 2017).

Additional dives on the escarpment of the adjacent São Paulo Ridge along a 1.5 km stretch of seabed between 2644 and 4219 m revealed an Antarctic minke whale skeleton at the foot of the ridge with a well-established (5- to 10-year-old) chemosynthetic community, the deepest natural whale fall studied to date (Sumida et al. 2016). Most of the 41 species found in association with the carcass were new to science, including the snail *Rubyspira*, polychaete worms, and a bone-eating worm *Osedax* spp. (Alfaro-Lucas et al. 2017, Alfaro-Lucas et al. 2018, Hasegawa et al. 2019, Shimabukuro & Sumida 2019, Shimabukuro et al. 2020). Perez et al. (2020b) described habitats and megafauna distribution along the escarpment, finding important associations with topography-related flow dynamics of key water masses. In 2018, there were a further two expeditions focused on the Alpha plateau as part of Marine E-tech, a joint Brazil-UK project focused on the study of ferromanganese deposit formation and associated biological communities. The focus of Marine E-tech was to collect baseline information with respect to the potential of future mining activities (Jovane et al. 2019); a complete review of the environmental baseline data available in the Rio Grande Rise and São Paulo Ridge region was prepared by Montserrat et al. (2019), with collated information concluding that both regions harboured diverse ranges of benthic communities.

Moving away from the Rio Grande Rise, the ATLANTIS project studied ABNJ in the south-west Atlantic between 42 and 48°S to the east of Argentina and north of the Falkland Islands (Malvinas) between 2007 and 2010. ATLANTIS was a sister project of RAP-Sur with the same focus to map VMEs in the Atlantic. The multidisciplinary work involved collecting high-resolution multibeam bathymetry data for the area, as well as performing a series of biologically focused benthic surveys (rock dredges, boxcorers, bottom trawls, and sediment collections) on the Patagonian Shelf and adjacent slope (both popular fishing areas). Cnidarians and sponges, both VME-indicator taxa, dominated the benthic megafaunal catch during the cruises. Of the Cnidaria collected, 33.7% were octocorals (Muñoz et al. 2012a). Four types of VME were identified in the study area: deep-sea sponge aggregations, cold-water coral reefs, coral gardens, and deep-sea rocky environments; the majority of which were located between 400 and 1000 m. These findings concur with those of a study conducted by the European Commission that concluded fished areas bordering the Argentine EEZ were likely to host VMEs between 200 and 1000 m due to the prevalence of favourable conditions for the formation of cold-water coral reefs and deep-sea sponge aggregations (Portela et al. 2010). The ATLANTIS project led to the identification of nine VME candidate areas for protection in south-west Atlantic ABNJ.

In 2009, the German DIVA 3 Expedition on board RV Meteor obtained macro- and megafauna samples using a box corer, epibenthic sledge, and Agassiz trawl in four areas in the Argentine and Brazil basins (Martínez Arbizu et al. 2015). Analysis of the epibenthic sledge samples revealed very high macrofaunal densities in the Argentine Basin and significantly lower values in studied areas of the Brazil Basin, related to differences in food supply (Kaiser et al. 2022a). Interestingly, historic samples collected by the RV Atlantis II revealed that abyssal tunicates from the Argentine Basin were more similar to Antarctic fauna than other Atlantic basins (Monniot & Monniot 1976). Samples collected from geographically close sites during DIVA 3 showed large variability in both macrofaunal density and composition, indicating strong natural variability that needs to be assessed with finer-scale sampling in the future. Similarly to previous DIVA expeditions, taxonomic knowledge gains were significant and included description of three polychaete species (Böggemann 2016) and a new isopod genus (Kaiser et al. 2018).

Within exclusive economic zones

List of nations

Northern South America (Venezuela, Guyana, Suriname, and French Guiana) The scientific literature focusing on offshore taxa from the northern South American coastline is extremely limited and it seems much of the research effort in the region has focused outside of the Central and South Atlantic in the Caribbean Sea and Gulf of Mexico. This said, the Venezuelan Atlantic front which includes the Gulf of Paria and the deltaic plains of the Orinoco River (the world's third largest flow) has been the focus of some research. The area covers 27,630 km^2 and constitutes one of the major wetlands in South America and one of the best-preserved ecosystems in the world (Miloslavich et al. 2011). Marine biodiversity knowledge in this area is limited and mostly reported in technical reports and local books. The first reports of deep-sea benthic species, from 214 m depth, are of the bivalve *Glossocardia agassizii* and the gastropod *Glyphostoma phalera* from 1884 located within the National Museum of Natural History at the Smithsonian Institution.

In the early 2000s, environmental baseline studies including marine biodiversity inventories with water quality and sediment characterisation were carried out in the area under the Plataforma Deltana project in response to the potential establishment of offshore and coastal developments by oil and gas companies (Martín et al. 2007). Despite limitations on taxonomic expertise, the project produced species lists for phytoplankton, zooplankton, ichthyoplankton, fish, and benthic communities from samples up to 1500 m depth (Bone et al. 2003, Martín & Díaz 2003, Pereira & García 2003, Severeyn & Romero 2005, Martín et al. 2007, Martín & Díaz 2007, Lodeiros et al. 2013). Specifically for deep-sea benthic communities, the Plataforma Deltana project collected nearly 15,000 organisms identifying 389 species of 22 taxonomic groups. Among the macrobenthos, the most abundant groups were Polychaeta and Peracarida which, when combined, summed more than 80% of the collected organisms (Martín et al. 2007).

Given the planned developments from the oil and gas industry in the Venezuelan Atlantic front, work has been done to identify the conservation priorities for ecosystems in this area (Klein & Cárdenas 2011). Most of the ecological 'conservation objects' identified in the area were coastal ecosystems (e.g., mangrove forests) and fisheries resources including crabs, shrimps, rays, sharks, oyster banks of *Crassostrea virginica*, and some fish species (Lasso & Molinet 2011). Other socio-economic conservation objects included indigenous settlements and areas used by indigenous populations that are important for industrial and artisanal fisheries (Klein & Cárdenas 2011).

The Surinamese EEZ has undergone some deep-sea exploration. The University of Miami undertook deep-sea expeditions in the tropical western Atlantic aboard the RV John Elliott Pillsbury, with cephalopod records coming from the Suriname EEZ (Voss 1975). There was also a series of research cruises conducted aboard the RV Oregon and RV Silver Buy between 1954 and 1970 that collected bathyal gastropods using trawls; while most of the study sites were outside the Central and South Atlantic, some samples were collected from the Surinamese EEZ (Voight & Walker 1995). Finally, sponges collected along the Guyana Shelf, but predominantly within the Surinamese EEZ, were described in Van Soest (2017). These were collected using a combination of trawls, dredges, and grabs on a variety of substrate types between 19 and 681 m during a series of expeditions led by the Dutch in the 1960s and 1970s. The majority of the 119 distinct species identified belonged to the Demospongiae, with 36 being new to science. When compared with neighbouring regions, approximately a third of the species were widespread throughout the western Central Atlantic, suggesting the region is well-connected (Van Soest 2017).

Brazil The large and morphologically complex deep continental margin off Brazil hosts a great variety of ecosystems, most of which are still poorly described (De Leo et al. 2020). For example, only four of the 161 submarine canyons have been the focus of biological and/or ecological studies such as the analysis of spatial patterns of abundance, biomass, and diversity of macro- and meiofauna (Fonsêca-Genevois et al. 2017, Lavrado et al. 2017, Bernardino et al. 2019). Biogeographic changes in deep-sea benthic assemblages are thought to be heavily influenced by the overlying water mass structure and marked latitudinal differences in productivity along the Brazilian margin (Bernardino et al. 2016, Sumida et al. 2020, Gaurisas & Bernardino, 2023). In general, the dominant benthic species of the central (19°S) and southern Brazilian margins are more similar than when compared to the northern deep-sea basin, partially supporting previous biogeographic helms proposed for the South Atlantic (Watling et al. 2013). In the Campos Basin off south-east Brazil, benthic assemblages exhibit high heterogeneity when compared to slope sediments, revealing that the canyons in high abundance on the Brazilian margin may represent an important habitat for non-slope species in the deep South Atlantic (Bernardino et al. 2019).

Given the extensive interests of the offshore oil and gas industry, studies of deep-sea biodiversity have typically concentrated on the sedimentary slope habitats of the southern and south-eastern margins (Cordes et al. 2016), leading to an increased recognition of the regional and basin-wide biodiversity of slope habitats. In these regions, the diversity of benthic communities, mostly meio- and macrofauna, has been shown to be higher on the upper slope and near areas of upwelling in the south-east, with diversity then decreasing towards the southern margin (i.e., from 21 to 34°S, see review by De Leo et al. (2020)). Slope depths between 200 and 1200 m also host an extensive diversity of ecosystems including pockmarks, seeps, cold-water corals, and submarine canyons (Almada & Bernardino 2017). Research resulting from fishing activity in the region found that the diversity of deep-water fish along the Brazilian margin and adjacent regions included 712 species (see review in Melo et al. 2020). Scientific exploration of the continental slope in southern and central regions in conjunction with fisheries by-catch records have shed light on the assemblage composition, abundance, and diversity patterns of fish, cephalopods, and crustaceans within the Brazilian EEZ (e.g., Perez & Wahrlich 2005, Costa et al. 2007, Haimovici et al. 2007, Serejo et al. 2007, Haimovici et al. 2008, Perez et al. 2013, Costa et al. 2015, Martins et al. 2017).

Cold-water coral-associated communities have been described along the south-eastern and southern margins, typically from records produced by monitoring the by-catch of deep-water fisheries, although a small number of research surveys have elucidated further data (Kitahara et al. 2020, Bernardino et al. in press). Pires (2007) investigated scleractinian coral diversity and distribution off the coast of Brazil with data compiled from the literature as well as newly collected data. Fifty-six species were reported, translating into a 4:1 ratio between azooxanthellate and zooxanthellate corals for Brazilian waters, which is higher than the usual ratio from the tropical-warm temperate western Atlantic (2:1) and the worldwide ratio (1:1). This suggests that Brazilian waters and likely other South American EEZs represent an area of high biodiversity of scleractinian cold-water corals. In the Campos Basin, reef-building corals have been extensively mapped and observed with geophysical instruments and ROV images (Cavalcanti et al. 2017). Although the northern and north-eastern Brazilian margins were previously considered unfavourable for cold-water corals due to the effects of the Amazon River plume, cold-water coral reefs seem to be common in the area (Pires et al. 2015), and habitat suitability models suggest that the north Brazilian continental slope is highly suitable for octocoral species (Barbosa et al. 2020). Dominant reef-building scleractinian species observed on the Brazilian margin include *Desmophyllum pertusum*, *Solenosmilia variabilis*, and *Madrepora oculata*. Observed Octocorallia richness comprises species from the families Primnoidae, Clavulariidae, Plexauridae, Alcyoniidae, Keratoisididae, Coralliidae, and Paragorgiidae (Pires 2007, Pires et al. 2015, Cavalcanti et al. 2017, Gaurisas & Bernardino, 2023).

The presence of cold seeps on the Brazilian margin has often been inferred from abundant geological (e.g., pockmark fields) and biological evidence, including records of chemosynthetic symbiont-bearing organisms (Shimabukuro et al. 2020) and of species endemic to chemosynthetic habitats such as the alvinocaridid shrimp, *Alvinocaris muricola* (Pereira et al. 2020b). This species is abundant in cold seeps in the south-east Atlantic and Gulf of Mexico, as well as being found in hydrothermal vent sites on the MAR. However, in the Brazilian EEZ, only one cold seep has been described to date at 1200 m on the Rio Grande Cone (Giongo et al. 2016). Two symbiont-bearing invertebrates were recorded in this seep: the tubeworm *Escarpia* sp. and the bivalve *Acharax* sp. (Giongo et al. 2016, Medina-Silva et al. 2018). In 2013, the seafloor of the São Paulo Plateau in the Campos Basin (20–23°S) was explored during the second leg of the Iatá-Piuna Expedition. Here, an asphalt seep was discovered, the third of its kind in the world (Fujikura et al. 2017). The reef-like structure was colonised by suspension-feeding epifauna, comprising hexactinellid sponges, keratoisid corals, brisingid starfish, and galatheid squat lobsters, with no sign of chemosynthetic symbiont-bearing organisms.

Biodiversity and ecological studies of seamounts and oceanic islands within the Brazilian EEZ (e.g., St. Peter and St. Paul Archipelago, Fernando de Noronha Island, Atol das Rocas, Vitória-Trindade Seamount Chain, and Trindade and Martim Vaz Islands) have typically focused on the shallow and mesophotic zones, which are dominated by maerl beds and shallow-water coral reef species (e.g., Serafini et al. 2010, Pinheiro et al. 2015, Pinheiro et al. 2017, Pimentel et al. 2020). Pinheiro et al. (2015) reviewed fish fauna reported during scientific dives in mesophotic areas and fishery surveys, revealing 171 species, many of them endemic to the islands. Venturing slightly deeper, a series of surveys with baited traps between 2012 and 2014 led to the first studies on the deep-water (300–700 m) flanks of the St. Peter and St. Paul islets, reporting bathymetric stratification of deep-sea fish and crustaceans (Nunes et al. 2016, Nunes et al. 2017, Pinheiro et al. 2020). There are a few records of deep-sea coral reef species associated with the seamounts, which are common to other slope areas at similar depths on the Brazilian margin, suggesting limited isolation of the cold-water coral fauna (Gaurisas & Bernardino, 2023, Bernardino et al. in press).

Uruguay Studies on the benthic ecology and biodiversity of the Uruguayan EEZ have been concentrated along the continental shelf and slope, although fauna of the deep continental margin have been the subject of numerous studies. Early research performed during the 1960s and 1970s included the RV Vema, RV Atlantis II, and the RV Walter Herwig I and II Expeditions. Fisheries surveys onboard national fishing vessels, as well as systematic joint surveys between Uruguay and Argentina, have provided population level information for benthic species of commercial interest and on the biodiversity of associated benthic fauna (Gutiérrez & Defeo 2003, Delgado & Defeo 2004, Gutiérrez et al. 2011). More recently, geochemical and sedimentary studies were undertaken aboard the German RV Meteor, and high-resolution, large-scale sampling was undertaken during a joint research cruise aboard the RV Miguel Oliver led by the Dirección Nacional de Recursos Acuáticos and the IEO.

Historic studies of some faunal groups elucidate interesting results from the Uruguayan EEZ. In 1971, the RV Atlantis II collected, among other taxa, bivalves between 200 and 5500 m. Results yielded 112 species, incorporating almost every known group occurring in other deep-ocean basins globally (Allen & Sanders 1996, Allen 2008). Of these, 38 species have only been recorded in the Argentine Basin, suggesting a potentially high degree of endemism, at least for deep-sea bivalves (Scarabino et al. 2015). Also using the material collected during the above-mentioned expeditions, recent work has synthesised information on the known diversity of deep-water ascidians (Scarabino et al. 2018) and pycnogonids (Scarabino et al. 2019) in the Uruguayan EEZ. For megabenthic gastropods (i.e., adult size >5 cm), the Uruguayan fauna includes species from different biogeographic provinces (Argentine, sub-Antarctic, and Subtropical; Carranza 2006, Carranza et al. 2008, 2010a,b), providing evidence that this area may act as a transitional zone as opposed to a rigid biogeographic boundary. Within the Crustacea, recent studies have reported 79 species, collected between 250 and 3800 m, of which 64% were shrimp taxa (suborder Dendrobranchiata and infraorder Caridea; Rotllant et al. 2020). Finally, of the polychaete fauna, Uruguayan waters share 33 families with Argentina and 22 with southern Brazil, indicating that the Uruguayan EEZ is dominated by taxa from sub-Antarctic regions to the south rather than those from the north (at least with respect to polychaetes, Rodriguez et al. 2014).

In relation to VMEs, the first records of cold-water corals in the region come from the HMS Challenger Expedition, with *Bathelia candida* reported from station 320 (a station straddling the modern-day Uruguayan and Argentine EEZs; Moseley 1881). More recently, mounds with associated *Desmophyllum pertusum* reefs, represented by both isolated pinnacles and aggregations (Carranza et al. 2012), were identified and were most abundant between 250 and 400 m. Their heights and diameters varied, respectively, from 20 to 24 m and from 450 to 1200 m (Carranza et al. 2012). Regarding chemosynthetic ecosystems, 2-dimensional reflection seismic data obtained during hydrocarbon exploration between 1970 and 2008 in the Uruguayan EEZ suggested that the presence of gas chimneys associated with a recent fault system was highly likely (Tomasini et al. 2011). Further evidence for the existence of chemosynthetic ecosystems in the Uruguayan EEZ is the description and presence of *Lamellibrachia victori*, a polychaete of the siboglinidae family (Mañé-Garzón & Montero 1986), as well as biological samples collected by the RV Miguel Oliver. These included the bivalves *Callogonia birmani* and *Graecina* sp., while other characteristic methane seep taxa (*Acharax* sp. and *Solemya notialis*) have been reported from the lower slope (Scarabino et al. 2015). Other studies reported a minimum of 41 unsampled pockmarks in the Uruguayan EEZ, and thus, there is perhaps an unsampled diversity of chemosynthetic ecosystems (López-Orrego et al. 2011).

Argentina Only a small fraction of the Argentine EEZ has been explored to date in relation to its benthic ecology and biodiversity yet despite this, the few benthic sampling efforts made so far indicate that the Argentine EEZ hosts high biodiversity and productivity as well as several VME-indicator taxa. Exploration of the Argentine EEZ began with the HMS Challenger Expedition, followed by the Swedish Antarctic (1901–1903), the British William Scoresby (1927–1931), and the Discovery (1926–1938) Expeditions in the early twentieth century. There were also several expeditions performed during the 1960s and 1970s, such as the RV Eltanin, RV Vema, RV Atlantis II 60, the Soviet Antarctic Expedition, and the Walter Herwig Expeditions among others. Detailed summaries of the surveys performed off the Argentine coast can be found in Gappa (2000), Gappa et al. (2006), Maggioni et al. (2018), and Doti et al. (2020b).

In 2005, the Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP) conducted the first benthic sampling within an Argentine submarine canyon aboard the fishery research vessel, BIP Capitan Oca Balda, as part of a stock assessment of the Patagonian scallop (*Zygochlamys patagonica*; Bremec & Schejter 2010). Samples were obtained using a dredge and yielded a total of 86 mega- and macrofauna taxa; biomass was dominated by *Z. patagonica* (~20%), echinoderms (16%), and sponges (10%), the latter of which when studied revealed two new species (Bertolino et al. 2007). Although no comprehensive work on the benthic biodiversity as a whole has been performed, the Mar del Plata is a well-studied submarine canyon system. During 2012 and 2013, three surveys led by Argentina's National Scientific and Technical Research Council (CONICET) aboard the RV Puerto Deseado were performed in the Mar del Plata submarine canyon system and adjacent area (Talud Continental I–III Expeditions), close to the Brazil-Falkland (Malvinas) Confluence Zone. Depths studied ranged from 200 to 3500 m, again resulting in the description of several new species and new records for the region (e.g., Cerino & Lauretta 2013, Pastorino 2016, Pastorino & Sanchez 2016, Pereira & Doti 2017, Lauretta & Penchaszadeh 2017, Maggioni et al. 2018, Martinez et al. 2019, Pereira et al. 2019, 2020a, Bernal et al. 2019, 2021, Teso et al. 2019, Rivadeneira et al. 2020, Roccatagliata 2020, Risaro et al. 2020, Flores et al. 2021). Reproductive features were also studied for several species of deep-sea cnidarians, echinoderms, and molluscs, mostly regarding protected development (e.g., Penchaszadeh et al. 2016, Berecoechea et al. 2017, Lauretta & Penchaszadeh 2017, Martinez & Penchaszadeh 2017, Rivadeneira et al. 2017, Penchaszadeh et al. 2017, Rivadeneira et al. 2020, Lauretta et al. 2020, Pertossi et al. 2021).

Cold-water corals have been recorded throughout the Argentine EEZ suggesting widespread distribution across multiple features. Sampling in the Mar del Plata submarine canyon system revealed the presence of cold-water corals throughout the depth range including scleractinians, octocorals (dominated by primnoids and sea pens), and 14 species of stylasterid (Bernal et al. 2021). Only one species of antipatharian was recorded (*Dendrobathypathes grandis*) in low abundances (Lauretta & Penchaszadeh 2017). While most of the scleractinian species were solitary and collected from soft-sediment habitats, the reef-building coral *Bathelia candida* was found at several stations (see also Durán-Muñoz et al. 2012). Furthermore, fossilised individuals of this species, along with *Flabellum thouarsii*, have been recorded from dredge and sediment cores collected on the outer shelf and middle slope regions of the northern Argentine continental margin (Garberoglio et al. 2020). Both species now inhabit the outer shelf and upper and middle slope regions of South America in the South Atlantic. As well as within submarine canyons, cold-water corals have also been recorded on the Patagonian Shelf (Portela et al. 2012, Muñoz et al. 2012a) and on Burdwood Bank (Schejter et al. 2020). Resulting from the SO260 cruise aboard RV Sonne in 2019, the largest known cold-water coral mound province was recorded between 900 and 1050 m, covering 2000 km^2 of seabed on the northern Argentine and southern Uruguayan continental slope (Steinmann et al. 2020). This aligns with previous isolated records of cold-water coral catches from similar depths along the Argentine continental slope (INIDEP 2020).

Burdwood Bank, located at the southern tip of Argentina, is another feature that has received recent attention. The notably high benthic species richness of the area was first recorded in 1908 when the Scotia (Scottish National Antarctic) Expedition retrieved a trawl weighing half a ton and comprising ~70 species within which sponges and bryozoans were dominant (Schejter et al. 2016). Later in 2002, the same high species richness was observed during the LAMPOS project, this time with samples dominated by sponges and cnidarians (Arntz & Brey 2003, Schejter et al. 2016). In 2013, the first Argentinian cruise to Burdwood Bank took place, tasked with creating an inventory of benthic diversity. High abundances of several VME-indicator taxa were recorded including corals, sponges, tunicates, and bryozoans, as well as high levels of endemism (Schejter et al. 2016). The expedition, led by CONICET, aimed to collect samples of benthic mega- and macroinvertebrates at central, buffer, and shelf break areas around Burdwood Bank. Benthic samples were collected using a bottom otter trawl elucidating 240 taxa, thus representing the most complete taxonomic inventory for the area (Schejter et al. 2016). Following this, many studies dealing with the taxonomy, biology, and biogeography of taxa reported in Schejter et al.'s (2016) inventory were published (e.g., Penchaszadeh et al. 2017, 2019, Schejter et al. 2017, 2020, Fraysse et al. 2018, García Alonso et al. 2018, López-Gappa et al. 2018, Taverna et al. 2018, Urcola & Zelaya 2018, Bremec et al. 2019, Di Luca & Zelaya 2019, Gordillo et al. 2019, Teso et al. 2019, Doti et al. 2020a, Pérez-Barros et al. 2020, Roccatagliata 2020). Furthermore and resulting from the designation of several Marine Protected Areas (MPAs) on Burdwood Bank, an intensive sampling programme of the benthic community ensued from 2013 (survey codes: CAV 2013, BBB 2016, PD-BB-ABR 2017). Data suggested that benthic communities of the shallower areas of Burdwood Bank were dominated by sponges and bryozoans, whereas the slopes of Burdwood Bank were instead dominated by cold-water corals (including alcyonaceans, scleractinians, and stylasterids), with many sites being considered coral gardens (Schejter et al. 2016, 2020). In addition to the already published information above, it is expected that further data on the benthic communities of Burdwood Bank will be available soon as many of the samples recently collected are still under study (Bax et al. 2022).

More recently, cruises GTGM-YTEC, led by CONICET and YPF TECNOLOGÍA, combined acoustic seafloor mapping with the collection of physical samples via box core in Sloggett submarine canyon, and the Malvinas and Colorado basins (Tassone 2017, Esteban et al. 2018, Principi et al. 2019). While mapped areas included those suitable for the recruitment of VME-indicator taxa (Tassone 2017, Esteban et al. 2018, Principi et al. 2019, Palma et al. 2021), this campaign also resulted in the discovery of active cold seeps in the Malvinas Basin, representing the first study of cold-seep benthic communities in the Argentine EEZ. Additionally, in 2019, the first box core sampling of chemosynthetic ecosystems in the Colorado Basin was undertaken (Esteban et al. 2018, Principi et al. 2019). Considering the many records of geomorphological features associated with fluid seepages (e.g., pockmarks, mud volcanoes) at the centre and south of the continental slope (Portela et al. 2012, Ormazabal et al. 2020, Isola et al. 2020, 2021), cold-seep benthic communities are potentially widespread throughout the Argentine EEZ.

Morocco including western Sahara region Cold-water coral habitats are well known in the Moroccan part of the Gulf of Cadiz, where they drape the outer fringes of mud volcanoes to form coral mounds (Somoza et al. 2021), located in close proximity to living chemosynthetic assemblages (Cunha et al. 2013). However, the majority of the cold-water coral assemblages are dead or belong to the Late Pleistocene age (Wienberg et al. 2009), when environmental conditions for cold-water corals deteriorated in the Gulf of Cadiz due to a significant drop in productivity associated with the Azores Front moving south-west and a decrease in aeolian dust (Wienberg et al. 2010). Major framework-building corals were and occasionally are *Desmophyllum pertusum* and *Madrepora oculata*, with few occurrences of *Dendrophyllia alternata* and *Dendrophyllia cornigera* being documented. The dead corals provide hard substrate and various macro- and microniches for many species across numerous phyla, as well as acting as feeding and nursery grounds (Rueda et al. 2016). In the same area, thousands of these so-called ‘mini-mounds’ were recently discovered, measuring on average 18 m in height in depths of approximately 720–980 m (Hebbeln et al. 2019). Again, there is almost no presence of live cold-water corals on these elevated structures. Such mini-mounds had been previously described from further south, near the Agadir Canyon in water depths of 678–873 m, where they are present in their hundreds. Known as the Eugen Seibold coral mounds at approximately 31°N (Glogowski et al. 2015), they are constituted largely of dead reef framework with some live colonies of *Desmophyllum pertusum* and *Madrepora oculata*. Live and dead cold-water coral samples were also identified from trawls in water depths between 657 and 1543 m during several MAROC Expeditions with RV VIZCONDE DE EZA between 2004 and 2006 (*pers. comm*. Fran Ramil). These, together with historic records from the NO TALISMAN Expedition in 1883, mean all occurrences of cold-water corals are located along the continental slope off the western Sahara region. Noteworthy are the deepest records in this area for some cold-water coral species such as *Caryophyllia ambrosia*, *Caryophyllia atlantica*, *Desmophyllum pertusum*, *Javania cailleti*, *Solenosmilia variabilis*, as well as the deepest Central Atlantic record for *Enallopsammia rostrata*, trawled at 2165 m by Princesse Alice II during her 1901 campaign off Morocco (Zibrowius, 1980).

Far less is known about *Dendrophyllia cornigera*- and *Dendrophyllia ramea*-dominated assemblages that were identified through the analysis of dredge samples collected from the NO Vanneau between 1923 and 1926 (Gruvel 1923, Maurin 1968). These assemblages are reported from many places along the Moroccan coast and seem to be related to the presence of rocky outcrops found between 70 and 160 m (Mhammdi et al. 2014). The corals are often colonised by the coral-inhabiting cirriped *Adna anglicum* (Zibrowius 1983). Historic records show that fishermen were warned of these coral locations due to the threats they pose to trawl nets, suggesting that they have long had substantial coverage in the region (Liouville 1924).

Mauritania and Senegal During the RV Meteor cruises M25/1971, M39/1975 and RV Valdivia cruise VA-10-2 between 1971 and 1990 off the coast of Mauritania, a 70 m thick ‘slope wall’ was mapped at around 500 m extending from the Tioulit Canyon system approximately 130 km towards Arguin Bank (Seibold & Fütterer 1982). Based on 3-dimensional seismic surveys of the Mauritanian EEZ by Woodside Mauritania Pty Ltd. between 1998 and 2003, Colman et al. (2005) presented detailed maps of a cold-water coral mound barrier off Mauritania, at least 190 km long. The entire outer shelf and continental slope off Mauritania was later bathymetrically mapped between 150 and 2000 m, thus covering 31,300 km^2, by the Spanish MAURIT Expeditions between 2007 and 2010 with the RV Vizconde de Eza (Ramos et al. 2017b, Sanz et al. 2017). These surveys showed the full lateral extension of the coral mound barrier to measure 405 km in length on the open slope. The summits of the mounds are 300–600 m wide and found at approximately 450 m depth, whereas the bases are much wider reaching up to 2 km across (Ramos et al. 2017b).

The 'slope wall' was linked to the presence of fossilised cold-water corals during RV Meteor cruise 58-1 in 2003 (Schulz et al. 2003), and core samples contained dead fragments of four reef-building scleractinian species: *Desmophyllum* sp., *Desmophyllum pertusum*, *Solenosmilia variabilis*, and *Madrepora oculata* (Colman et al. 2005). In 2002, a survey of the area with a towed camera identified vast areas of coral rubble at two sites on the Mauritanian margin. While the observed coral was dead, the rubble supported epibenthic invertebrate communities and fish assemblages, and the soft-sediment communities around the base of the mounds included sea pens and hydroids (Colman et al. 2005). A subsequent survey in 2003 revealed the presence of live coral polyps and a single living colony of *Desmophyllum pertusum* on one mound (Colman et al. 2005). The mound structure itself also gave rise to epibenthic invertebrate communities including echinoids (*Cidaris* sp.) and tube worms. In 2010, several areas of cold-water coral habitat in Mauritania's submarine canyons and the open slope coral mound barrier were the focus of a detailed ROV survey during the RV Maria S. Merian MSM16/3 cruise (Westphal et al. 2012). Analysis revealed that while live coral communities on the open slope coral mound barrier are present, they were mostly confined to the summit areas of individual mounds and their densities reduced with distance from the summit. *Desmophyllum pertusum* and *Madrepora oculata* were accompanied by a diverse and dense octocoral community comprising *Acanthogorgia armata*, *Acanthogorgia granulata*, *Paramuricea* spp., *Thesea talismani*, and *Swiftia* phaeton (Sampaio et al. 2022).

Live cold-water coral density in this region has been reported as highest in locations characterised by rough topographies such as the headwalls of slide scars and submarine canyon flanks and shoulders (Wienberg et al. 2018). The above-mentioned cold-water coral assemblage is present in these locations but with a larger (older) scleractinian framework, accompanied by dispersed *Dendrophyllia cornigera* colonies. Goecke et al. (2016) also documented intense recolonisation of recently settled *Desmophyllum pertusum* and *Madrepora oculata* colonies in symbiotic combination with *Eunice* spp., as well as the carnivorous sponge *Cladorhiza corallophila*, on rocky substrate within canyon shoulders. Corallivory on *D. pertusum*, *M. oculata*, octocorals, and sponges is common in this region and is driven by solenogastrids, nudibranchs, calliostomatid, eulimid and pyramidellid gastropods, asteroids, and echinoids (Hoffman & Freiwald 2018, Hoffman et al. 2019). Published information on the cold-water coral-associated community reported approximately 860 species, but this figure is steadily increasing. For a full review of the Mauritanian benthos, see Ramos et al. (2017a).

North-west Africa – The Gambia, Guinea-Bissau, Guinea, Sierra Leone, and Liberia A literature search for the deep-sea and/or offshore environments within the Gambian, Guinea-Bissaun, Guinean, Sierra-Leonean, and Liberian EEZs provides extremely limited numbers of studies. Most focus on describing the geology of the region, particularly in relation to oil and gas.

Otter trawl samples from between 20 and 1000 m collected during the GUINEA-BISSAU 0810 survey in 2008 aboard the RV Vizconde de Eza showed that decapod biomass and abundance peaked between 200 and 500 m, after which it decreased (Muñoz et al. 2012b). Seven decapod assemblages were identified driven primarily by depth but also influenced by sediment type. Similarly, demersal fish assemblages on the Guinea-Bissau continental shelf and slope are also structured by depth (Amorim et al. 2002).

Gulf of Guinea – Côte d'Ivoire, Ghana, Togo, Benin, Nigeria, Cameroon, Equatorial Guinea, Gabon, Congo Republic, and Democratic Republic of the Congo A total of 17 cruises have been carried out by French deep-sea scientists between 1998 and 2012 in the Gulf of Guinea (Western African), focusing on the Congo deep-sea fan and cold seeps within this area. Prior to scientific exploration of the deep sea in this region, continental margins along the Gulf of Guinea were first explored by oil and gas industries and the RV Pillsbury Deep-sea Expedition to the Gulf of Guinea during 1964 and 1965 (Chesher, 1966).

The first campaign of French cruises in the Gulf of Guinea, ZaïAngo, were led by IFREMER in collaboration with TOTAL Fina Elf (a multinational oil and gas company) and ran from 1998 to 2001. It comprised seven cruises (ZaïAngo 1, ZaïAngo 2, ZaïAngo-Sar, ZaïAngo-Car, ZaïAngo-OBS-SMT, ZaïAngo-Rov1, and ZaïAngo-Rov2), the focus of which was largely to conduct a geological survey of the area (Savoye et al. 2009). Specifically, the goals were to define the deep structure of the Congo-Angola margin using seismic surveying techniques, define ocean-bottom micro-topography using high-resolution side-scan sonar, and provide images (both visual and acoustic) of the surface sediments on the seabed (Savoye et al. 2000, 2009). The ZaïAngo cruises resulted in the detection of various gas hydrate areas (pockmarks) and the first images of deep-sea benthic fauna in the area.

Results from the ZaïAngo cruises led to the selection of sites along the west African margin ranging from 350 to 4800 m for further study (these areas spanned both EEZs and ABNJ). The resulting programme of eight cruises, BioZaire (BioZaire 1, Biozaire 2, BioZaire 3, ZaïAngo-Obs-Biol1, ZaïAngo-Biol2, ZaïAngo-Rov, Bio2recup, and Bio2recup2), targeted the west equatorial African margin between 2001 and 2005 and focused on characterising benthic faunal community structure in relation to the physical and chemical processes in the region (Sibuet & Vangriesheim 2009). A total of 11 sites were surveyed in an attempt to measure and understand the physical, chemical, and biological setting. Sites included areas earmarked for oil and gas extraction, sites both within and away from the influence of the Congo submarine channel, cold seeps and pockmarks, and lobe areas on the abyssal plain. Sites were surveyed using standardised sampling methodologies (e.g., benthic trawling) together with more modern equipment such as the ROV *Victor 6000*. The BioZaire cruises led to the discovery of one of the largest cold seeps near the Congo channel, the Regab pockmark at 3160 m (Olu et al. 2007a, Ondréas et al. 2005). The distribution of benthic assemblages within the sample sites was also mapped (Olu et al. 2007a).

In 2011, the Regab pockmark was revisited during the West African Cold Seeps cruise, again led by IFREMER. During this cruise video, mosaic mapping was used to identify three main types of megafaunal communities in the Regab site, each inhabiting its own area. Mussel beds were recorded in more central areas of the cold seep experiencing a high flux of methane; these were followed by tubeworm fields, and finally, vesicomyid clam-dominated communities where the sulphide flux is lowest (Marcon et al. 2014). Characterisation of epifauna and megafauna from the Regab site revealed that symbiont-bearing species were dominated by mytilids including *Bathymodiolus* sp. aff. *boomerang* (Olu et al. 2007a,b), two vesicomyid clam species (Cosel & Olu 2008, 2009, Krylova & Cosel 2011), and siboglinid polychaetes (Andersen et al. 2004). Non-symbiont-bearing and vagrant communities were dominated by a range of megafaunal species including alvinocarid shrimp (Komai & Segonzac 2005), holothurians (Thomas et al. 2020), and gastropods (Warén & Bouchet 2009). Other taxa observed at the Regab site included one zoarcid fish species (*Lycodes* sp.), two species of galatheid crustacean (Macpherson & Segonzac 2005), and *Branchipolynoe* cf. *seepensis*, a commensal polychaete of the mussel *Bathymodiolus* sp. aff. *boomerang* (Gaudron et al. 2017).

In sites further afield from the Regab pockmark, numerous benthic and benthopelagic fish were recorded at depths of 3000–4000 m (Olu et al. 2009). At other pockmark sites around 600 m on the Gabon margin, dominant species included vesicomyid bivalves and gastropods (Warén & Bouchet 2009). Similarly to the Regab pockmark, this site (Guiness) was revisited during the West African Cold Seeps cruise, which resulted in the identification of previously undescribed species (Duperron et al. 2013, Gaudron et al. 2017).

Besides reducing habitats in the Gulf of Guinea, the presence of deep-sea scleractinian coral (namely *Desmophyllum pertusum*) was first reported close to the Congo Canyon at a depth of 380 m during the 1950 Galathea Expedition aboard the HDMS Galathea (Zibrowius 1980, Sibuet & Vangriesheim 2009). During the BioZaire programme, one site at 400 m was revisited and surveyed using a combination of multibeam bathymetry, side-scan sonar, high-resolution seismic techniques, and ROV dives. Surveys revealed the presence of carbonate mounds colonised by *D. pertusum*.

Video analysis showed high fish diversity was associated with these structures (Le Guilloux et al. 2009, Sibuet & Vangriesheim 2009), as well as the presence of other VME-indicator taxa including antipatharians (*Stylopathes* sp.) and hexactinellid sponges (*Aphrocallistes* sp.). Similarly, a 70 m high cold-water coral mound was discovered at 400 m off the Ghanaian coast. This mound extends over 1400 m perpendicular to the main current direction and, when last observed, was topped by a thriving *D. pertusum*-dominated reef, accompanied by patches of live *Madrepora oculata* and *Solenosmilia variabilis* (Buhl-Mortensen et al. 2017).

Environmental baseline surveys executed by the oil and gas industry have been undertaken since the 1990s, and there now exists an extensive, but largely unpublished, body of information on the fauna of bathyal depths of the continental margin regions of West Africa. When shared with scientists, these datasets can also shed light on the biodiversity of the Gulf of Guinea continental margin. For example, Total E&P Nigeria Ltd (2007) reported that their samples of the macrofaunal community of the Usan field, located in the far east of the Nigerian EEZ approximately 130 km from the island of Bioko, consisted of molluscs (38.6%), arthropods (22.0%), protozoans (17.6%), and annelids (16.3%). Through science-industry collaboration via the SERPENT project (Gates et al. 2017), the first description of epibenthic megafaunal assemblages on the Nigerian continental margin took place (again within the Usan field), revealing communities dominated by echinoids and crustaceans (Jones et al. 2013).

In 2012, as part of the Norwegian Oil for Development Programme to assess the impacts of offshore hydrocarbon production on ecosystems (Bianchi et al. 2016), samples were taken aboard the RV Dr. Fridtjof Nansen along a bathymetric gradient extending across the shelf and slope off the Ghanaian coast (Jóźwiak et al. 2020, Stępień et al. 2021). Macrofauna were collected using a van Veen grab between 25 and 1000 m depth. Analysis of the Tanaidacea and Cumacea from these samples revealed high levels of diversity in both taxa, with most species undescribed (Jóźwiak et al. 2020, Stępień e t al. 2021). Since many species appeared to be rare and species accumulation curves did not attain saturation, a large portion of species in the region have likely not been discovered.

Like much of the Gulf of Guinea, the scientific literature for the Nigerian EEZ is lacking, but fisheries provide an insight into marine life here. The Niger Delta is home to large artisanal shrimp fisheries (Olaoye & Ojebiyi 2018); further offshore, there are demersal fish populations including *Cynoglossus browni*, commonly known as the Nigerian tonguesole (Akintade et al. 2021). In deeper waters, large populations of drift fish and lantern fish are prominent (Elegbede 2021). To further understand and develop its fisheries resources, Nigeria has acquired the RV Bayagbona.

Angola The Angolan continental shelf represents a subtropical transition zone between the Equatorial Atlantic and the BCLME (Hutchings et al. 2009). In addition to the Angolan aspects of the Gulf of Guinea exploration outlined above, exploration of offshore areas within the Angolan EEZ has commenced through both scientific and industry-driven exploration. Higgs et al. (2014) were able to use industry ROVs to undertake a study of the megafaunal scavenger communities associated with three natural food falls (one whale shark and two mobulid rays). The carcasses supported moderate communities of scavenging fish (up to 50 individuals per carcass), mostly from the family Zoarcidae. There was no evidence of whale fall-type communities with the exception of putative sulphide-oxidising bacterial mats. Additional studies of the macrofaunal scavenger communities of the Angolan margin have also been undertaken (Duffy et al. 2016, Horton 2004, Horton & Thurston 2014), again made possible through the use of industry-collected data.

In 2016, the ANNA Expedition (M122) with the German RV Meteor detected a large cold-water coral mound province south of the Cuanza River, which extends over 60 km along the Angolan continental margin (Hebbeln et al. 2017), showing similarities to cold-water coral reefs found slightly further north (Le Guilloux et al. 2009). During the expedition, high-resolution mapping of the province revealed that it consisted of numerous coral mounds and ridges, located at depths between 250 and

500 m and reaching heights of up to 100 m. Video dives with the MARUM ROV *Squid* recorded thriving cold-water coral reefs on top of the mounds dominated by *Desmophyllum pertusum*, *Madrepora oculata*, and Caryophyllidae solitary corals. At depths around 250 m, live *D. pertusum* occurred widely as scattered small colonies, whereas at deeper depths of 330–470 m, the coral mounds were covered by dense *D. pertusum* reefs (Hebbeln et al. 2020). Two colour morphs of *D. pertusum* colonies were present: white-tissued and occasionally red-tissued morphs. Although *M. oculata* is comparably rare, some relatively dense patches were documented, and the species was observed forming exceptionally large colonies reaching over 1 m high (Orejas et al. 2021). Hydrographic sampling using CTDs and benthic lander systems indicated that these Angolan coral reefs are today exposed to hypoxic conditions (0.5–1.5 mL/L dissolved oxygen) in the centre of the local oxygen minimum zone (Hanz et al. 2019, Hebbeln et al. 2020). Corals thriving under such low oxygen conditions have never been observed before, neither in nature nor in laboratory experiments. Other recorded cnidarian groups included hydroids, pennatulids, antipatharians (likely *Parantipathes* sp.), actiniarians in high densities on coral rubble or as symbionts on hexactinellid sponges, and octocorals, with Stolonifera (*Clavularia* sp.) and gorgonians (Acanthogorgiidae and Plexauridae) being most abundant. Overall, suspension-feeders were the most dominant and conspicuous benthic group observed off Angola. In contrast, shallower areas between the coral mounds were characterised by soft bottoms with or without coral rubble and were dominated by sponges. Locally, other filter-feeders such as oysters (*Neopycnodonte zibrowii*) were present in high abundance. Predators were represented mostly by crustaceans and asteroids. Ophiuroids (mostly detritus feeders) were present in the soft-bottom areas as well as in the rocky boulders present on the shallower mounds. Even though the Angolan reefs tend to have high biodiversity, many faunal groups commonly found on better oxygenated Atlantic coral mounds were missing here (Hebbeln et al. 2017).

Asphalt mounds are formed from seepage of hydrocarbons associated with subsurface salt structures and are present on the Angolan margin. Epifaunal communities associated with these features are dense, including some chemosynthetic taxa where there was active seepage (Jones et al. 2014). Angola's asphalt mounds increased habitat heterogeneity in the area providing substratum for epilithic megafauna, increased local α- and β-diversity, and therefore, may play an important role in maintenance of regional sizes of populations of epifaunal species (Jones et al. 2014).

Using the RV Dr. Fridtjof Nansen, the EAF-Nansen Programme has surveyed the Angolan EEZ multiple times since 1994, typically focusing on assessing demersal fish stocks (Bianchi et al. 2016). Additionally, a number of demersal fish surveys have been conducted in this region, often associated with areas of oil and gas extraction. Milligan et al. (2020) used 7.5 years of photographic time-series data from the Deep-ocean Environmental Long-term Observatory Systems (DELOS; Vardaro et al. 2013) to demonstrate recurrent, seasonal changes in the abundance of demersal fishes at 1400 m depth on the Angolan slope. Changes were correlated with overlying patterns of net primary productivity, suggesting strong bottom-up trophic control of the deep-living fish assemblage. Fishes from 11 families were identified, with dominant taxa including macrourids, synaphobranchid eels, and halosaurids. Baited camera studies from the continental slope (1297–2453 m depth) identified 31 species from 17 families including Somniosidae, Synaphobranchidae, Moridae, and Zoarcidae, all of which are widely distributed through the Atlantic Ocean (Jamieson et al. 2011, Jamieson et al. 2017).

Namibia The Benguela VI and VII research cruises were carried out under the Namibian Region Research Project in the 1980s, and Uriz (1988) characterised the sponge fauna from trawl samples from between 100 and 500 m depth. This work described an abundance of sponge fauna on the Namibian shelf, describing 75 species from the classes Hexactinellida and Demospongiae.

During the ANNA Expedition in 2016, a cold-water coral mound province was mapped southeast of the Walvis Ridge at around 21°S that extends over 80 km along the outer Namibian shelf between 160 and 270 m (Hebbeln et al. 2017). The province consists of more than 1200 coral mounds with heights of a few metres to up to 20 m, arranged on top and west of a large north-east–south-west-trending escarpment (Tamborrino et al. 2022). Video observations and benthic sampling revealed that the coral mounds are made up exclusively of fossilised *Desmophyllum pertusum* framework from between 9500 and 4500 years ago (Tamborrino et al. 2019). No live corals were observed and the epifaunal community living on the reef framework was of low diversity, likely reflecting the extremely low oxygen conditions in this region (<0.15 mL/L dissolved oxygen; Hanz et al. 2019). Nevertheless, the dead reef framework still provides habitat for communities adapted to near anoxic conditions on the west African margin. Most conspicuous were the masses of yellow, cheilostome bryozoan patches, likely belonging to the genus *Metroperiella*, that covered coral skeleton and were highly fluorescent under ultraviolet light stimulation (Wienberg et al. 2023). Some coral mounds had larger aggregations of an erect-flexible and weakly calcified flustrellid bryozoan, possibly of the genus *Klugeflustra*. Other commonly found sessile organism groups were actiniarians, zoanthids, several hydroid species, some thin encrusting sponges, ascidians, and serpulid and sabellid polychaetes. The associated sessile megafauna was also found to be low in diversity (both taxonomically and functionally), constituting five commonly occurring sponge species. The mobile fauna was represented by asteroids and ophiuroids (with *Amphiura grandiquama* and *Ophiactis luetkeni* most abundant), *Macropipus australis*, the stomatopod *Pterygosquilla armatus*, shrimp species, pycnogonids, amphipods, cumaceans, and holothurians. An interesting feature was the high local abundance of a 5 to 10 cm long gobiid fish, *Sufflogobius bibarbatus*, that lived and hid underneath coral framework in great numbers. Other fish encountered in the coral mounds included representatives from the genera *Lophius* and *Merluccius*. Occasionally, swarms of carangid fishes (probably *Trachurus*) were observed. Notably large quantities of sunken jellyfish were also observed during ROV dives.

Benthic invertebrate data associated with the Namibian Ministry of Fisheries and Marine Resources hake fishery surveys dates back to at least 1990, although data from other fisheries such as monk and crab may also be accessible. However, the taxonomic resolution of this data is low, with most samples identified to phylum level; however, in cases where finer-scale taxonomic groups were readily identifiable, for example, Asteroidea, these were recorded. Recently, the Ministry has embarked on a process to establish a benthic invertebrate collection and monitoring programme to run alongside their existing fisheries survey programme. The motivation for this new programme is to meet the conditional requirements of the Marine Stewardship Council (MSC) for certification of the Namibian hake fishery, one of which calls for the gathering of baseline data on the benthic invertebrate fauna associated with fisheries and the identification of VMEs. The first sample collection (identified to higher taxonomic resolution) using standard trawling procedures was in November 2021 aboard the RV Mirabilis, Namibia's fisheries research vessel; this was closely followed by further sampling during the hake surveys in January and February 2022. Approximately 99% of individuals were identified to species level during these surveys, although this still needs to be verified by taxonomic experts. Images were also collected from each location where invertebrates were physically sampled. The samples were preserved in formalin with the aim of subsequently acquiring taxonomic verification.

South Africa South Africa's rich marine biodiversity has long been recognised, with current estimates of more than 13,000 species (Sink et al. 2019). Overall estimates of endemism range from 26% to 33%, and although there is considerable variability among taxa, South Africa is reported to have the third highest endemism after New Zealand and Antarctica (Costello et al. 2010).

Most of South Africa's offshore research has been driven by management requirements of extractive industries including fisheries and petroleum. Fishery-independent demersal research trawl surveys have been conducted annually since 1984 by the relevant government fisheries department (currently the Department of Forestry, Fisheries and Environment (DFFE)) to determine abundance indices of important demersal fish resources including hake (*Merluccius* spp.), kingklip (*Genypterus capensis*), monk (*Lophius vomerinus*), and sole (*Austroglossus pectoralis*). These annual surveys span from the South African-Namibian border in the north to approximately 27°E (Port Alfred) and from 30 m inshore to the 500 m depth contour; however, since 2011, the surveys have been extended to a maximum of 1000 m (DEFF 2020). All vertebrates and cephalopods retained in the catch are identified to species level where possible, and the catch weight and size composition, per gender, is recorded (DEFF 2020). Several decades of these regular surveys result in fairly comprehensive demersal megafauna diversity information from South Africa's unconsolidated shelf and shelf edge in the south-east Atlantic region. Similar to other south-west African nations, the EAF-Nansen Programme first visited the South African EEZ in 1994 and carried out work assessing demersal fish stocks (Bianchi et al. 2016).

Species composition of demersal fish assemblages on South Africa's west coast is thought to be influenced mostly by depth, with two main assemblages present above and below 300–400 m, the depth taken to represent the edge of the continental shelf (Roel 1987, Atkinson et al. 2011). Shallower shelf assemblages are variable between summer and winter, whereas deeper assemblages are homogeneous in species composition throughout the year (Roel 1987). Clear geographic distinctness in assemblages north versus south of Cape Columbine was also observed, attributed to benthic terrain differences (Atkinson et al. 2011).

Demersal fish and cephalopod assemblages on the Agulhas Bank, located off the south coast of South Africa, are well-studied for the Central and South Atlantic (Badenhorst & Smale 1991, Smale et al. 1993, Yemane et al. 2010, Currie et al. 2019, 2020). Fish and cephalopod assemblages can be split into three demersal groups: inshore (shallower than 100 m), shelf (± 90 to 190 m), and shelf edge/upper slope (deeper than 200 m), likely driven by temperature and oxygen variability (Smale et al. 1993). Overall diversity declines from shallow waters to around 80 m where it increases to 150 m, followed again by a decline; below 300 m, there is an increase in heterogeneity of the demersal fish community (Yemane et al. 2010). Analysis of time-series data across three decades (1986–2016) revealed a mean westward shift in location and a reduced extent of demersal fish populations on the Agulhas Bank (Currie et al. 2019). The historical data included many more reef-associated species compared to newer data that mostly included species associated with unconsolidated sediments or both reef and non-reef habitats, perhaps indicating that a century of industrial trawling on the Agulhas Bank has altered the benthic habitats and, indirectly, fish assemblage composition (Currie et al. 2020).

South Africa's offshore benthic invertebrates have, in the past, been poorly studied and local taxonomic studies have been sparse. However, since 2007, marine invertebrates have been increasingly retained, recorded, and identified as part of research demersal trawl surveys conducted on the west and south coasts of South Africa (DEFF 2020). Routine monitoring of benthic invertebrates was formally implemented in 2011, led by the South African Environmental Observation Network (SAEON) in collaboration with DFFE. Regular surveys of this vast area within South Africa's EEZ have enabled a rapid increase in local knowledge of offshore invertebrate benthic biodiversity and contributed towards the classification and description of South Africa's marine ecosystems. For example, knowledge of azooxanthellate corals in South African waters has significantly increased thanks to recent efforts, with the number of known species rising from 77 to 108 including 28 new South African records, three new species, and a new genus (Filander et al. 2021). Data and knowledge from the routine SAEON/DFFE monitoring of benthic invertebrates were collated into South Africa's first field guide to offshore marine invertebrates published in 2018 (Atkinson & Sink 2018). Ongoing surveys continue to expand local knowledge and a new initiative is underway to advance molecular knowledge of these species. As comprehensive demersal research invertebrate data has only been collected since 2011, detailed studies of these communities are currently in preparation. However, from the records of the 410 trawled epifaunal species across twelve phyla, dominant groups were identified as decapod crustaceans, molluscs, and echinoderms (Atkinson & Sink 2018).

The distributions of 22 potential VME-indicator taxa (Atkinson & Sink 2018) have been mapped, drawing from invertebrate research trawl data and museum records for reef-building and non-reef-building scleractinian corals, bamboo corals, stylasterids (*Errina*, *Errinopsis*, *Inferiobata*, and *Stylaster* spp.), bottlebrush primnoid corals (*Thouarella* spp.), sea fans (of the family Melithaea), seapens of the genus *Anthoptilum*, and habitat-forming sponges and bryozoans. Confirmed VME habitats from South African waters include *Suberites* spp. sponge grounds on the western margin (Samaai et al., 2017, 2021).Other biodiversity-focused research includes benthic macrofauna research (Karenyi 2014, Karenyi et al. 2016) and characterisation of marine habitats using visual tools such as submersible, ROV, and towed camera systems (Sink et al. 2019).

In addition to scientific research, the South African EEZ has a long history of offshore oil and gas exploration. Visual tools are frequently used by the oil and gas sector to survey proposed exploration sites in both unconsolidated and rocky terrain at depths exceeding local research capacities. For example, a dedicated *in situ* survey of a localised oil production wellhead located on the Agulhas Bank revealed significant differences in benthic fauna within and beyond a 250 m radius of the wellhead and raised concern over alien or invasive species present in high abundance on the wellhead infrastructure (Sink et al. 2010). As is the case for many Central and South Atlantic bordering nations, it is likely that there exists a substantial, but largely unpublished, body of information on the fauna in deep-sea ecosystems within the region.

Selvagens Islands (Portugal) and the Canary Islands (Spain) Knowledge and understanding of the marine environment in the Selvagens and Canary Islands are poor due to limited scientific exploration, especially of mesophotic and deep-sea ecosystems. In May and June 1991, the RV Seward Johnson visited Madeira, the Selvagens, and the Canary Islands (Reed & Pomponi 1991). Using the *Johnson-Sea-Link I* submersible, the aim was to collect benthic invertebrates, such as lithistid sponges (Carvalho et al. 2015), for bioprospecting purposes to depths as deep as 914 m. Dives revealed that dominant communities providing structural habitat in the region included sponges, gorgonians, and solitary scleractinians. Later in 2010, a second deep-sea expedition was undertaken to explore benthic habitats surrounding the islands. Unfortunately, the ROV *Luso* was lost after a couple of dives and the mission was terminated (EMEPC/M@rbis/Selvagens Expedition). In 2015, data collected across 12 drop-camera deployments between 112 and 2294 m depth revealed the presence of 17 families of deep-water fishes (24 different taxa), with crustaceans (mostly shrimp) reported as the most abundant mobile invertebrates (Friedlander et al. 2016). Shallower locations between 100 and 300 m showed high relief basalt dominated by sponges, gorgonians, and black corals, while deeper waters were characterised by mostly flat sandy areas or low to steep relief basalt slopes dominated by grenadiers and cutthroat eels. Notably, the Azores Chromis (*Chromis limbata*) accounted for 10% of the total biomass in the Selvagens Islands and was more than four times dominant (by weight) in the deeper areas surveyed compared to shallower waters. A single occurrence of the smalltooth sand tiger shark (*Odoontaspis ferox*) was reported at 1200 m.

In the Canary Islands EEZ, Concepcion Bank (Banco de la Concepción) is the best-studied feature owing to the seven research cruises between 2009 and 2013 that surveyed here aboard the RV Vizconde de Eza, RV Miguel Oliver, and RV Angeles Alvariño. The multidisciplinary surveys were part of the LIFE project, INDEMARES, and included multibeam mapping, environmental data collection using a CTD, and sampling of soft- and hard-substrate habitats using box cores, multicore, and ROVs (Almón et al. 2014). The geological and biological processes acting on the seamount were documented alongside the geomorphology (Rivera et al. 2016). The substrate typically comprised rocky outcrops, sediment patches of varying thickness, and accumulations of dead coral and sand dunes. Due to the complex hydrodynamic regime around the seamount retaining productive water, biodiversity here is high (Rivera et al. 2016). The INDEMARES project resulted in 498 species being recorded on Concepcion Bank, with cnidarians and sponges being the most conspicuous. Also recorded were numerous species endemic to Macaronesia including *Antipathella wollastoni*, *Corallium tricolor*, and *Isozoanthus primnoides*. Most of the benthic communities described here occur in bathyal depths from 200 to 3000 m. In hard-substrate areas, the assemblages were dominated by several cnidarians including antipatharians, with a strong dominance of the genus *Stichopathes*, as well as gorgonians such as *Callogorgia verticillata* and *Narella bellissima*. Sponges were also well-represented on the bank, with observations of large hexactinellids, mainly *Asconema setubalense* (Martín-García et al. 2022), as well as lithistid (stone) sponge assemblages comprising *Leiodermatium lynceus* and *Neophryssospongia nolitangere*. Mixed communities were also present including one dominated by the sponge *Pheronema carpenteri* and the gorgonian *Paramuricea biscaya*. Scleractinian cold-water corals including *Dendrophyllia cornigera* were also present. In addition to the live coral communities, dead framework supporting diverse epifaunal assemblages was observed comprising mostly *Desmophyllum pertusum* and *Madrepora oculata*, with occasional live thickets also documented (Rivera et al. 2016). Other VME-indicator taxa observed included *Corallium niobe* and *Corallium tricolor* and several species of bamboo corals. In soft-substrate areas, solitary corals were abundant including *Flabellum chunii*.

Cabo Verde The Cabo Verde archipelago is naturally fragmented, isolated from permanent continental influences and possesses a relatively rich biodiversity, which is normally characterised by diverse populations despite low abundances. Apart from its rich marine biodiversity, Cabo Verde also hosts high numbers of endemic species in the context of the Macaronesian region (e.g., Duda & Rolan 2005). This is thought to be due to the combination of the tropical environment, which prevents large sea-surface temperature variations, and the archipelago's biogeographical isolation from west African shores, mainly due to the presence of the north-west African Upwelling (Freitas et al. 2019). Although there have been several expeditions here, published marine biodiversity information is still scarce (Freitas et al. 2019). However, Senghor Seamount situated to the north-east of the island of Sal in the Cabo Verde EEZ has been surveyed.

In 2009, biological communities on Senghor Seamount were surveyed using an ROV during cruise M79/3 of RV Meteor (Christiansen et al. 2011). Dives undertaken on the summit and upper slopes of the seamount found a diverse range of habitats and communities. At a depth of ~320 m on the north-eastern edge of the summit plateau, a small number of fish and mobile fauna were observed, while the rest of the megabenthic community was relatively scarce. Along the other slope transects, a mixture of sponges and hard and soft corals were observed on protruding rock formations, while ophiuroids were seen in high densities on softer sediments (Christiansen et al. 2011, Chivers et al. 2013). With regard to the macrofaunal communities, polychaetes dominated, often comprising over 70% of the total number of individuals collected (Chivers 2014); on the northern flank of the seamount, polychaete communities were particularly diverse, with 135 putative species being identified from over 950 individuals (Chivers et al. 2013). Comparison of the macrofaunal data from four different transects revealed that abundance and biomass was higher at mid-slope depths on the southern flank of the seamount compared to the eastern flank which may have been a result of increased current speeds and greater physical disturbance (Chivers 2014).

The biodiversity and distribution of demersal fish communities around Cabo Verde has also been studied along the islands' shelf break and slopes (Menezes et al. 2004), seamounts, and adjacent abyssal plain (e.g., Christiansen 2012, 2013). Results of multiple investigations suggest the region hosts a high abundance of deep demersal fish (Henriques et al. 2002, Menezes et al. 2015), including the occurrence of rare or poorly known species (Vieira et al. 2013). Further experimental field surveys onboard RV Poseidon investigated the demersal fisheries around Senghor Seamount and adjacent abyssal plain (Christiansen 2012, 2013). Using longlines, traps, and trawls, 26 fish species were caught belonging to 18 families, seven of which were new records for the Cabo Verde deep-sea fish fauna. The results provided a better understanding of the biogeographic patterns of deep-water fish species and highlighted the waters around Cabo Verde as an important transition zone between northern and southern Atlantic fauna (Vieira et al. 2018).

In 2021, the iMirabilis2 Expedition took place in the southern part of the Cabo Verde archipelago and represented the first survey dedicated to the investigation of benthic fauna of the slopes of Fogo and Brava islands as well as Cadamosto Seamount (Orejas et al. 2022). The expedition was conducted aboard the RV Sarmiento de Gamboa. During the expedition, benthic megafaunal communities occurring on hard substrate were surveyed using the ROV *Luso*. Cadamosto Seamount is seismically active (Grevemeyer et al. 2010) and is characterised by young volcanic features with the presence of volcanic boulders and extensive pillow lavas as well as iron-rich hydrothermally altered rocks (Hansteen et al. 2014). This seamount displayed the highest diversity of the three survey sites, although species composition and abundances differed significantly across the flanks. Nevertheless, most hosted sponge aggregations and coral gardens, the latter comprising *Metallogorgia* spp., as well as plexaurid and bamboo corals. *Enallopsammia rostrata* was typically recorded as scattered colonies, although a large coral garden comprising this species was recorded at 1600 m on the north-west flank. The north-east flank displayed the highest diversity and density of cold-water coral species, hosting different species of antipatharians and bamboo corals to the other flanks. The summit of Cadamosto Seamount sits at approximately 1400 m, with the western side dominated by white stick-shaped carnivorous sponges in high densities. The slope of Fogo Island revealed varying species composition across location and depth. The base of the slope was characterised by soft sediment with sporadic *Anthomastus* spp. colonies. On the slope, the substrate changed to include boulders, with the same cold-water corals present as on Cadamosto Seamount. *Acanella arbuscula* was recorded in high densities across all locations on the southern side of Fogo Island between 1830 and 1950 m, alongside sponges and cold-water corals. Sea pens and holothurians dominated the community in soft-sediment habitats at around 1800 m. Although the substrate type at Brava Island reflected that of Fogo, this was the least diverse feature in comparison. The community was largely dominated by sea pens, ophiuroids, and sponges, although in the shallowest areas, *Metallogorgia* spp. were observed as well as large colonies of bamboo corals (some over 1 m in height). No large aggregations of any species were detected. A first version of a catalogue for the benthic fauna documented during the iMirabilis2 Expedition is available online (Vinha et al. 2022).

Other Oceanic Islands – Sao-Tome and Principe and Annobón Island (Equatorial Guinea) The RV Pillsbury Deep-sea Expedition to the Gulf of Guinea during 1964 and 1965 (Chesher 1966) sampled the fauna of Sao-Tome and Principe and Annobón Island; however, despite the name, it appears that samples were largely collected in shallow marine and freshwater habitats (e.g., Holthuis 1966). Based on the available literature, it seems that no other deep-water work has taken place in the EEZs of these oceanic islands.

Falkland Islands (Malvinas) (United Kingdom) Deep waters of the Falklands Maritime Zone (FMZ) remain relatively unexplored, with limited sampling compared to that focused on the shallower habitats around the islands (Brewin et al. 2020); instead, sampling efforts have often represented components of larger sampling regimes, for example, the Biogeographic Atlas of the Southern Ocean (De Broyer et al. 2014). Resultantly, available literature for the FMZ typically comprises reports from a few stations within broad-scale surveys which has hindered the quantification and mapping of benthos in the FMZ. However, as part of marine spatial planning initiatives (Bax et al. 2022) and an ecosystem-based approach to management planning objectives (Baylis et al. 2021), the South Atlantic Environmental Research Institute (SAERI) has undertaken a series of baseline surveys of key areas within the FMZ.

Burdwood Bank is a shallow submerged plateau region at depths of ~50 to 150 m, surrounded by deeper waters located in the south of the FMZ, straddling the boundary of the Argentine EEZ. In 2018 and 2020, SAERI and the British Antarctic Survey (BAS) collaborated on Darwin Initiative-funded cruises JR18003 (Sands et al. 2019) and JR19002 (Scourse et al. 2020) to characterise the eastern Burdwood Bank, collecting high-resolution bathymetry, imagery, and physical specimens. Diverse habitats were identified including areas with abundant stylasterid and scleractinian corals, with preliminary results suggesting that Burdwood Bank hosts both high benthic carbon storage and sequestration potential with high biological diversity compared to other parts of the Patagonian Shelf and ABNJ to the north of the FMZ (Bax et al. 2022).

Like other areas of the Central and South Atlantic, there is a history of collaboration with industry in the exploration of the FMZ. SAERI, in collaboration with the Falkland Islands Fisheries Department and Consolidated Fishes Limited, have undertaken three research cruises to collect data to support MSC certification of the Patagonian toothfish (*Dissostichus eleginoides*) fishery. Imagery and by-catch data were collected from across the shelf region and used to develop broad-scale habitat and VME-indicator taxa maps for depths ranging from 200 to 3000 m (Brewin et al. 2020, Pearman, 2021). Additionally, a number of habitat and environmental baseline surveys have also been conducted to support offshore exploration of oil and gas (FOGL 2011a,b, Noble Energy 2014a,b,c). These surveys comprised the collection of small-scale patches of high-resolution bathymetry, image data, and grab samples of both fauna and sediment.

VME-indicator taxa recorded from the FMZ include sponges (Goodwin et al. 2011, Brewin et al. 2020, Pearman et al. 2022), bryozoans, cnidarians (predominantly alcyonaceans), stylasterids (Brewin et al. 2020, Pearman et al. 2022), and scleractinians (Cairns & Polonio 2013, Brewin et al. 2020, Pearman et al. in review). In many cases across the Falkland Plateau, VME-indicator taxa form VME habitats including scleractinian coral reefs, sea pen fields, coral gardens (Brewin et al. 2020, Pearman et al. 2022), and chemosynthetic communities (Noble Energy 2014a,b,c). In 2019 and 2021, VMEs comprising field-like aggregations of the stylasterid corals, *Errina* sp., were identified at mesophotic depths (~40 m) around Bird Island, a small land mass lying due south of West Falkland (Bax et al. 2022). Mesophotic ecosystems are largely unexplored in the FMZ, as is the case in most of the Central and South Atlantic, and the lower depth limit of most light-dependent species is unknown (Goodwin et al. 2011, Bayley et al. 2021). However, densities of stylasterids appeared similar to fields found in other locations such as the Patagonian fjords in Chile and East Antarctica (Bax & Cairns 2014), suggesting that Bird Island (and other unexplored locations) may host important mesophotic coral biodiversity.

St Helena, Ascension and Tristan da Cunha (United Kingdom) Deep-water exploration of the UKOT of Saint Helena, Ascension and Tristan da Cunha began with the HMS Challenger Expedition. A total of 39 species, many of which were identified as cold-water corals, were collected from station 344 at approximately 768 m, located within the EEZ of Ascension Island at ~7°S (Murray 1895). Further south at ~39°S, 105 species were collected from station 135 at 658 m in the Tristan da Cunha EEZ, demonstrating a high diversity of benthic taxa (Murray 1895).

More recently, BAS and the Centre for Environment, Fisheries and Aquaculture Science (Cefas) have jointly led mid-Atlantic cruises focusing on the UKOT. Five research cruises were undertaken between 2013 and 2019 (Barnes et al. 2013, 2015, 2019, Morley et al. 2018, Whomersley et al. 2019). Surveys in 2013, 2015, 2018, and 2019 sampled within the EEZs of Tristan da Cunha and/or Saint Helena across multiple topographic features, while the 2015 and 2017 surveys sampled around Ascension Island. All cruises involved the collection of high-resolution multibeam bathymetry, water property data via CTD deployment, physical sample collection by mini-Agassiz trawl, and seabed imagery between 75 and 1020 m captured using a drop camera. Analysis of the benthic assemblage structure from the flanks of the oceanic islands and seamounts in all three EEZs of the UKOT revealed that those from Ascension and St Helena were less diverse than those from Tristan da Cunha (Bridges et al. 2021), although there was more within-depth-stratum variation in communities in the tropics (Bridges et al. 2022a). Tropical communities were dominated by cold-water coral reef-associated ophiuroids, soft-bottom cup corals, prawns, and cidarid urchins, whereas temperate communities were dominated largely by filter-feeding taxa such as encrusting sponges, hard-bottom *Caryophyllia* spp. cup corals, massive structure-forming hexactinellid sponges, hydroids, and non-reef-associated ophiuroids (Bridges et al. 2021). Alongside many VME-indicator taxa, VMEs in the form of *Desmophyllum pertusum* reef, *Solenosmilia variabilis* reef, coral gardens, and hard-bottom cup coral fields comprising solitary scleractinians were all observed (Bridges et al. 2021). Such assemblages in just the 3% of Ascension's seabed shallower than 1000 m surveyed have been estimated to store 43,000 tonnes of blue carbon proving how important the benefits from nature (ecosystem services) can be in these habitats (Barnes et al. 2019).

Following on from the 2019 survey, a joint cruise led by Cefas, Ascension Island Government and Saint Helena Government with the RRS Discovery is currently surveying deep-water ecosystems in the EEZs of Ascension Island and Saint Helena (DY159, October - December 2022; Whomersley et al. in prep). Focusing largely on the oceanic islands themselves and/or surrounding seamounts, a towed camera system collected video footage between 130 and 1157 m, revealing high diversity of species and ecosystems in both EEZs. In Ascension Island EEZ, observations included dense *D. pertusum* reef with associated epifauna including large numbers of the glass sponge, *Aphrocallistes* sp.; sea pen and pencil urchin (*Cidaris* sp.) fields; as well as rocky habitats with lower densities of octocorals and crinoids. Further south in the Saint Helena EEZ, dive videos revealed extensive patches of dead *D. pertusum* with scattered colonies of live polyps; mixed substrate areas hosting octocorals, sea pens, and crinoids; and soft-substrate sea pen fields. In addition to the video data, grab samples containing coarse, calcareous sediments with low epi- and infaunal density were collected from between 3200 and 3600 m in the Ascension Island EEZ.

Additionally, as part of a National Geographic Pristine Seas Expedition, in partnership with the Tristan da Cunha Government and the Royal Society for the Protection of Birds (RSPB), an expedition took place to Tristan da Cunha in early 2017 (Caselle et al. 2018). Similarly, this cruise collected data on oceanographic conditions, biodiversity via the use of SCUBA surveys, drop cameras, and pelagic baited remote underwater video systems (BRUVS). A total of 21 species were observed within the 23 2-hour-long deep-water drop-camera deployments, with structure-forming taxa, including sea pens, crinoids, whip corals, and gorgonians, present at 40% of the deployments. Many species of fish were also recorded in several deployments including bluenose warehou (*Hyperoglyphe antarctica*), lantern sharks (*Etmopterus granulosus*), bluntnose sixgill shark (*Hexanchus griseus*), grenadiers (family Macrouridae), deep-water cod (*Physiculus karrerae*), and cutthroat eels (*Synaphobranchus* sp., likely *brevidorsalis*). Interestingly, there were distinct differences in communities above and below 750 m aligning with a change in dominant water masses.

Although largely focused on the geology, there are records of surveys within the Ascension Island EEZ focusing on the hydrothermal vents. Based on three cruises (M64/1 in April to May 2005, M68/1 in May 2006, and M78/2 in May 2009) aboard the FS Metoer, Lilliput vent field is thought to measure approximately 1000×250 m in size and is located at 1500 m depth on a ridge segment (Haase et al. 2009). Sampling methodologies included multibeam echosounders, CTDs, ROVs, TV-guided grabs, and autonomous underwater vehicles (AUVs). Imagery and physical samples were collected to satisfy the geological aims of the cruises; although these have not yet been formally analysed with respect to the biology, preliminary observations suggest areas of active and inactive venting, both hosting low megafaunal diversity (*pers. comm.* Amelia Bridges). Also with a geological focus, cruise CD169/05 aboard the RRS Charles Darwin took place in 2005 (German & Parson 2006). Sampling included use of a TOBI deep-tow vehicle, CTDs, and an AUV that collected images from 5 m above the seafloor (German et al. 2008). Again, it is unclear whether the images were analysed in relation to the biology. Biological samples collected during research cruises aboard the RV Meteor (M64/1 in May 2005 and M78/2 in May 2009) and RV l'Atalante

(MARSUED IV in January 2008) were investigated in relation to the genetic connectivity of bivalves and their symbionts from the northern and southern MAR (Breusing et al. 2016). Alongside the physical specimens, image data were also collected and reported in van der Heijden et al. (2012) showing diverse assemblages of chemosynthetic organisms.

Summary of broad-scale biodiversity patterns

The southern hemisphere is extremely data-limited compared to the northern hemisphere (Howell et al. 2020a), and the Central and South Atlantic is no exception to this. This said, the above information demonstrates that a significant level of research has been carried out in this region, however data are not often accessible. It is clear that the Central and South Atlantic is a biodiverse region supporting a range of benthic assemblages and species (Figure 3), many of which are protected under various legal instruments (e.g., VMEs and marine reserves).

Early interbasin comparisons have suggested that the South Atlantic deep sea is more speciose than the North Atlantic due to its geological history and openness to immigration from the Indo-Pacific area (Wilson 1998, Culver & Buzas 2000, Gage 2004). Studies that have characterised broad-scale distribution patterns of the South Atlantic have typically done so as part of such interbasin comparisons (Culver & Buzas 2000). A frequent result is that latitudinal diversity gradients observed in the North Atlantic are less clear in the South Atlantic, perhaps due to a lack of data, but also due to strong interregional variation (Rex et al. 1993, Gage 2004) and possible hemispherical asymmetry (Chown et al. 2004). For example, the south-west Atlantic (Argentine Basin) displays exceptionally high diversity compared to other regions and basins across a range of taxa (Rex et al. 1993, dos Santos et al. 2020).

Understanding how diversity changes with latitude represents one of the oldest ecological challenges. Early work investigating latitudinal diversity gradients collected physical samples from the Central and South Atlantic, typically comprising grab or sledge samples from soft-substrate ecosystems, with results identifying the tropical deep sea to be more diverse than temperate and polar regions (Rex et al. 1993, Culver & Buzas 2000). While this may be the case for soft-substrate areas (or may not, see Gray 2002), this gradient is not apparent in hard-substrate ecosystems which can show a peak in diversity at temperate latitudes driven by heightened primary production (Bridges et al. 2022a). However, productivity is not the only driver of latitudinal diversity gradients. Habitat heterogeneity at the basin-scale will, in part, dictate where areas of high or low diversity occur. For example, the distinct lack of hydrothermal vents along the southern MAR may yield lower diversities in the south, but reef framework, whether dead or alive, will support complex epifaunal communities, and thus increase overall diversity where they occur (Buhl-Mortensen et al. 2010). Furthermore, a basin's role in the evolution of life in the deep sea will shape its diversity. The South Atlantic is older than other basins (e.g., the North Atlantic), and therefore, speciation has had longer to occur, leading to the evolution of more species compared to other basins (Menzies et al. 1973, Hessler et al. 1979, Danovaro et al. 2014).

This said, the information above illustrates that hard-substrate habitats in the tropics are not devoid of life, with seamounts *across* the Central and South Atlantic hosting diverse ranges of benthic assemblages (Victorero et al. 2018, Ramiro-Sánchez et al. 2019, Bergstad et al. 2019, Bridges et al. 2021). One particularly interesting pattern drawn from the summary above is the prevalence of extensive dead scleractinian reefs in parts of the eastern Central and South Atlantic (Durán-Muñoz et al. 2014, Bergstad et al. 2019, FAO 2022b). It appears that much of the scleractinian framework is dead along the north-west African margin and on structures further south (Guinea Seamount Chain and Walvis Ridge) away from continental influence. However, some areas of live reef thrive (e.g., off Angola and Ghana); almost all seamounts host cold-water coral communities, with *Enallopsammia rostrata* repeatedly reported in abundance. Opposingly, the south-west Atlantic, particularly the Brazilian margin, hosts extensive living scleractinian reef systems (Kitahara et al. 2020) at depths between 400 and 800 m in areas of carbonate mounds associated with methane oxidation and under high pelagic productivity (Bernardino et al. in press).

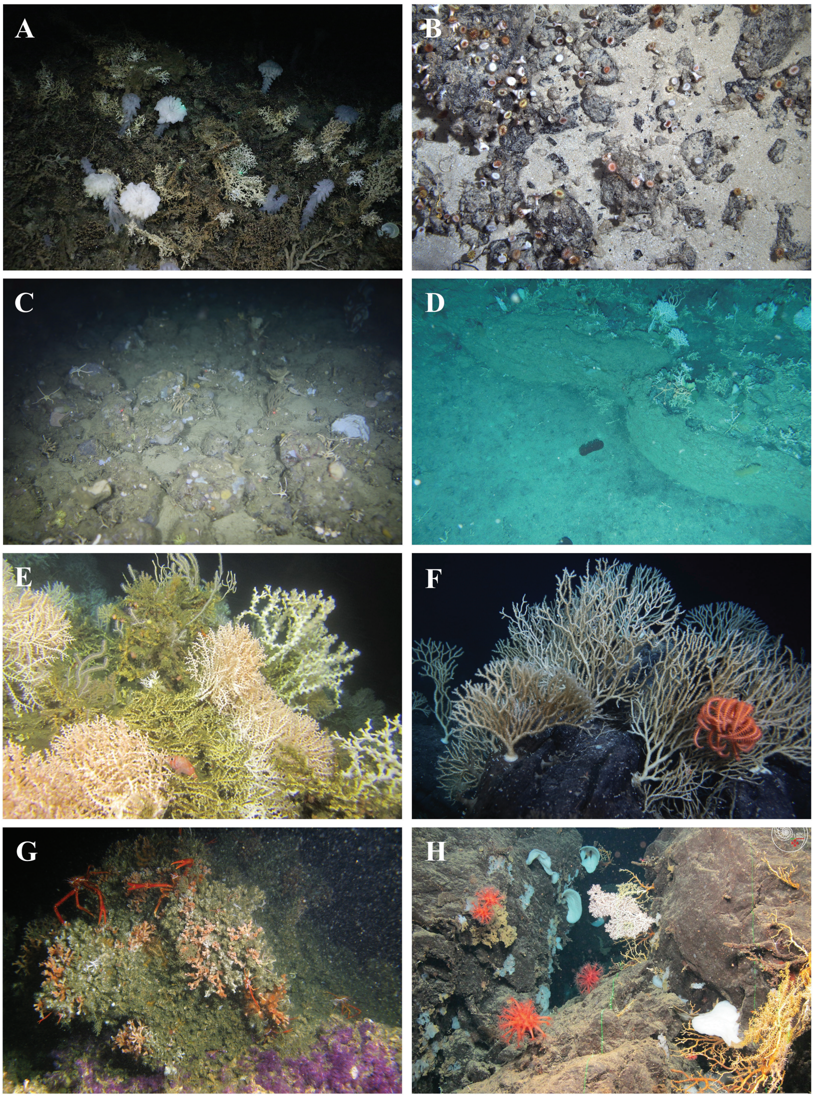

Figure 3 Examples of some of the benthic ecosystems observed in the Central and South Atlantic. (A) Complex of scleractinian reef (*Desmophyllum* sp.) and glass sponge fields (*Aphrocallistes* sp.) from 460 m depth on Grattan Seamount, Ascension Island, image copyright belongs to Ascension Island Government. (B) Hard-bottom cup coral field at 320 m on Crawford Seamount near Tristan da Cunha, image copyright belongs to Tristan da Cunha Government. (C) Bryozoans and sponges characterise the rocky shelf edge at 290 m on the south-western margin of South Africa, image copyright belongs to South African Environmental Observation Network. (D) Cold-water coral assemblage comprising individuals from Stylasteridae, Primnoidae, and Scleractinia observed at 1250 m on the Falkland Plateau, image copyright belongs to Noble 2014a,b,c. (E) Cold-water coral reef, dominated by *Desmophyllum pertusum* and *Madrepora oculata*, growing on top of a coral mound at 350 m on the Angolan margin, image copyright belongs to MARUM ROV Squid (Bremen, Germany). (F) *Sarostegia oculata* garden with a Brisingidae seastar from 790 m on the Rio Grande Rise, image copyright belongs to JAMSTEC. (G) *Desmophyllum pertusum* reef at 556 m off Mauritania (Tanoûdêrt Canyon) colonised by many organisms, among a large *Clavularia* cf. *borealis* colony and *Eumunida bella*, image copyright belongs to Tomas Lundälv, Tjärnö Marine Laboratory, University of Gothenburg, Sweden. (H) Soft corals and sponges dominate bedrock at 1880 m on the flanks of Cadamosto Seamount within the Cabo Verde EEZ, image copyright belongs to iMirabilis2, IEO, CSIC/EMPEC/iAtlantic project.

The North and South Atlantic share taxa, with similar seamount benthic assemblages identified in both hemispheres (Bridges et al. 2021), as well as cold-seep communities (Olu et al. 2007b). The key feature separating the two basins is the Romanche FZ on the MAR. While this may act as a biogeographical barrier for some taxa (e.g., Cardoso et al. 2014), the Romanche FZ facilitates water circulation in the Central Atlantic and therefore may also play a key role in structuring deep North and South Atlantic communities as well as characterising dispersal patterns and connectivity (German et al. 2011, van der Heijden et al. 2012). The eastern and western Atlantic also appear somewhat connected, with several taxa shared across regions (Olu et al. 2010, Krylova & Sahling 2010, Teixeira et al. 2013, Thomas et al. 2020). For example, similarities in the demersal fish communities of the Rio Grande Rise in the south-west Atlantic and the Walvis Ridge in the south-east Atlantic have been highlighted (Parin et al. 1995, Balushkin 2009, Prokofiev & Kukuev 2009). Coined by Polyakov et al. (2017), the term 'atlantification' refers to the encroachment of Atlantic taxa into the polar regions. While this is widespread in the Arctic literature, there are no available references to atlantification in the Antarctic literature. This could be, at least in some part, due to the significant barrier provided by the Antarctic Circumpolar Current both physically and physiologically, although this may be less pronounced in deeper waters (Dueñas et al. 2016). Nevertheless, range shifts and invasive species moving into polar regions are important topics and perhaps represent a major connection between the south-west Atlantic and the Southern Ocean.

Summary of human activities in the region

Although it is clear that the Central and South Atlantic supports a diverse range of species and habitats, including those boasting protection, and despite little being known about the connectivity of ecosystems and their environmental drivers in this broad region, human industries that extract resources from the natural environment are also present. Here, we summarise the current anthropogenic activities and management regimes for ABNJ and EEZs.

Fishing

Regional Fisheries Bodies (RFBs) are organisations responsible for the management of fisheries across large areas of ocean and three are relevant to this review (Figure 4). The two RFBs responsible for bottom fisheries in the Central Atlantic, the Fisheries Committee for the Eastern Central Atlantic (CECAF) and the Western Central Atlantic Fishery Commission (WECAFC), differ from the South East Atlantic Fisheries Organisation (SEAFO) as the first two are entirely advisory in nature, adopt non-binding recommendations, and cover fisheries in areas both within and beyond national jurisdiction. Many states bordering the Central and South Atlantic are not referred to by name in the following section because they do not partake in large-scale, deep-water fisheries.

Fishing in the Central Atlantic

Scientific advice for fishing upon non-highly migratory species in the Central Atlantic is coordinated by CECAF and WECAFC. Established in 1967 and 1973, respectively, the objectives of both CECAF and WECAFC are to promote sustainable use of living marine resources within their areas of competence through proper management and development of fisheries and fishing operations. Unlike SEAFO, neither organisation has any regulatory authority and so cannot implement catch limits or technical measures such as bottom fishing closures.

The upwelled waters off the north-west African continent support productive, artisanal fisheries that represent a key food source for the west African population (FAO 2004, Olaoye & Ojebiyi 2018). However, in recent years, there has been an increase in industrial fishing effort in west African EEZs by other nations including Russia and Denmark, made possible by international agreements (Zeeberg et al. 2006). These fisheries typically target pelagic stocks including sardines (Clupeidae)

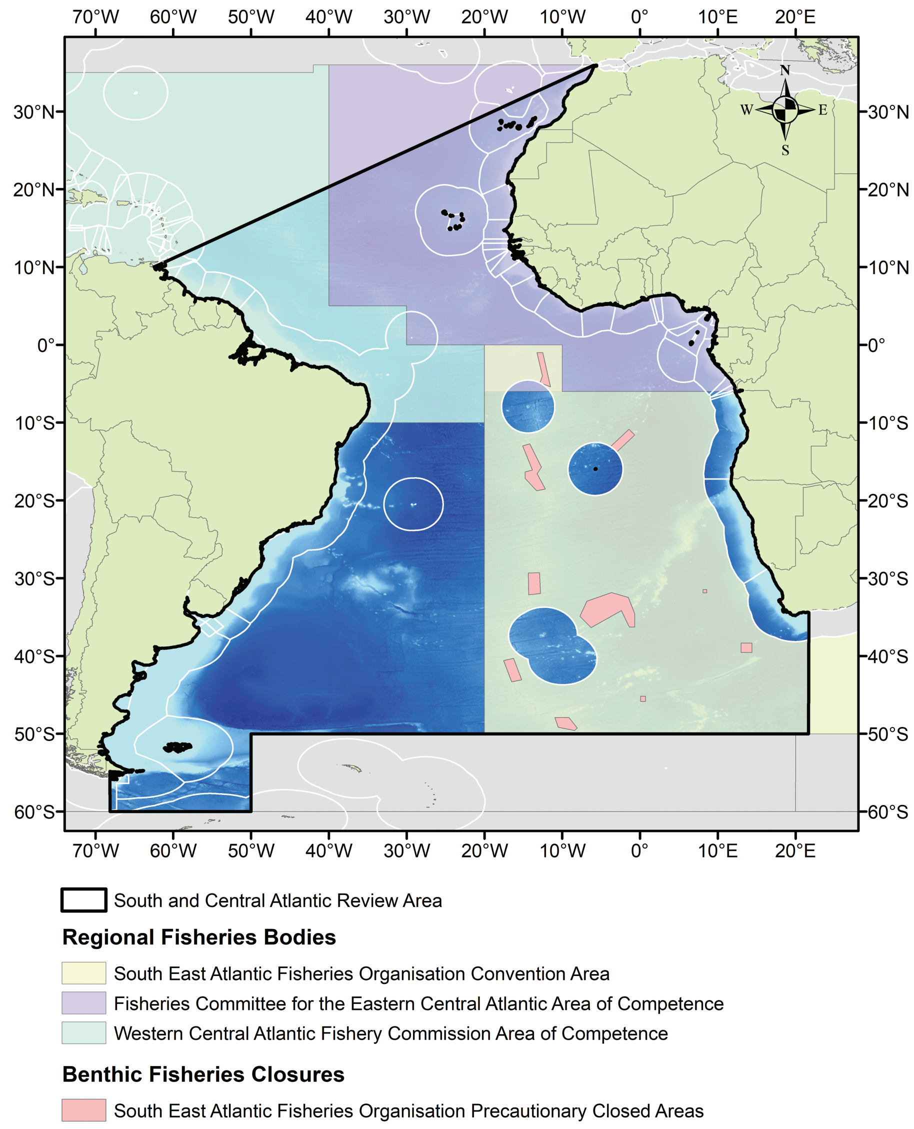

Figure 4 Regional Fisheries Bodies (RFBs) relevant to the Central and South Atlantic. Precautionary closures within the South East Atlantic Fisheries Organisation (SEAFO) Convention Area are also shown. Underlying bathymetry from GEBCO 2020 Grid. Map drawn in WGS84.

and horse mackerel (*Trachurus trachurus*), though by-catch of non-target species is reportedly high (Zeeberg et al. 2006). Also important are the offshore tuna, coastal demersal finfish, and coastal shrimp fisheries (Olaoye & Ojebiyi 2018).

In ABNJ, there are few benthic fishable features present in the Central Atlantic, meaning fishing activity is typically restricted to sections of the MAR as other areas are too deep for demersal fishing gear (FAO 2020). This results in the reported catches of deep-sea species using bottom-contact gear being comparatively small against other regions (FAO 2020). Deep-water fisheries in the eastern Central Atlantic date back to the seventeenth century for species such as European hake (*Merluccius merluccius*) and black scabbardfish (*Aphanopus carbo*), although these were, and continue to be, exclusively within national jurisdiction (FAO 2020). Seamount fisheries were developed in the 1970s around the Canary Islands, but again, these were primarily mid-water trawls targeting pelagic stocks. More recently, states with large, ocean-going fleets such as China and Russia report catches of alfonsino (*Beryx splendens*), a demersal fish often associated with cold-water coral reef habitat, off the north-west African continent, likely from areas both within and beyond national jurisdiction (FAO 2020). There are no records of deep-water fishing in the western Central Atlantic.

Fishing in the South-east Atlantic

SEAFO was established in 2003 and is the Regional Fisheries Management Organisation (RFMO) responsible for sustainably managing fisheries and marine life resources in the south-east Atlantic within its Convention Area (Figure 4). The Convention Area applies only to ABNJ, which includes both the Area and the High Seas, and not the EEZs of bordering nations. Valdivia Bank, Vema, Discovery, and Meteor Rise seamounts along with some more isolated seamount complexes, such as Ewing and Molloy, are target areas for deep-sea fisheries in this region (FAO 2009).

Over recent decades, the south-east Atlantic has been the subject of increasing fisheries exploitation due to its rich nature and relatively short commercial fishing history (1950s+) when compared to other oceanic regions (Thompson et al. 2017). All present fisheries in the SEAFO Convention Area (Figure 4) occur on or around seamounts (Thompson et al. 2017), with the majority of bottom fishing activity falling into three distinct areas: the Valdivia Bank seamount complex, the Discovery seamounts, and the Meteor seamounts (see Figure 1 for locations).

Alfonsino (mainly *Beryx splendens*) and southern boarfish (*Pseudopentaceros richardsoni*) are caught using bottom and mid-water trawls on the top and along the slopes of Valdivia Bank between 200 and 700 m. Anchored lines of 400 Japanese beehive pots (roughly 7.7 km long) are also used to catch deep-sea red crab in the region (mainly *Chaceon erytheiae*); again, this is largely focused around Valdivia Bank between 280 and 1150 m. For 10 years from 1995, bottom trawls were used to target orange roughy (*Hoplostethus atlanticus*) on Valdivia Bank, Ewing Seamount, and the north-eastern section of the Walvis Ridge. Further south, there is fishing for Patagonian toothfish *(Dissostichus eleginoides*) on and around the Discovery seamount complex. These areas have all been identified as hotspots of biodiversity (Bergstad et al. 2019, Buhl-Mortensen et al. 2019). Although fishing effort has been increasing and catches are highly variable, the annual catches for all species have been declining since 2010 (Thompson et al. 2017). While this is inline with many global fisheries (Froese et al. 2012), overfishing is a particularly pertinent issue for deep-sea fisheries. This is because the target species are typically long-lived, reaching sexual maturity later than many other species, and thus, it is more difficult to replenish populations on timescales relevant to fisheries management. Research quota is available for some species like orange roughy, but in 2019, only the red crab and Patagonian toothfish fisheries were active.

SEAFO has adopted measures to ensure that illegal, unregulated, and unreported (IUU) fisheries are limited in their Convention Area by implementing an authorised vessel list and adding to the IUU vessel list compiled by the North East Atlantic Fisheries Commission, the Northwest Atlantic Fisheries Organisation, and CCAMLR. IUU fishing is likely to affect VMEs and other benthic habitats as the lack of adherence to rules suggests that the reporting of by-catch and location data would not be shared. However, it is worth noting that although SEAFO contributes to the list, instances of non-compliance (and therefore IUU fishing) are not actively searched for, and it is therefore likely that IUU fishing in the region is underestimated. Since 2005, SEAFO has also mandatorily implemented a vessel monitoring system (VMS). Additionally, it has adopted a protocol for the retrieval and reporting of lost gear, a source of damage to some benthic habitats, including VMEs (Roberts & Hirshfield 2004). Although there is little evidence to determine the effect of fishing on benthic ecosystems in the south-east Atlantic, bamboo coral gardens on Discovery seamount were found to be severely damaged by sea urchin hyperabundance, thought to be driven by overfishing in the region (Buhl-Mortensen et al. 2021).

Within EEZs, many west African nations bordering the South Atlantic rely heavily on inshore fisheries for food provision, although some have expanded their fleets to allow for the creation of deep-water fisheries. Off south-west Africa, key deep-water fisheries include the Namibian-South African hake (*Merluccius* spp.) fishery (Paterson et al. 2013, Durholtz et al. 2015), Namibian large-eye dentex (*Dentex macrophthalmus*) fishery (Potts et al. 2010), and Namibian deep-water shrimp fisheries (Konda 2008).

South Africa has both an inshore and offshore demersal trawl sector targeting hake and other fish species on the west coast and the Agulhas Bank down to 900 m. The offshore trawl grounds extend in an unbroken band along the west coast of South Africa, from approximately 300 m depth off Hondeklipbaai to the southern tip of the Agulhas Bank, with effort concentrated on the shelf edge (Sink et al. 2019) and diminishing northwards. On the south coast, offshore trawlers operate on the edge of the Agulhas Bank with efforts concentrated offshore of Gqeberha (Sink et al. 2019). The offshore trawl fishery uses demersal otter trawls to target primarily two hake species, *Merluccius capensis* and *Merluccius paradoxus* (Payne 1986, Payne & Punt 1995). The South African demersal longline fishery also targets deep-water cape hake and operates along the west and south coasts with effort concentrated along the shelf edge. Lines are generally 30 km in length, and contain between 6000 and 14,000 hooks (Japp 1989) deployed at depths of 200–400 m (Fairweather et al. 2006, Petersen et al. 2008).

Communities of large ocean states such as those living on Saint Helena and Tristan da Cunha are extremely isolated, and therefore, a large portion of their economies rely on fishing (Glass 2014, SHG 2016). The Tristan da Cunha rock lobster (*Jasus tristani*) fishery is MSC certified and represents the main economic income for islanders (Glass 2014). Inshore boats as well as larger vessels from Cape Town use traps to catch the target species with little to no by-catch (typically only small numbers of two species of octopus). Around Saint Helena, commercial fishing has a reasonably long history (Edwards 1990). Today, pole and line is the only fishing method permitted within its EEZ, targeting yellowfin, bigeye, albacore, and skipjack tuna as well as wahoo. Fishing largely takes place around the island, but in recent years, larger boats have begun to fish for tuna species around Bonaparte and Cardno seamounts (SHG 2016). Tuna fishing around St Helena uses locally caught live bait of a number of scad or mackerel species (mainly *Decapterus* spp.). Besides a small component of recreational fishing and a catch-and-release sports fishery, no fishing occurs within the Ascension Island EEZ (AIG 2021).

Fishing in the South-west Atlantic

ABNJ in the south-west Atlantic represents one of the few areas in the world where there is no RFB, and therefore, responsibility falls upon bordering states to cooperate in the management of High Seas fisheries (FAO 2009), mainly on the Patagonian Shelf, Rio Grande Rise, and some isolated seamounts. The major High Seas bottom fisheries in the region principally target Argentine hake (*Merluccius hubbsi*) and Argentine shortfin squid (*Illex argentinus*), mainly undertaken by Spanish and Taiwanese vessels, respectively (Portela et al. 2010, Vilela et al. 2018). Although the fisheries in this area target squid and hake on sandy bottoms, some trawls may extend beyond the shelf break and therefore pose a threat to VMEs (European Commission 2007). Little is known about the impacts caused by bottom-towed gear in the region (Pires et al. 2015), although findings from the ATLANTIS project determined that 99% of fishing effort in their study area was targeted at depths shallower than 300 m, assessed using commercial fishing data and VMS. A number of nations actively fishing the area have reported large catches of non-target species including elasmobranchs (FAO 2009). Other current bottom fisheries in the region include a longline fishery on the Patagonian Shelf for Patagonian toothfish (*Dissostichus eleginoides*) between 37 and 56°S (Brewin et al. 2020), the Patagonian scallop (*Zygochlamys patagonica*) fishery between 36 and 42°S (Campodónico et al. 2019, INIDEP 2020), and fisheries on individual seamounts for which data are not available (Clark et al. 2007).

Fisheries within EEZs of countries bordering the south-west Atlantic are similar to those in ABNJ, largely targeting hake species (*Merluccius* spp.), monkfish (*Lophius gastrophysus*), Patagonian toothfish (Brewin et al. 2020), and deep-water crustaceans including the geyonid crabs (*Chaceon* spp.) and deep-sea aristeid shrimps (Pezzuto et al. 2006, Perez et al. 2009). Brazil developed upper bathyal fisheries (200–1000 m) between 2000 and 2008 across the south-eastern and southern continental margins (23–30°S), but these declined afterwards mostly due to overfishing (Perez et al. 2009). Within the Argentine EEZ, large areas are open to trawling despite very little being known about the impacts (Bertolino et al. 2007, Schejter et al. 2016, INIDEP 2020).

Deep seabed mining

Deep seabed mining (DSM) refers to extraction activities whereby minerals and deposits are removed from the seabed in water depths greater than 200 m. Mineral resources of economic interest, such as iron, cobalt, nickel, copper, manganese, zinc, lithium, and rare earth elements, occur in seabed deposits in the form of polymetallic nodules (PMN), seafloor massive sulphides (SMS), and cobalt-rich ferromanganese crusts (CRC).

PMN enriched with nickel, copper, and manganese predominantly occur on the surface of sediment-covered abyssal plains at water depths of 3500–6500 m (Hein et al. 2013); SMS containing copper, lead, zinc, gold, and silver are found on hydrothermal vents ecosystems, between 1000 and 4000 m (Ramirez-Llodra et al. 2007); and CRC, a source of iron, manganese, cobalt, copper, nickel, and platinum, are found on the slopes and summits of seamounts in water depths of 400–7000 m, although the most economically viable CRCs for extraction are reported to occur between depths of 800 and 2500 m (Hein et al. 2009, 2013).

The communities found on active hydrothermal vents are currently recognised as rare and vulnerable biodiversity hotspots (UNGA Resolution 61/105, UNGA 2007), and potential future DSM activities may therefore be restricted to inactive or extinct SMS deposits (Van Dover et al. 2020). Similarly, seamounts serve as habitat for numerous VMEs (Watling & Auster 2017, 2021), and while there is a requirement to protect VMEs from fishing activities, no such requirement exists for mining activities. Although less studied, the communities and species on PMN are distinct to adjacent seafloor fauna (Mullineaux 1987, Amon et al. 2016, Vanreusel et al. 2016, Simon-Lledó et al. 2019), with many nodule-associated taxa new to science (e.g., Dahlgren et al. 2016, Gooday et al. 2017, Grischenko et al. 2018). DSM activities are expected to have impacts on biodiversity and ecosystem structure, processes, and services (Armstrong et al. 2012, Thurber et al. 2014, Jones et al. 2017, Le et al. 2017). The impacts of DSM on biodiversity will depend on the type of mining and the proximity of certain ecosystems, although it is understood that it will likely drive overall losses in biodiversity (Van Dover et al. 2017, Miller et al. 2018). In general, our understanding of the potential extent and magnitude of the impacts of DSM is in its early stage as the affected ecosystems are not fully understood (Levin et al. 2020).

In ABNJ, contracts for the exploration of seabed mineral deposits are issued by the International Seabed Authority (ISA). Two such contracts have been issued in the Central and South Atlantic. The first was to the Government of the Russian Federation in 2012 for the exploration of SMS on the MAR (Figure 5). Later in 2014 and 2018, IFREMER and the Government of the Republic of Poland were also issued contracts for the exploration of SMS on the MAR, although the respective contract areas fall outside the boundary of what we consider the Central and South Atlantic in this review. The MAR is home to many confirmed and inferred hydrothermal vents, although the suitability of these for mining SMS deposits has yet to be affirmed (Figure 5).

The second area under contract for mining exploration in the Central and South Atlantic is the Rio Grande Rise, also referred to by the ISA as the ‘South Atlantic seamounts exploration area’. Here, the Companhia De Pesquisa de Recursos Minerais, a state-owned company sponsored by the Brazilian

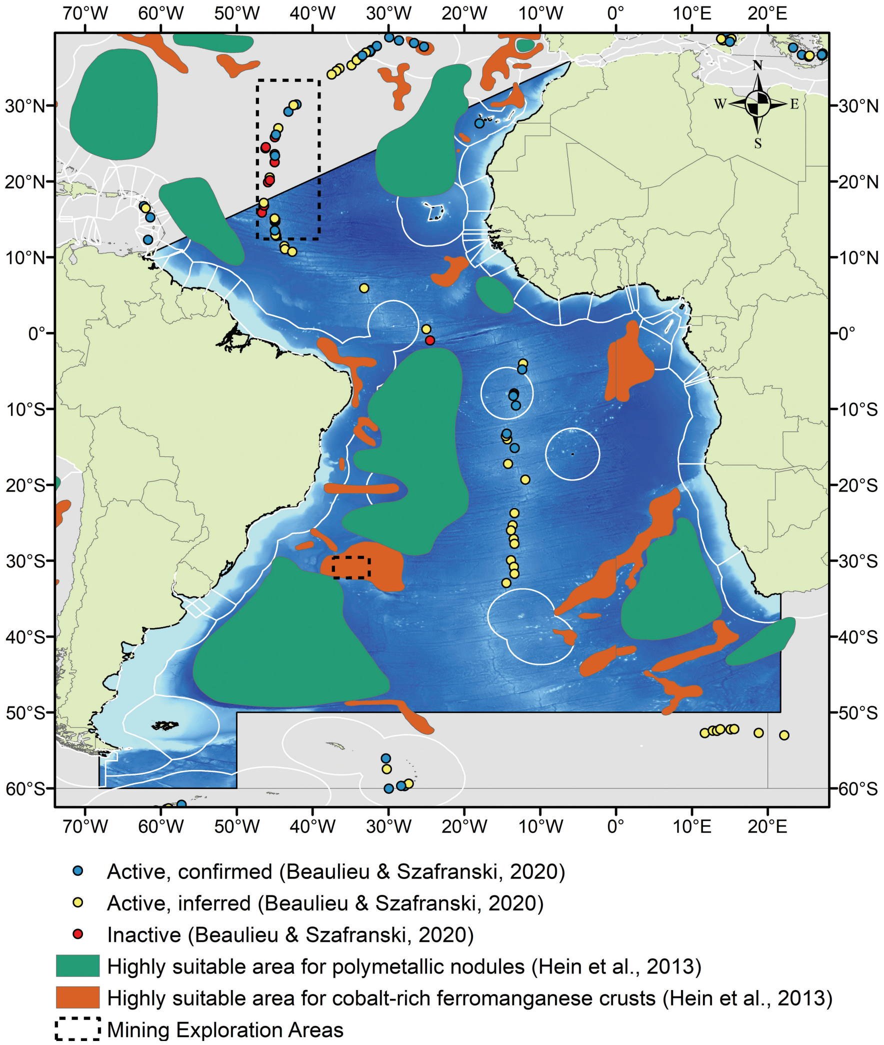

Figure 5 Hydrothermal vent locations from the InterRidge database (Beaulieu & Szafranski 2020) and permissive areas for the development of polymetallic nodules and cobalt-rich ferromanganese crusts as identified by Hein et al. (2013) in the Central and South Atlantic. Overlaid are the current exploratory mining licence areas in the region. White lines depict national Exclusive Economic Zones. Underlying bathymetry provided by GEBCO 2020 Grid. Map drawn in WGS84.

government, was granted a 15-year contract for exploration of CRC deposits on the Rio Grande Rise in 2015 (Perez et al. 2020a). Interest in exploring mineral resources on the Rio Grande Rise has intensified since 2009, when the Prospecting and Exploration of Mineral Resources in the International Area of Atlantic South and Equatorial programme was established under the Ministry of Mining and Energy of Brazil. One of the aims of this programme was to map the occurrence of CRCs on the Rio Grande Rise, and the application for the current exploration contract was based on the findings of this. Although this represents the only CRC exploration contract in the region, Hein et al. (2013) identified additional large areas of seabed in the Central and South Atlantic with suitable conditions for the occurrence of CRCs and PMN (Figure 5). Additionally, PMN have been reported in a range of settings including abyssal ecosystems in the Cape Basin and Cape Passage (Rogers 1985). However, there is no dedicated prospecting or exploration targeting PMN at present in west African EEZs.

Oil and gas

The Central and South Atlantic region is rich in natural resources including oil and gas deposits below the seabed (Bernardino et al. 2020). Exploration of oil and gas deposits is a global industrial activity in the deep ocean (Cordes et al. 2016, Zhang et al. 2019), and deep-water areas have become the focus of increased exploration as more easily accessible resources have become depleted and technology has improved. Offshore exploration areas at depths greater than 1500 m are termed 'ultra-deep waters' and these operations, active since the 1990s, are also focused in the South Atlantic off Brazil and West Africa (Zhang et al. 2019, Bernardino et al. 2020). Globally, most deep-water oil resources are concentrated in the Atlantic basins off Brazil, the Gulf of Mexico, and West Africa. These Atlantic deep-water basins have been named the 'golden triangle' and have the largest potential for future explorations (Zhang et al. 2019, Bernardino et al. 2020).

The waters off eastern Brazil represent an area with some of the highest oil reserves in the world, with the majority of deep-water oil and gas operations located in the Campos Basin (Zhang et al. 2019, Figure 6). Since the first large-scale operations began in the 1970s, there has been an almost continuous discovery of new resources. In Brazil, over 80% of the country's total annual oil production has been extracted from deep and ultra-deep presalt oil fields (Almada & Bernardino, 2017, Perez et al. 2020a). Many of the leased areas offshore along the Brazilian margin overlap with vulnerable habitats including cold-water coral reefs and submarine canyons, representing a management challenge (Almada & Bernardino, 2017). Although less productive, it is believed that there are oil and gas reserves further south in the Argentine EEZ. Unlike Brazil, these are in their

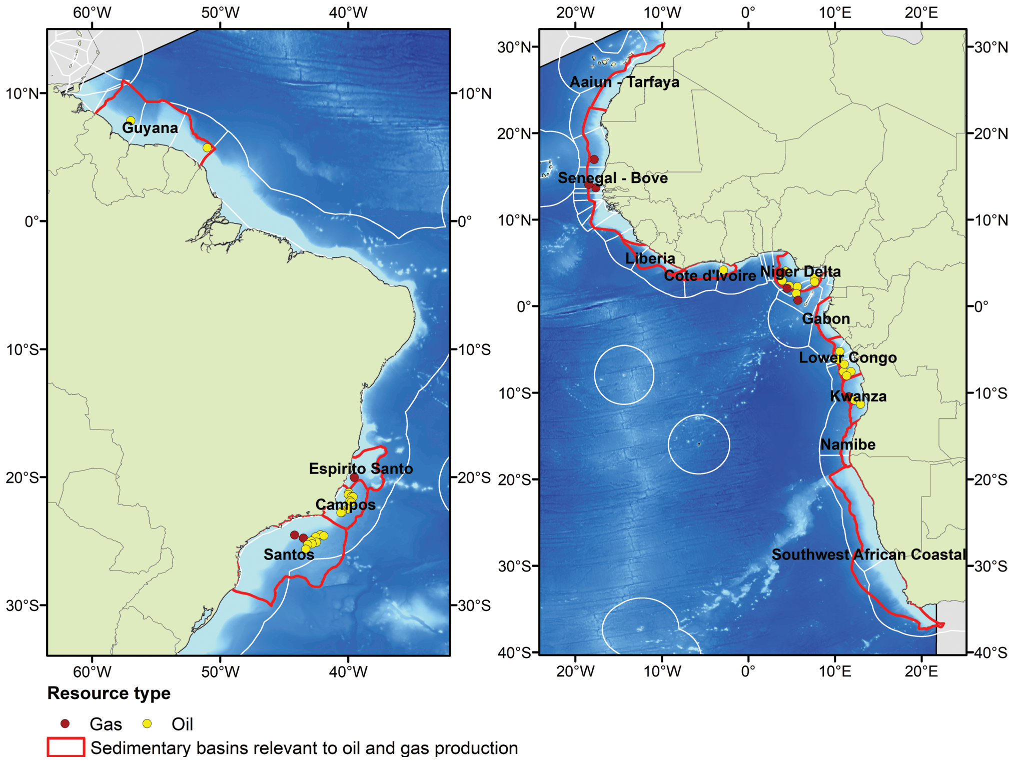

Figure 6 Distribution of major deep-water oil and gas fields and the sedimentary basins important for their development – basin names are labelled in black. Resource field locations were georeferenced from figures within Zhang et al. (2019). White lines depict national Exclusive Economic Zones. Underlying bathymetry provided by GEBCO 2020 Grid. Map drawn in WGS84.

exploratory stages with granted exploration licences comprising a total surface of 225,000 km^2. Similar to Argentina, the deep-water oil and gas industry off the north-eastern South American continent has also been in its discovery stage since 2010 with oil fields discovered in the EEZs of Guiana, Suriname, and French Guiana (Zhang et al. 2019, Figure 6).

Much of the west African continental margin has undergone exploration by the oil and gas industry resulting in the presence of numerous oil wells being developed since the 1990s due to large deep-sea hydrocarbon reservoirs (Figure 6; Savoye et al. 2009, Le Guilloux et al. 2009). Between 1995 when exploration began and 2012, 180 fields had been discovered (Guoliang et al. 2012), with the richest deposits located in the Gulf of Guinea from the Nigerian EEZ to the northern Angolan EEZ (Huaicun 2014, Zhang et al. 2019). While Nigeria remains the largest exporter of oil in the Gulf of Guinea region, in more recent years, the focus has shifted from the Niger Basin to the Senegal and Côte d'Ivoire Basins in the north and the Kwanza Basin off northern Angola in the south (Figure 6; Zhang et al. 2019).

In South Africa, offshore oil and gas exploration started in the 1960s with leases expanding rapidly between 2007 and 2014; as a result, more than 90% of the marine domain around South Africa is currently covered by leases. Operation Phakisa (meaning 'hurry up' in Sotho) is a government-led blue economy initiative that is fast tracking oil and gas exploration as part of the development of South Africa's ocean economy (Findlay 2018). Environmental baseline and impact assessment surveys, in support of oil and gas exploration, have been conducted in South Africa's EEZ since around 1998 with regular ongoing surveys.

All current oil and gas fields under lease fall within EEZs and the management of this industry therefore depends on national regulations. Environmental impacts of operations in deep-water ecosystems may affect biodiversity (species diversity, abundance, biomass, etc.) and this is usually assessed through means of an environmental impact assessment (EIA; Cordes et al. 2016). Data collected by contractors and consultants for the purpose of oil and gas EIA is often not made public, and therefore, the peer-reviewed literature on impacts of offshore oil and gas on benthic diversity is limited. However, as with all extractive industries in the deep sea, it is understood that there are likely to be negative impacts on certain ecosystems including those constituting VMEs (e.g., Vad et al. 2018), especially when there is overlap between these and leased areas (Almada & Bernardino 2017).

Other industries

In addition to demersal fishing and oil and gas extraction, seabed habitats in South Africa and Namibia experience pressure from offshore mining (diamonds and other minerals) in depths of up to 150 m. There is also increasing interest in phosphate mining in both South African and Namibian waters, with several leases for exploration already granted in South Africa (Sink et al. 2019).

Submarine communication cables are 17–22 mm in diameter that have been placed on the seafloor to transmit telecommunication signals between countries. These fibre-optic cables are the backbone of telecommunications, enabling over 98% of international communications (ICPC 2016); their role in connecting the world's population and providing the infrastructure to enable a global economy has been widely recognised (e.g., Carter 2010, UNGA 2015, ICPC 2016). The network of cables in the Central and South Atlantic connects countries within and between Africa and South America, with the three main intercontinental cables being the South Atlantic Cable System (connecting Angola and Brazil), the South Atlantic Inter Link (connecting Cameroon and Brazil), and the EllaLink (connecting Brazil and Europe; TeleGeography 2022). In addition, from South Africa, cables connect west with east Africa, as well as Africa with Asia through India and Malaysia. These networks of cables occur both within and beyond national jurisdiction.

The International Cable Protection Committee (ICPC) is a non-governmental organisation and forum established in 1958 with the primary goal of promoting the security of submarine cables through the exchange of technical, legal, and environmental information. It comprises both governments and commercial entities, representing cable owners and operators globally. Over the years, the ICPC has participated in multiple reviews of the environmental impacts of submarine cables, which have found that these structures are not considered to cause major damage to the seabed, with only minor impacts on benthic communities (e.g., see review by Carter 2010, Burnett et al. 2015, UN 2016). In waters deeper than 2000 m, cables are laid directly on, rather than in, the seabed (Burnett et al. 2015) and therefore cause minimal disturbance. In addition, cables are laid to avoid fragile ecosystems identified during route planning (Burnett et al. 2014).

Area-based management

Area-based management tools (ABMTs) represent one way of spatially regulating where particular industries can operate, of which MPAs are an example. MPA is an umbrella term for which the definition varies depending on the level of protection given, the activities/threats it is designed to protect against, and the defining body. The number of MPAs across the world's ocean has increased in the last five decades, although coverage in the Central and South Atlantic has, overall, lagged behind global efforts (Figure 7). While the usefulness of MPAs in some circumstances is demonstrable, their use has also been criticised, especially in remote areas, for providing the illusion of protection when no active protection is occurring (Agardy et al. 2011, Marques & Carranza 2013).

Extended continental shelf claims

Before touching on the various management mechanisms applicable to ABNJ and EEZs, the Commission on the Limits of the Continental Shelf (CLCS) should be mentioned. Where the continental shelf extends further than 200 nm and consequently out into ABNJ, states may submit a request to the CLCS, a technical body created by UNCLOS, to extend their EEZ to the outer limit of the continental shelf (CLCS 1997). Approval of this submission would result in the state exercising

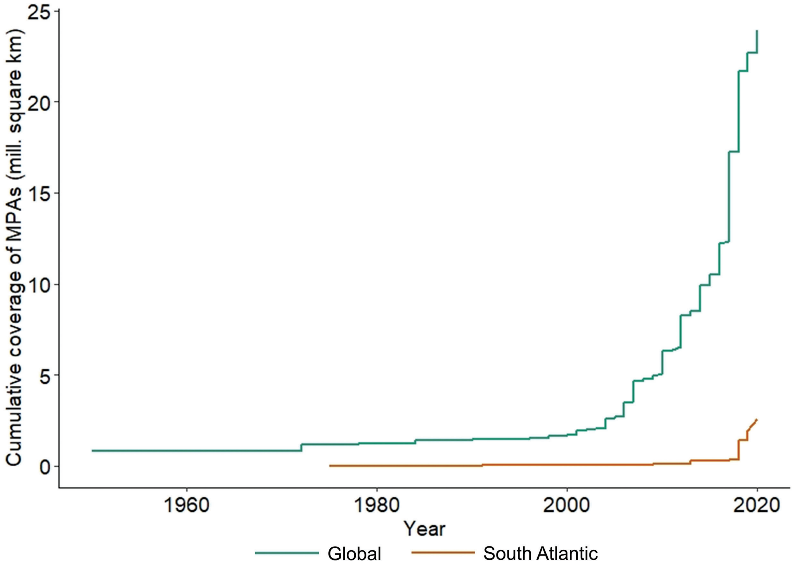

Figure 7 Cumulative coverage of MPAs globally and in the Central and South Atlantic from 1950 to 2020. Data from UNEP-WCMC & IUCN (2021).

sovereign rights, including protection and exploitation, over the new area of seabed but *not* the water column above it; there is currently no legal framework for states to make sovereign claims over the water column adjacent to their 200 nm EEZ (CLCS 1999).

The only countries bordering the Central and South Atlantic that to date have *not* made submissions to the CLCS are Morocco (including the western Sahara region), Liberia, Togo, Cameroon, Equatorial Guinea, Venezuela, the Congo Republic, and the Democratic Republic of the Congo. Of the remaining nations that have made submissions, most have requested extensions that run relatively parallel to their current EEZ boundary (Figure 8).

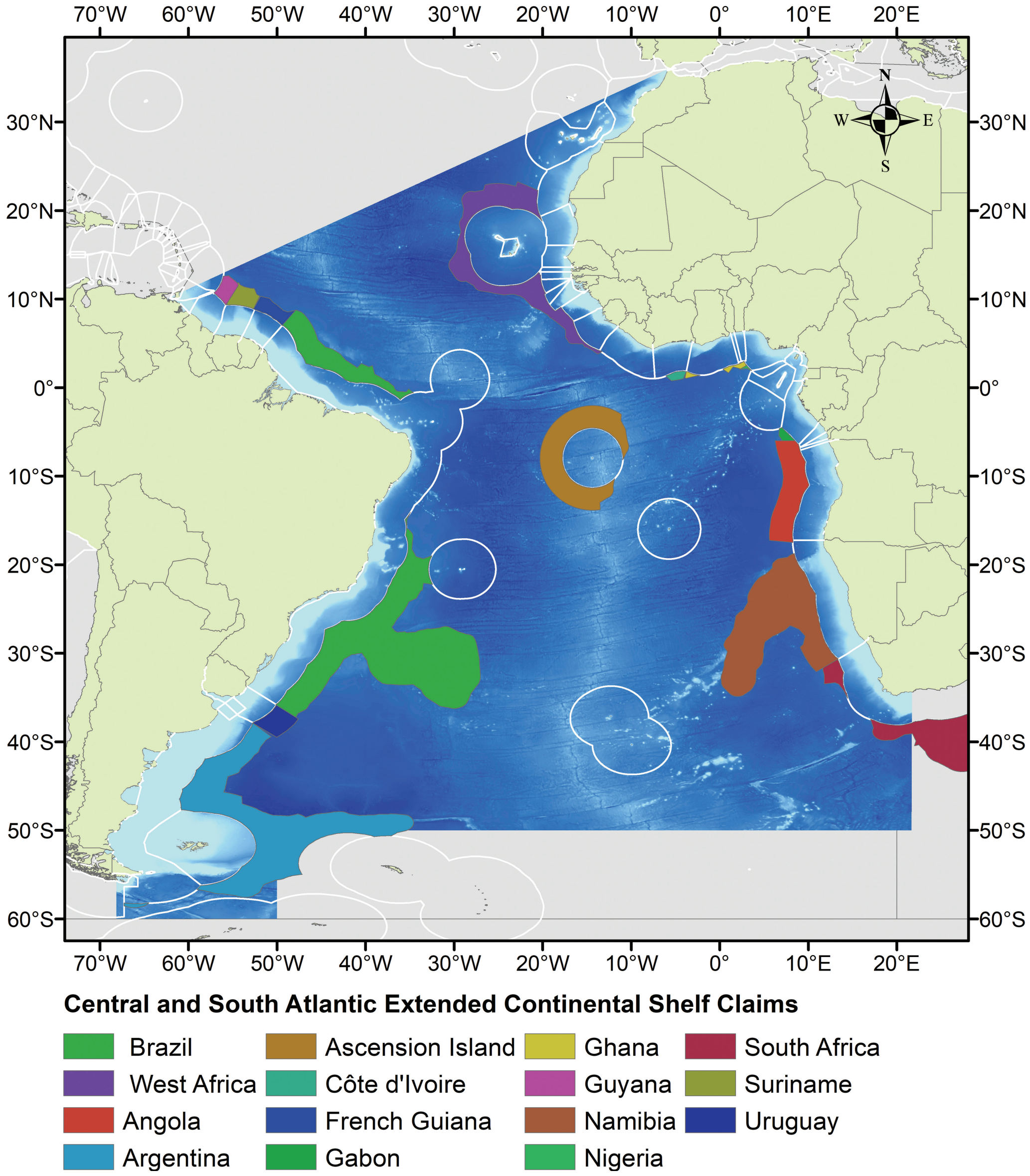

Figure 8 Claims submitted by Central and South Atlantic bordering nations to the Commission on the Limits of the Continental Shelf. Bordering nation EEZs are depicted by white lines. Bathymetry provided by GEBCO 2020 Grid. Map drawn in WGS84.

In the east Atlantic, South Africa, Namibia, and a combined application by west African nations (Cabo Verde, The Gambia, Guinea, Guinea-Bissau, Mauritania, Senegal, and Sierra Leone) have the largest spatial coverage (Figure 8). The Namibian request is particularly notable as it claims a large area of the Walvis Ridge. In the South-west Atlantic, Brazil, Uruguay, and Argentina have all submitted claims to extend their EEZs by vast areas.

Area-based management in areas beyond national jurisdiction

UNCLOS outlines the rights and responsibility of member states regarding the oceans. Although it contains clauses pertaining to the conservation of living resources in ABNJ (Part Y, Section 2), the Convention lacks the legal framework from which to implement ABMTs, including but not limited to MPAs. However, other pieces of legislation focused on specific sectors do have the legal capability to 'close' areas to specific activities, for example, fisheries closures in RFMO Convention Areas. These AMBTs are often not considered MPAs because they can only protect from damage caused by individual sectors.

Ecologically or biologically significant marine areas

The Convention on Biological Diversity (CBD) was signed by the international community in Rio de Janeiro, Brazil, in 1992 and came into force in December 1993. It has three main objectives: the conservation of biological diversity; the sustainable use of the components of biological diversity; and the fair and equitable sharing of the benefits arising out of the use of genetic resources. In 2010, the Aichi Biodiversity Targets were adopted under the CBD, number 11 of which stipulates that "by 2020, at least […] 10 percent of coastal and marine areas, especially areas of particular importance for biodiversity and ecosystem services, are conserved through effectively and equitably managed, ecologically representative and well-connected systems of protected areas […]". To ensure that the protected areas would be informed by scientific knowledge, the CBD held regional workshops and invited scientists to identify Ecologically or Biologically Significant Marine Areas (EBSAs) that were "in need of protection in open ocean waters and deep-sea habitats". EBSAs are designated by the CBD, and although they boast no legal protection, the classification flags them as areas that serve important purposes to support the healthy functioning of the ocean. Although the CBD has no framework for designating MPAs in ABNJ, EBSAs are not limited to EEZs and can therefore be designated in ABNJ. In 2008, the Contracting Parties of the CBD established guidelines for defining EBSAs: uniqueness or rarity; special importance for life-history stages; importance for threatened, endangered, or declining species and/or habitats; vulnerability, fragility, sensitivity, or slow recovery; biological productivity; biological diversity; and naturalness (CBD 2009).

Two workshops held in Brazil and Namibia in 2012 and 2013 focusing on the 'Wider Caribbean and Western Mid-Atlantic' and the 'South East Atlantic', respectively, resulted in the identification of 49 EBSAs that cover areas in the Central and South Atlantic. Of these, seven are located adjacent to the South American coast, 38 are reasonably adjacent to the west African coast, and four extend significant distances into ABNJ (Figure 9). Most EBSAs are entirely within EEZs, but 11 are transboundary.

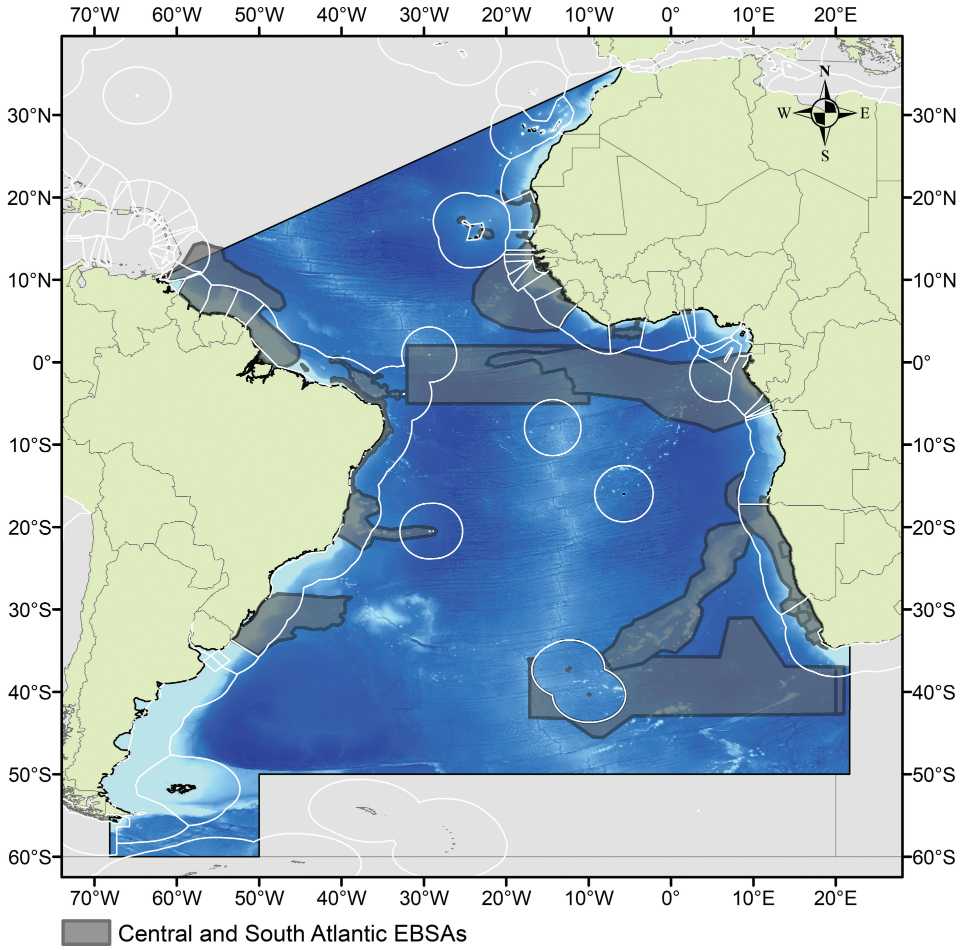

Figure 9 Central and South Atlantic EBSAs identified by CBD Contracting Parties in 2012 and 2013. A full list of these EBSAs with accompanying information is available on the CBD website (https://www.cbd.int/ebsa/). EEZs denoted by the white lines. Underlying bathymetry provided by GEBCO 2020 Grid. Map drawn in WGS84.

Fisheries closures

In 2006, UNGA Resolution 61/105 called

> upon States to take action immediately, individually and through regional fisheries management organisations and arrangements, and consistent with the precautionary approach and ecosystem approaches, to sustainably manage fish stocks and protect vulnerable marine ecosystems (VMEs), including seamounts, hydrothermal vents and cold-water corals, from destructive fishing practices.

RFMOs were tasked with identifying where VMEs occur/are likely to occur in their Convention Areas, and then acting to prevent significant adverse impacts (SAIs) within their jurisdiction. This legislation gives RFMOs the capacity to close certain areas to fishing activities to prevent damage to VMEs. With relevance to the Central and South Atlantic, it is important to note that CECAF and WECAFC are not RFMOs and therefore do not have the authority to implement fisheries closures.

SEAFO have adopted a precautionary approach to conservation measures in the form of a set of VME closures “constituting a biogeographically representative selection of subareas likely to have VMEs" (Figure 4). These closures were focused towards seamounts and seamount complexes with summit depths of less than 2000 m. A suggested list of 13 closures was compiled in October 2006 in response to UNGA Resolution 61/105 using the criteria of a high chance of VMEs and known history of fishing exploitation. The SEAFO Scientific Commission agreed to close 10 of the 13 seamounts to all forms of bottom fishing during 2007–2010 through the adoption of Conservation Measure 06/06 (CM 06/06 2006). In 2010, Discovery seamount complex was reopened, boundaries were changed to create larger closures, and five new areas were closed along the MAR. Along with the suggestion of more closures in 2007, SEAFO recommended that for trawling to resume in any closed areas, VMEs should be mapped, and proposals for mapping, exploratory fishing, and resumption of commercial fishing should be submitted to the SEAFO Scientific Committee for consideration. This means that areas outside of the current fishing footprint are subject to increased regulations. In 2016, the first VME closure was established based on data from a scientific research cruise on Valdivia Bank (FAO 2016), and consequently, only longlines and pots are permitted. SEAFO currently has 12 VME areas closed to bottom fishing or selected gear types, totalling 3.2% of the Convention Area (Figure 4).

Although the International Guidelines for the Management of Deep-Sea Fisheries in the High Seas (FAO 2009) provides examples of taxa indicative of VMEs, there are no universal technical definitions in terms of metrics or thresholds for abundance/density (Auster et al. 2011). This proves problematic when RFMOs are tasked with closing areas to avoid SAIs to VMEs; hence, the main solution to reducing SAIs is the 'move-on' rule. This protocol states that vessels using bottom fishing gears are required to move at least 2 nm away from the end point of the trawl/tow in the direction least likely to result in more encounters when they encounter a VME-indicator species above 'threshold levels' (defined individually by each RFMO). The incident is reported to the corresponding RFMO Executive Secretary who informs all Contracting Parties and archives the location information. If the encounter took place outside an existing fishing area, a temporary closure is implemented pending examination by the RFMO Scientific Committee. This strategy relies solely on the reporting of encounters to SEAFO by fisheries observers, and it is therefore imperative that observers are permitted to work freely and safely aboard vessels (Bell et al. 2019).

The International Commission for the Conservation of Atlantic Tunas (ICCAT) is an Atlantic-wide RFMO that manages highly migratory species and can implement closures in the South Atlantic down to 60°S, although these closures are not relevant to demersal fisheries as the focus species within ICCAT are pelagic. Although there is no RFMO in the south-west Atlantic to which bottom fishing vessels report, the European Commission states that all vessels working in the south-west Atlantic fishing under EU member state flags are subject to monitoring including onboard observers, and Argentina states that their fleet operating within the High Seas of the south-west Atlantic uses VMS. However, the High Seas near the Argentine EEZ have been identified as a hotspot for the disablement of fishing vessel tracking systems, evidencing concerns of IUU fishing whereby vessels illegally enter neighbouring EEZs (Welch et al. 2022). Interestingly, this study also highlighted areas off the west African coast, suggesting that IUU fishing may exert pressure on benthic ecosystems throughout the Central and South Atlantic.

Deep seabed mining

The responsibility of regulating, controlling, and managing deep-sea mining activities in the Area, the seabed outside states' jurisdictions, lies with the ISA, an autonomous organisation established in 1994 under UNCLOS acting on behalf of all humankind (UN 1982).

The ISA develops and establishes regulations for each phase of mining activities: prospecting, exploration, and exploitation, collectively referred to as the Mining Code. Through the designation of Areas of Particular Environmental Interest (APEIs), the ISA has the capacity to close areas of the seafloor to seabed mining activities in order to conserve regional biodiversity. At present, the only APEI network that has been established is located in the Clarion-Clipperton Fracture Zone (CCZ) in the north-eastern Pacific and was declared through a regional environmental management plan (REMP) for the area (ISA 2012).

In April 2022, a draft REMP for the northern MAR with a focus on polymetallic sulphide deposits was made available for public consultation (ISA 2022). It is designed to provide "conservation and management measures and tools across the region in the Area of the northern MAR to ensure the effective protection of the marine environment from harmful effects that may arise from activities in the Area" (ISA 2022). In it, the ISA outlines scientific criteria for identifying Areas in Need of Protection (AINP) and Sites in Need of Protection (SINP). AINPs are defined as "large-scale areas of ecological importance due to their uniqueness and/or biodiversity", while SINPs are "fine-scale sites, where vulnerable marine ecosystems have been identified" (ISA 2022). The Romanche FZ is a proposed AINP to be "protected from direct or indirect impacts from exploitation of mineral resources in the Area". SINPs identified in the REMP mostly include known hydrothermal vent fields, six of which fall within the boundaries of the Central Atlantic defined in this review (Logatchev 1, Logatchev 2, Semyenov 2, Irinovskoe, Ashadze 1, Ashadze 2; ISA 2022).

Shipping

Finally, several mechanisms for protecting biodiversity in ABNJ through ABMTs exist through the International Maritime Organisation (IMO), a specialised agency of the UN responsible for regulating shipping. These are the designation of Special Areas or Emission Control Areas and Particularly Sensitive Sea Areas (PSSAs). Through the IMO, the International Convention for the Prevention of Pollution from Ships (MARPOL) was adopted in 1973 and entered into force in 1983. MARPOL applies to shipping both within and beyond national jurisdiction and is focused on the prevention of pollution to the marine environment from both operational and accidental causes.

Under MARPOL, certain areas of the sea are defined as Special Areas based on their oceanographic and ecological conditions (MARPOL Annex I, II, IV, V). In these areas, mandatory methods must be adopted to prevent pollution to the sea, and accordingly, these Special Areas are provided greater protection than adjacent areas. Most Special Areas occur within EEZs, but two lie within ABNJ, in the Antarctic and Mediterranean Sea.

The IMO can also designate PSSAs, areas that need "special protection through action by IMO because of its significance for recognised ecological or socio-economic or scientific reasons and which may be vulnerable to damage by international maritime activities" (IMO 2005). The designation of a PSSA is accompanied by associated protective measures, which may be legally binding and include actions such as strict rules on operational discharges, areas to be avoided, or rerouting measures. Importantly, the attributes of the area used to qualify it as a PSSA must be at risk from international shipping activities (IMO 2005).

While the IMO has the ability to designate PSSAs and Special Areas in ABNJ, no such designation of the former has yet occurred, with only two occurrences of the latter. It is unclear how these ABMTs may be applied to ABNJ in the future (Gjerde & Rulska-Domino 2012), but the IMO has indicated its cooperation with the Biodiversity Beyond National Jurisdiction (BBNJ) process (IMO 2018).

Area-based management in national waters

The 1981 Convention for Cooperation in the Protection, Management and Development of the Marine and Coastal Environment of the Atlantic Coast of the West, Central and Southern Africa Region (henceforth referred to as the Abidjan Convention) was adopted under the United Nations Environment Programme (UNEP) Regional Seas Programme. Contracting Parties from the Central and South Atlantic are Angola, Democratic Republic of Congo, Republic of Congo, Gabon, Namibia, and South Africa. The Abidjan Convention extends only to the ocean areas of its Contracting Parties within national jurisdiction, but notably includes areas within extended continental shelf claims. To date, the regulatory framework within the Convention has been developed solely to prevent and address issues of marine pollution. However, in 2014, a Memorandum of Understanding (MOU) was signed within which the Contracting Parties of the Abidjan Convention "aimed to give support to the development of a Marine Protected Areas Protocol". Additionally, an MOU was signed in 2013 between the Convention for the Protection of the Marine Environment of the North-East Atlantic (the OSPAR Convention) and the Abidjan Convention, acknowledging the importance of cooperation between the Atlantic-bordering-states in both hemispheres in the protection of the marine environment. Therefore, although the Abidjan Convention is not directly responsible for the designation of any MPAs in national waters or ABNJ, the Convention demonstrates an openness by Contracting Parties towards the conservation and sustainable use of marine resources (Ribeiro 2017).

In 2004, the CBD formed the Programme of Work on Protected Areas, which, for marine biodiversity, aims to identify and preserve high-quality representative selections of marine habitats through the establishment of a coherent network of MPAs (CBD 2004). This requirement has since been ratified into national law across many nations, for example, the Marine and Coastal Access Act (2009) in the UK. This Act, as well as synonymous Acts in other countries, allows for the creation of MPAs to conserve biodiversity within EEZs. This said, unlike other collections of states with bordering seas, such as Europe, there is no combined management plan for bordering EEZs in the Central and South Atlantic. However, there are some examples of intergovernmental initiatives such as the BCC that involves Angola, Namibia, and South Africa to promote human and ecosystem wellbeing. Additionally, transboundary agreements for fisheries do exist such as the proposed joint management of the Namibian and South African hake (*Merluccius* spp.) fishery and the Argentine-Uruguayan Common Fishing Zone.

With regard to MPAs, bordering states of the Central and South Atlantic are at various stages of their marine spatial planning processes, and therefore, the spatial coverage and level of protection varies. Off the west African coast, protection varies significantly. For example, the Gulf d'Arguin region in Mauritania harbours Africa's largest shallow-water MPA, Banc d'Arguin National Park, and a proposal suggesting five regions as MPAs within the Mauritanian EEZ, covering 0.7% of the area, is under negotiation (Ramos et al. 2018). The latter would contribute to further protection of areas within the CCLME which, at present, sees only 0.77% of its ~98,000 km^2 area protected (Heileman & Tandstad 2009). Côte d'Ivoire has also taken its first step in marine spatial planning, designating its first MPA covering 2600 km^2 in September 2020 after declaring its intention to create five MPAs. Further south in Gabon, the very large Reserve Aquatique du Grand Sud du Gabon was designated in 2017, covering 12% of Gabon's EEZ. Meanwhile, South Africa designated an additional 20 MPAs in 2019, increasing protection from 0.4% to 5% of their waters (Kirkman et al. 2021).

Some large ocean states and territories also play important roles in regional conservation efforts. In the Central Atlantic, a key MPA is that of the Selvagens Island Marine Nature Reserve that covers 12 nm around the islands and is the largest MPA with full protection in the Atlantic north of the equator at 2677 km^2. Also in the Central Atlantic, Concepcion Bank in the Canary Islands EEZs was declared as Site of Community Interest in 2014, as part of the *Natura 2000* network. Further south, the UKOT of Saint Helena, Ascension, and Tristan da Cunha has protected approximately 1.6 million km^2 of ocean. This comprises the entire EEZs of Ascension Island and Saint Helena which are IUCN category I and VI MPAs, respectively, and the Marine Protection Zone at Tristan da Cunha which protects 91% of the EEZ as a no-take zone with small cutouts around some features where demersal longline fishing is allowed. This protection was designated as part of the Blue Belt Programme, a 4-year global project that now provides long-term protection to around 4.3 million km^2 of marine environment globally.

Along the South American coast, Brazil, Uruguay, and Argentina all have MPA networks. In 2018, Brazil announced the designation of four new MPAs that increased the coverage of MPAs from 1.5% to 24.5% of the EEZ. The largest of these was the Área de Proteção Ambiental do Arquipelago de Trindade e Martim Vaz that offers varying levels of protection to the Trindade and Martim Vaz archipelago, covering 100% of the archipelago's EEZ and 11% of Brazil's total marine area. In 2022 at the UN Ocean Conference in Lisbon, Portugal, Uruguay's Minister of Environment announced the designation of a new MPA covering 12,000 km^2 of ocean, 60% of which will be a no-take zone. This designation significantly increases the coverage of MPAs in the Uruguayan EEZ and is part of Uruguay Azul 2030, a programme that commits Uruguay to expanding its total protected areas to 30% by 2030. In 2014, the National System of MPAs of Argentina was formed, aimed at protecting and conserving representative marine habitats and ecosystems under a single, integrated management and governance system. The resultant MPAs target the preservation of areas with high diversity and vulnerability as well as areas valuable for breeding and spawning of fish species of commercial interest. Currently, MPAs only exist along the southern section of the continental slope, namely Namuncurá-Burdwood Bank I and II and the Yaganes MPA located off the southern tip of Tierra del Fuego, extending southwards into the Drake Passage. In the Falkland Islands (Malvinas), proposed Marine Managed Areas (MMAs), including the eastern Burdwood Bank (adjacent to the Namuncurá MPA), are being consulted upon in 2022 and if implemented would encompass 15% of the Falklands Maritime Zone (Bax et al. 2022). Within the Gulf of Paria and Orinoco Delta region on the Venezuelan Atlantic coast, there are two areas under special conservation regulations. These are the Turuépano National Park in the Gulf of Paria and the Orinoco Delta National Park, which is also a Biosphere Reserve (Bone et al. 2004, Miloslavich et al. 2003). The latter is largely terrestrial although there are calls to extend the protection into the oceanic area to allow for the protection of the marine benthic and nektonic communities (Klein & Cárdenas 2011).

Knowledge gaps and future research

By combining the summaries of biodiversity and human impacts above, gaps can be identified where further research is required to support sustainable development. In the following sections, we identify and discuss knowledge gaps, and recommend future research and management considerations based on the summaries above.

Gap analysis

To examine the sampling effort across the Central and South Atlantic, metadata, including much from the summaries above, were compiled from known sources identified through a literature search and information provided by members of the Challenger 150 Central and South Atlantic Regional Scientific Research Working Group. The metadata, available in Bridges et al. (2022b), contained information on several variables including location, gear type (drop camera, towed system, etc.), sample depth, project/cruise, and target group (epifauna or macrofauna). Major patterns show that EEZs of bordering nations have been exposed to higher sampling effort than ABNJ (Figure 10).

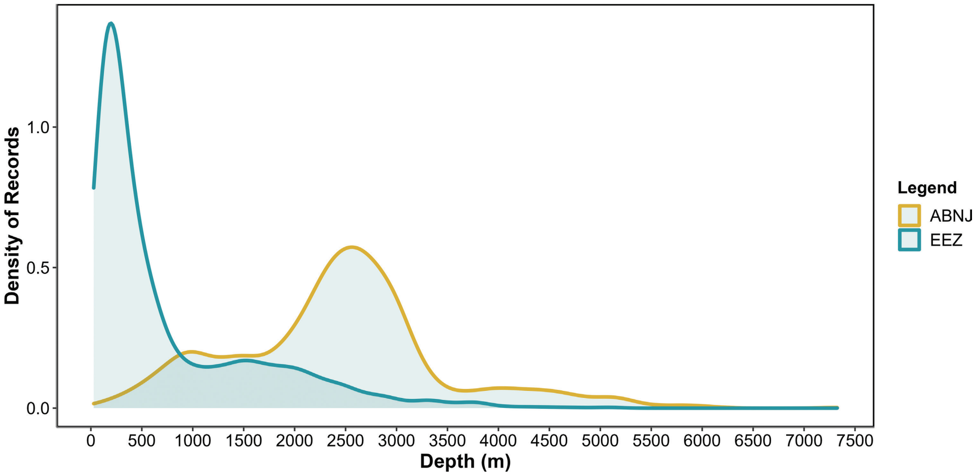

Figure 10 Density of records plotted by depth and area. Kernel density values were multiplied by 1000 for ease of reading. Values: Areas beyond national jurisdiction (ABNJ) n=1251; Exclusive economic zone (EEZ) n=2557.

The bias towards shallower sampling in EEZs is also clear and unsurprising. It is likely that the peak in ABNJ sample effort around 2500 m reflects targeted research towards seamounts and similar topographic features of interest.

When mapped, it becomes clear that large ocean areas are void of sampling, with topographic features in ABNJ that appear comparatively heavily sampled including the Walvis Ridge in the south-east Atlantic and the Rio Grande Rise and Patagonian Shelf in the south-west Atlantic (Figure 11A).

To understand where the majority of open-access benthic species records lie for in the Central and South Atlantic, a broad-scale low-resolution gap analysis was performed. The distribution records for different macrofaunal taxa (Gastropoda, Bivalvia, Polychaeta, Oligochaeta, Aplacophora, Monoplacophora, Polyplacophora, Scaphopoda, Amphipoda, Tanaidacea, Isopoda, and Cumacea) and megafaunal taxa (Pycnogonida, Tunicata, Echinodermata, Anthozoa, Hydrozoa, Porifera, Decapoda, Cheilostomatida, Cephalopoda, and Vertebrata) were extracted from the open-access database, Ocean Biodiversity Information System (OBIS).

Data were downloaded for the world and then subset using the Central and South Atlantic sub-area (Figure 1). Using the occurrence() function in the 'robis' package (Provoost & Bosch 2019), data were downloaded specifying a minimum depth of 30 m. The 'obistools' package hosts a number of functions to assist users in cleaning OBIS data (Provoost & Bosch 2018). Functions used in the cleaning of this dataset were check_onland() with a buffer of zero to remove any erroneous records on land and check_depth() with a depth margin of 100 to remove any records farther than 100 m from the seabed. A total of 2,052,302 macrofaunal and 13,010,731 megafaunal records were extracted from OBIS, which after cleaning reduced to 1,773,466 macrofaunal and 11,368,490 megafaunal distribution records.

It is immediately clear when the sampling effort map (Figure 11A) and the OBIS records maps (Figure 11B) are compared that there are significant discrepancies. Areas where there is congruence between the sampling effort and OBIS records trends are the Patagonian Shelf and

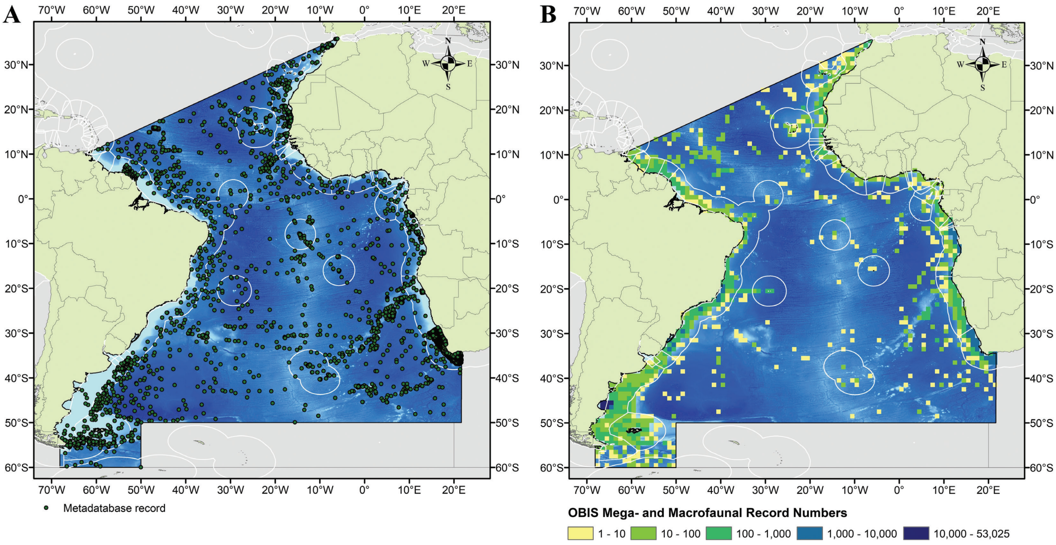

Figure 11 (A) Sampling effort mapped for the Central and South Atlantic using metadata compiled from known sources identified through a literature search and information provided by members of the Challenger 150 Central and South Atlantic Regional Scientific Research Working Group (Bridges et al. 2022b). (B) Open-access records in the Ocean Biodiversity Information Service (OBIS) for mega- and macrofauna in the Central and South Atlantic. Underlying bathymetry provided by GEBCO 2020 Grid. Map drawn in WGS84.

the southern African continental margin, with both datasets showing these are likely the best-sampled regions in the Central and South Atlantic. Additionally, both datasets identify the Gulf of Guinea region, specifically in the east off the coasts of Côte d'Ivoire to Nigeria, as particularly data-limited.

The contrast between sampling effort and OBIS records is further highlighted in Figure 12, and is likely in part due to datasets collected during research cruises not being uploaded to OBIS, resulting in a lack of open-access data across the region for major faunal groups (Kaiser et al. in prep). While the Walvis Ridge is identified as one of the heavily sampled features in the basin (Figure 11A), the vast majority of this data is not listed in OBIS resulting in marked disconnects in data collection and data availability to inform future science (Figure 12). Similar concerns were raised by Carranza et al. (2022) where authors showed that 72% of the material collected by the German RV Walther Herwig I and II in the south-west Atlantic during the 1960s and 1970s is not open access, with a large majority still undetermined at species or genus level.

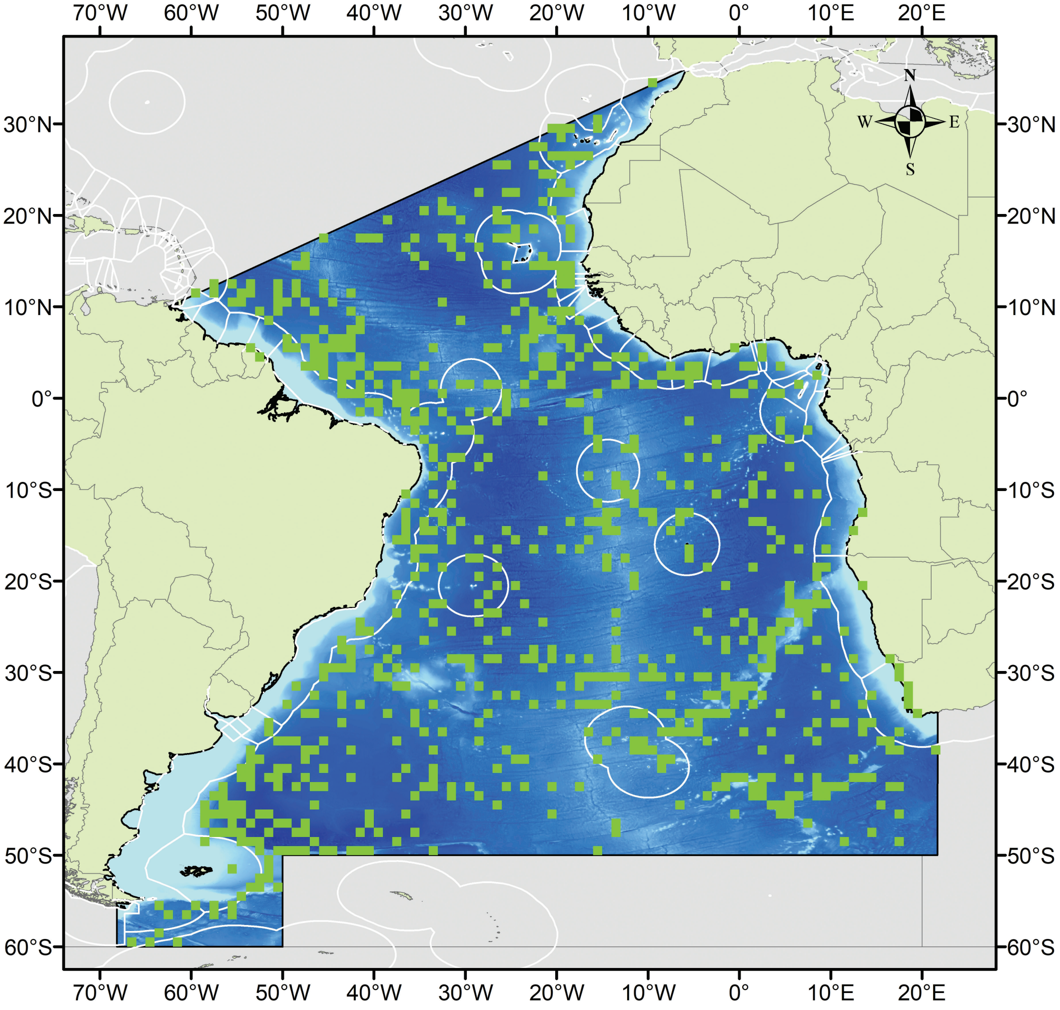

Figure 12 Locations in the Central and South Atlantic where the metadata (available in Bridges et al. 2022b) shows sampling effort, but there are no records in OBIS. Records were binned into 1-degree cells. Underlying bathymetry provided by GEBCO 2020 Grid. Map drawn in WGS84.

Howell et al. (2020b) outline a blueprint for a global deep-sea field programme and identify essential ocean variables (EOVs) that should be stratified, and data collected within each stratum. The two key variables they identify are latitude, as a proxy for climate-related variables, and depth. When the density of OBIS records for both faunal groups is plotted against these EOVs, the resulting patterns are similar (Figure 13). Both the mega- and macrofaunal records display a large drop in record number in the Central Atlantic between approximately 0 and 20°S, bottoming at around 10°S. This concurs with the summary of information above for the Central Atlantic in ABNJ and within the EEZs of much of the Gulf of Guinea and north-east South America. It is important to indicate that the latitudinal panels in Figure 13 display edge effects, hence the strongly sloped nature of the density plots.

For records with depth, unsurprisingly the overwhelming pattern is a reduction in record density with increasing depth for both groups due to the technical challenges associated with sampling at greater depths. This concurs with results of Kaiser et al. (in prep) who also reported the most dominant gaps in macrofaunal data for the region to be between 200 and 6000 m. More nuanced is the slight peak in records around 4000 m, likely reflecting early trawl, grab, core, and sledge sampling on soft-substrate abyssal plains.

When mapped, the megafaunal and macrofaunal OBIS records for the Central and South Atlantic show similar patterns (Figure 14). It is likely that the drop in record density in the Central Atlantic somewhat reflects the lack of OBIS records for the Brazilian margin just south of and around Cabo Branco (Figure 14). As was demonstrated in Figure 10, EEZs are exposed to higher sampling effort than ABNJ, and this is particularly pronounced in the macrofaunal records (Figure 14B).

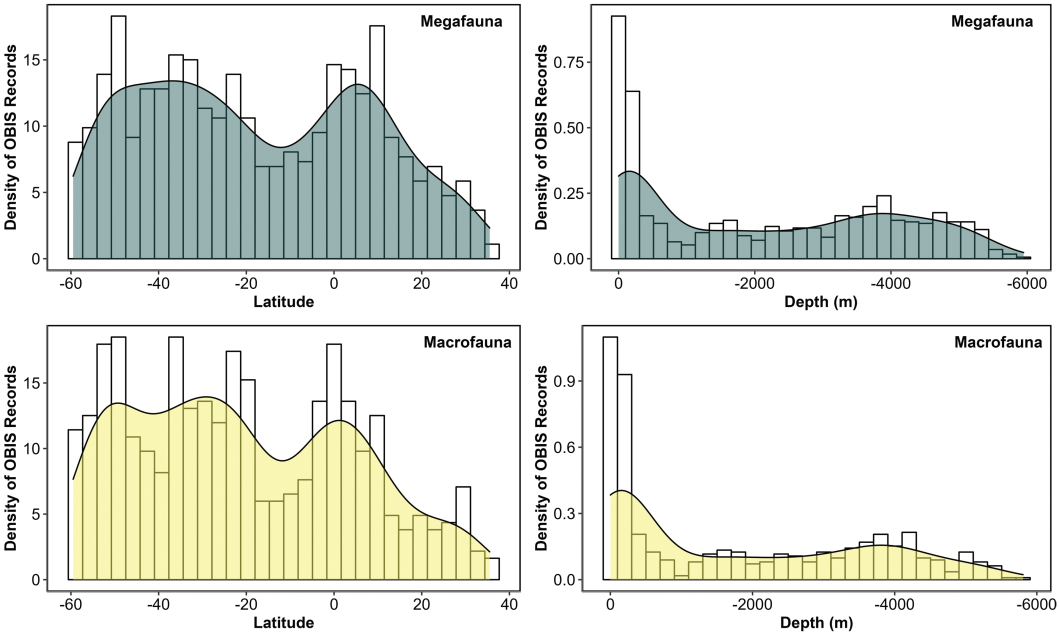

Figure 13 Density of records in the Ocean Biodiversity Information Service (OBIS) against latitude and depth for the Central and South Atlantic. The top two panels (blue) display the megafauna data and the bottom two panels (yellow) the macrofauna. Kernel density values were multiplied by 1000 for ease of reading.

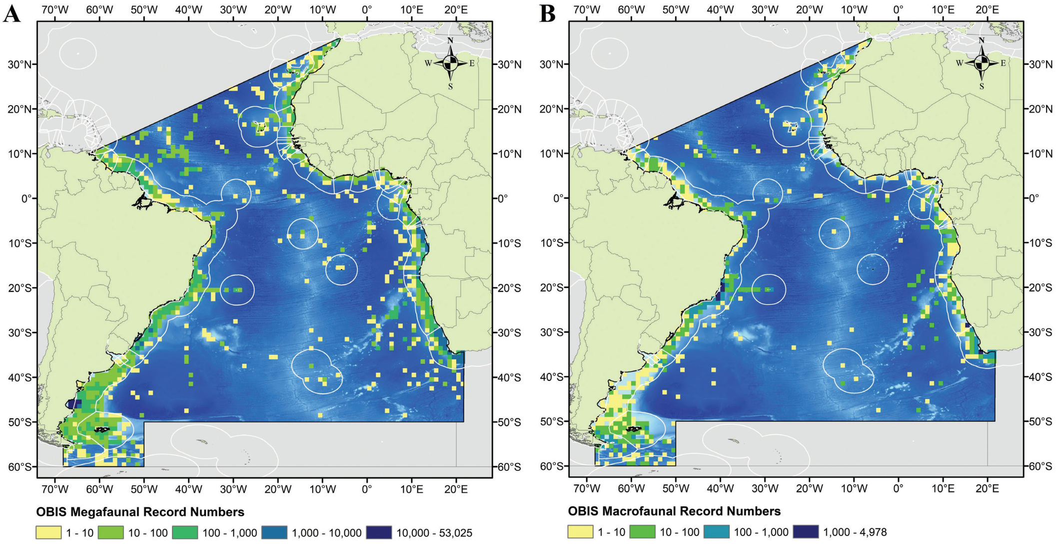

Figure 14 Open-access records in the Ocean Biodiversity Information Service (OBIS) for mega- (A) and macrofauna (B) in the Central and South Atlantic.

Summary of knowledge gaps

Our review has identified significant data gaps concerning the benthic ecology of the Central and South Atlantic. ABNJ is undersampled, as are the deeper parts of nations EEZs. In particular, the region off the north-west African coast, including the Gambia, Guinea-Bissau, Guinea, Sierra Leone, Liberia, and parts of the Gulf of Guinea are poorly sampled and/or known, as well as north-east South America, including the EEZs of Venezuela, Guyana, Suriname, and French Guiana. In general, there is a large drop in the number of open-access data records in the Central Atlantic between approximately 0 and 20°S, bottoming at around 10°S, and a general reduction in record density with depth. There are also significant gaps in knowledge of deep-water regions of all oceanic island territories, but particularly Sao-Tome and Principe, and Annobón Island, which form part of the Guinea Seamount Chain.

The UN Ocean Decade aims to deliver "the science we need for the future we want". Making decisions around use of the marine environment necessitates, we can predict (model) the potential outcomes of different scenarios. Baseline ecological data form the input to all biological ecosystem models and maps. Predictions rely on models of the ecosystem that can approximate reality. Bias and gaps in our baseline data severely limit our ability to approximate reality, and thus, generate accurate predictions of possible outcomes (Howell et al. 2020b). Howell et al. (2020b) provide a blueprint for deep-ocean science for the next decade identifying the need to fill data gaps. Our review suggests that for the Central and South Atlantic, scientists should prioritise the areas identified above for research in order to reduce bias in available deep-sea data.

While reducing bias is important for our ability to forecast and achieve a '*predictable ocean*' in line with the aims of the Ocean Decade, it is not the only consideration when prioritising research effort. Human use of the region is also biased towards certain areas and it may be prudent to focus research effort in those areas under the most pressure. The north-east South American region is both data-limited and subject to oil and gas activities, with recent exploration interests near the Amazon Delta. Neighbouring ABNJ is also data poor and identified as a region of potential mining resource (PMN), although not currently licenced for exploration. The north-west African coast is also a data-limited region, and yet supports significant fisheries as well as oil and gas activities.

In ABNJ, bottom-contact fisheries tend to focus on topographic highs like the Guinea Seamount Chain in the data poor region between 0 and 20°S, the Walvis Ridge and the Rio Grande Rise, as well as other seamounts. These areas overlap with potential mining resources (CRC) although not all are currently licenced for exploration. The Cape, Argentine, and Brazilian basins in ABNJ are all data poor and support potential mining resource (nodules), although not currently licenced for mining. Collection of data in these areas therefore provides potential gains in achieving the Ocean Decade outcomes of a "predictable ocean, a healthy and resilient ocean, and a productive ocean".

Future challenges for sustainable management

Overall lack of knowledge

The logistical challenges associated with undertaking deep-sea science mean that this realm is far less understood than shallow-water and terrestrial ecosystems. Consequently, there are fundamental biological and ecological questions that remain unanswered in the deep sea, including: what is the diversity of life in the deep ocean?; how are population and habitats connected?; and what are the roles of living organisms in ecosystem function and service provision? (Howell et al. 2020a). The lack of answers to these central questions hinders conservation efforts of deep-sea ecosystems in all ocean basins, particularly when technological advancements often outpace scientific ones. However, in those basins that remain undersampled, typically in the global south, this combined with low-resolution environmental data and lack of knowledge represents a key stumbling block for managers (Bridges, 2022). Additionally, the likely high number of records that are either not open access or that remain unprocessed in natural history collections compound this issue (*sensu* Figure 12, Carranza et al. 2022).

Climate change

Climate change represents a significant threat to the deep ocean due to forecast changes in temperature, water mass structure, and nutrient concentrations (Sweetman et al. 2017). These changes will drive alterations to both the biotic functioning and carbon sequestration capacity of the deep ocean resulting in impacts to both ecological and social systems (Smith et al. 2008).

Species can respond to climate change in several ways including shifting their geographical ranges and adapting physiologically or behaviourally (Mora et al. 2013). Previous dramatic climate events captured in the fossil record have demonstrated that despite its perceived remoteness, the deep sea is subject to the effects of rapid climate change (Robinson et al. 2005, Yasuhara et al. 2008, Margolin et al. 2014, Portilho-Ramos et al. 2022). Additionally, based on *in situ* experiments in areas with different productivity regimes in the western Pacific, Nomaki et al. (2021) concluded that benthic faunal abundance and food web structure are negatively affected by a climate change-driven shifts in phytodetritus composition from diatoms to cyanobacteria at higher latitudes, while enhancing prokaryotic metabolism and microbial organic matter cycling.

Specific to the Central and South Atlantic, Ríos et al. (2015) presented the first observation-based acidification trends in Atlantic water masses along meridional lines from 50°S to 36°N. Results confirmed that pH changes are largely determined by anthropogenic activity, with the largest decrease in pH recorded in the SACW, a prevalent water mass across the South Atlantic. Deep, bottom waters appeared to be less affected with lower change in pH values. Similarly, differences in subsurface temperature have also been observed in the south-west Atlantic extending into the bottom layers, and this has the potential to impact the distribution of protected and commercially valuable species (Franco et al. 2020).

Furthermore, modelling exercises have revealed that continental margins of the Central and South Atlantic will experience significant effects of climate change by 2100. These effects include warming, acidification, and lower productivity in most areas, as well as deoxygenation in some areas (Sweetman et al. 2017). For example, on the south-east Brazilian margin where the largest deep scleractinian reef systems have been identified, predicted warming and lower productivity are expected to exert a significant influence on coral productivity and reef health (Sweetman et al. 2017, Bernardino et al. in press). Sweetman et al. (2017) also predict that in the South Atlantic, slope sediments are expected to warm by an average of 1°C and maintain a lower pH (range of −0.1 to −0.3). Pelagic productivity and POC export will also decrease between 0.1 and 5 mg C m^2/day, representing a 4%–30% decrease compared to present day conditions. The decreased food availability may result in major changes in benthic biodiversity and ecological processes at the seafloor over large areas of the Atlantic (Smith et al. 2008, Nomaki et al. 2021). Although available models commonly suggest that the chemical and biological conditions in the deep Atlantic will be more challenging for a range of organisms, it is likely that some regions may offer refuge for a subset of its biodiversity to thrive, for example, some oxygen minimum zones in the region host high biodiversity (Hanz et al. 2019). However, our understanding of these 'refuge' ecosystems and climate resilience is poor, and therefore, it is difficult to say whether their influence will stem significant shifts in the benthic biodiversity.

Overlapping industries

Many areas in the deep ocean are exposed to cumulative or multiple pressures from different sectors (Halpern et al. 2019), and thus, there is the potential for overlap between industries such as fishing and mining (van der Grient & Drazen 2021).

In the Central and South Atlantic, industries already overlap within EEZs of bordering nations. Andrews et al. (2021) undertook a review of the overlap between artisanal fisheries and oil and gas, showing that there is significant overlap within both the west African and east South American EEZs. To manage these overlapping interests along the Argentine continental slope, an agreement was made between the sub-secretariats for both industries in 2019. The agreement constituted the basis for forming a commission of experts to develop an environmental impact assessment of oil and gas on fisheries (INIDEP 2020). While the interaction between industries is somewhat manageable within EEZs as they are governed by a single state, the situation in ABNJ is rather different. Management of ABNJ is entirely sector-based and lacks the legal framework to develop one governing authority responsible for overseeing all industrial activities. It is hoped that a new treaty on BBNJ, currently under negotiation, may support cross-sectoral management (particularly regarding ABMTs) to promote a holistic approach to the use and conservation of ABNJ (UN 2022).

Recommendations to consider in sustainable management

Recommendation 1: Develop strategic, collaborative sampling programmes to address key knowledge and spatial gaps

Howell et al. (2020b) define a set of EOVs over which stratified sampling would facilitate the answering of fundamental questions about life in the deep oceans. As outlined in Section 7.1, further sampling is required in the Central and South Atlantic in order to achieve samples across all strata. Therefore, strategic, collaborative sampling programmes could play a key role in advancing science and conservation in this region, for example, targeting areas identified in this review as under-/unsampled such as ABNJ and EEZs in the Central Atlantic and the deeper regions of most EEZs. To ensure participation in and longevity of such sampling programmes and the continuing advancement of deep-sea science globally, it is crucial that these programmes involve significant capacity-building elements to stop 'parachute science' (Harden-Davies et al. 2022).

Recommendation 2: Build capacity to participate and progress in deep-sea research to ensure that no nation is left behind

Sustainable management will only succeed when all nations have the capacity to support decision-making at a national level and to participate in international processes. A lack of skills, knowledge, infrastructure, and technology, among others, limits deep-sea research and prevents sound environmental management (e.g., Sink et al. 2021). A commitment to capacity development in the Atlantic is reflected in the Belém Statement, a joint declaration by the European Union, Brazil, and South Africa promoting collaborative scientific efforts in the Atlantic Ocean to improve marine scientific research in the region. In addition, there are a number of capacity development opportunities through the UN Ocean Decade, including Challenger 150, the Deep Ocean Observing Strategy, and the Deep Ocean Stewardship Initiative. Initiatives within these programmes seek to address discrepancies in capacity to partake and progress in deep-sea science. Such initiatives should draw from or promote analyses of capacity development requirements, so that efforts are driven by self-identified needs, and where possible, should be coordinated to avoid duplication of effort and a haphazard approach to capacity development. The current review could support design of future research campaigns by/with scientists from/working in bordering regions to advance deep-sea science in the Central and South Atlantic. Such research should be supported by meaningful international collaborations that empower local scientists to undertake research in their waters, through co-developed research questions and plans, shared data, and joint outputs.

Recommendation 3: Promote ocean-basin-scale management

The importance of ocean-basin-scale management has been increasingly recognised over recent years, see for example, the Frontiers in Marine Science Research Topic “Managing Deep-sea Ecosystems at Ocean Basin Scale”. This management approach recognises that both threats to natural habitats and ecological trends do not adhere to geopolitical boundaries, and as such, nature conservation needs to adopt a transboundary approach. This may include, for example, incorporating factors such as connectivity of ecosystems into marine spatial planning frameworks (*sensu* Leiva et al. 2022). Of course, the management of oceans at the basin-scale requires baseline knowledge on biodiversity throughout the basin that can be used to underpin management tools such as predictive models. Consequently, recommendation three here is underpinned by recommendation one.

Recommendation 4: Adopt a multifaceted approach to conservation using a variety of management tools

Once knowledge and spatial gaps are filled, either through new sampling programmes or the application of novel techniques (*sensu* Bridges 2022), marine spatial planners will be able to devise appropriate strategies for the conservation of marine living resources. While the authors appreciate that these future strategies should include some level of static, area-based management to protect sessile benthic ecosystems, this approach is not equally effective for all taxa, and therefore, a wider range of protection measures should be considered (Boerder et al. 2019). For example, seasonal protection regimes, gear modifications, or reduction in fishing effort may be the most effective tools for the conservation of migratory (e.g., pelagic fishes) and endangered (e.g., sharks and seabirds) taxa. Additionally, considering resilience to climate change in marine spatial planning is crucial if we are to develop coherent protection networks. In the North Atlantic, climate change has been identified as a significant threat to the efficacy of ABMTs, and the same will apply in the Central and South Atlantic (Johnson et al. 2018). Thus, a multitude of approaches should be considered by managers to ensure the efficacy of protection regimes at the wider ecosystem level against future challenges, particularly those associated with migratory species and climate change.

Recommendation 5: Incorporate the socio-economic needs of bordering nations into realistic management plans

Much of the conversation in conservation science is dominated by the ecological merit of areas for protection, but it is also important to consider socio-economic and cultural factors in protection strategies to ensure sustainable and equitable use of the oceans going forward. While it is difficult to disentangle the linkages between the deep ocean and humanity in many cases, some services that the deep sea provides are more obvious (La Bianca et al. 2023). The implementation of any ABMT such as an MPA will likely result in some level of displacement of anthropogenic activity. For example, fishing displacement effects of MPAs, particularly large-scale MPAs, can discriminate against small-scale commercial fisheries (SSCFs). SSCFs are less able to move into new areas than larger, offshore vessels, because of the additional economic costs of travelling to more distant grounds or lack of the necessary infrastructure (Stevenson et al. 2013, Barreto et al. 2020). This is an example of an impact that should feed into the decision-making process, via stakeholder engagement, where the realism of proposed MPAs/MPA networks are considered. This is particularly important in many less-developed countries and/or large ocean states where extractive industries represent the main source of economic income and often an important food resource, and therefore, blanket bans on all extraction activities are not a viable solution. This issue also intersects with over-exploitation of fisheries and climate change-induced range shifts of commercial species. Many coastal communities are highly vulnerable, across a range of social and economic factors, to needing to travel further to reach fishing grounds (Townhill et al. submitted).

Recommendation 6: Consider how multiple sectors can be managed holistically

In the Central and South Atlantic, there are several processes that the above considerations should apply to, for example, the ISA's development of a REMP for the region. As highlighted above, there is a distinct possibility of multiple sectors overlapping in the Central and South Atlantic in the future – this is not just the case for extractive activities but also for areas that may be protected in one sector but not another. With ABMTs included in the draft BBNJ Agreement and likely to enter into force in the coming years, what remains unclear is how the coordination of conservation and extraction activities in ABNJ will work post-ratification, nor is it known what organisation(s) will have this responsibility. It is important that whoever it is considers how MPAs in ABNJ and existing measures interact with one another, for example, existing fisheries closures implemented by SEAFO.

Conclusion

While the Central and South Atlantic is home to a high diversity of benthic organisms and ecosystems, comparatively little is known about this region, as is the case for much of the global south. Despite this, industry continues to advance both deeper and further offshore, often into scientifically unexplored areas. The rapid development of new technologies to facilitate the expansion of extractive industries in deep water, combined with the global effects of climate change altering ecosystem function, threatens benthic ecosystems in the Central and South Atlantic deep sea. To understand how these pressures may manifest themselves and to have a chance of conserving these ecosystems in the future, we must invest in the scientific exploration of data-limited regions such as the Central and South Atlantic.

Despite what many hoped would be the final round of negotiations, talks in August 2022 failed to produce an agreed text for a treaty on the conservation and sustainable use of biodiversity beyond national jurisdiction. Although progress was made, areas of sensitivity and contention remain, including the process for establishing MPAs in ABNJ, implementation of EIA, and equity issues around resource exploitation. The sixth session of formal talks is set to commence in early 2023, and delegates will need to reach consensus on these and other issues to finalise the treaty text. Nevertheless, the UN Decade of Ocean Science for Sustainable Development provides the ideal backdrop to significantly drive forward scientific exploration, sustainable management, and blue growth. With the progression of the BBNJ negotiations, alongside significant in-country initiatives to manage marine resources sustainably around the Central and South Atlantic, the scientific community can support these initiatives through synthesising best available data and providing expert input into future management plans. We hope that this review serves to inform future research in the Central and South Atlantic by summarising existing works, identifying knowledge gaps, and informing policy and ecosystem protection mechanisms.

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