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FISH, cephalopods and associated habitats of the Discovery rise seamounts, Southeast Atlantic

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ABSTRACT

In February 2019, seamounts of the Discovery Rise, SE Atlantic (41–45°S, 3°W - 3°E), were explored in support of the application of the Ecosystem Approach to Fisheries Management in the Southeast Atlantic Fisheries Organization (SEAFO) Convention Area. Video records of the seafloor were produced by the Video-Assisted Multi-sampler System (VAMS) along 15 valid transects conducted in plateau and flank areas of Shannon, Tablemount, Discovery and Heardman seamounts at depths ranging from 394 to 1839 m. Nine benthic seascapes were classified and described based on substrate hardness, texture, slope, physical and biological modifiers as observed in the video images. Predominant water masses were estimated from temperature, salinity and dissolved oxygen vertical profiles obtained by CTD casts in the vicinity of each transect. A total of 366 fishes were seen (total observation time = 25.0 h) and classified in 32 morphotypes, included in 9 orders and 12 families. Most fish morphotypes (14) were included in the Macrouridae family. Family Moridae, on the other hand, included 65.3% of all fish records (239), with two particularly abundant morphotypes: *Laemonema* sp. (116) and *Guttigadus* sp. (92). Thirteen cephalopods were observed and classified in five morphotypes; the oegopsid squid *Moroteuthopsis ingens* was the most abundant of them (6). Despite the taxonomic uncertainties associated with video identifications, the explored region was found to contain a mixture of tropical – subtropical and subantarctic faunas of the Atlantic. Similarities of fauna composition and non-directional beta diversity estimates revealed some degree of seamount identity, but 57.5–61.9% of morphotypes were shared among seamounts (Jaccard = 0.425, Sørensen = 0.381). Fishes and cephalopods were more frequently observed on the shallower plateau areas under the influence of warmer and more oxygenated Antarctic Intermediate Waters. Depth and related factors did not influence richness, but dissimilarities in fauna composition between video transects increased with increasing depth intervals. Spatial habitat heterogeneity may have accounted for the increased beta diversity within seamounts. The most widely explored Tablemount seamount contained the most diverse observed sites, but also a considerable spatial variability likely associated with seascape heterogeneity. In two sites (transects 11 and 14), there were exceptionally high aggregations of the morid cods *Laemonema* sp., at the shallowest 'gravely' site explored (397 m), and *Guttigadus* sp., at a site of intermediate depth (1020 m) covered mostly by soft sediments. Neither of these species (or congenerics) have been previously classified as 'seamount-aggregating" species. On the other hand, the Patagonian toothfish (*Dissostichus eleginoides*) and other commercial species known to aggregate in these seamounts were not found in the explored areas.

1. Introduction

Ocean basins may contain up to hundreds of thousands of seamounts of varying heights, and morphologies, most of them yet to be explored (Wessel, 2007; Yesson et al., 2011; Kvile et al., 2014). These features disrupt the generally plain abyssal floor, exposing benthic habitats to upper levels of the water column and important vertical environmental gradients. They also interpose and, depending on their size and morphology, modify deep water current flow producing local circulation regimes and biophysical processes (White et al., 2007; Rogers, 2018). The advection of suspended food particles to seamount flanks, entrapment of vertically migrating zooplankton and micronekton on seamount

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summits and local enhancement of primary and secondary production, as induced by the upwelling of nutrient-rich deep water, are amongst the processes that sustain rich megafauna communities, mostly formed by benthic suspension feeders (e.g. cold-water corals and sponges) and fish (see reviews in Genin, 2004; Pitcher et al., 2007; Clark et al., 2010a; Consalvey et al., 2010; Rogers, 2018). In some regions these communities attract top predators (e.g. whales, sharks and billfish) (Morato et al., 2010) including humans, that have established fisheries regimes targeting pelagic and benthopelagic fish and crustaceans, most notably, orange roughy (*Hoplostethus atlanticus*), alfonsinos (*Beryx* spp.), oreo dories (Family Oreosomatidae), toothfish (*Dissostichus* spp.), geryonid crabs and others (Clark et al., 2007; Clark, 2009). These fisheries have often been regarded as unsustainable both because seamount stocks are generally considered to be low productivity, producing "boom-and-burst" fisheries, and because bottom fishing gear may cause irreversible damage to benthic communities (Koslow et al., 2000; Clark and Koslow, 2007; Clark et al., 2016, 2019). In that sense, management of bottom fishing activities on high-seas seamounts, mostly conducted by Regional Fisheries Management Organizations (RFMOs), have focused on conservation of these communities, adopting measures that should reduce damage to "Vulnerable Marine Ecosystems" (VMEs), as defined by UN General Assembly resolutions (e.g. UNGA 61/105 and

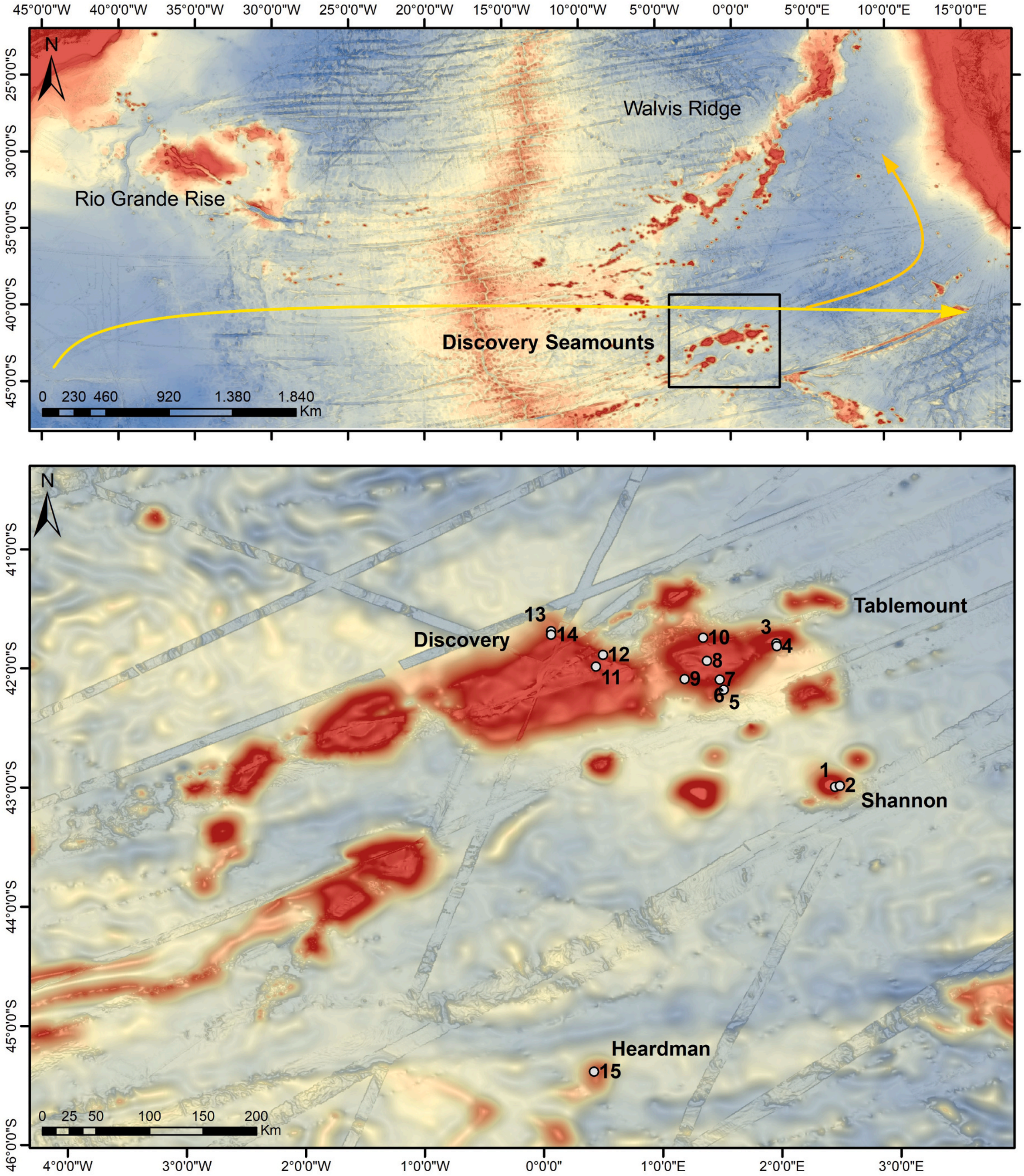

Fig. 1. South Atlantic Ocean seafloor (top map) with area explored (box) in January–February 2019, during the investigation of Vulnerable Marine Ecosystems in the convention area of the Southeast Atlantic Fisheries Organization (EAF-Nansen Programme). The South Atlantic Current and the Banguela Current, carrying AAIW (~500–1220 m), are indicated by yellow and orange solid arrows, respectively. The Discovery Rise seamount complex (bottom map), include the Discovery, Tablemount, Shannon and Heardman seamounts. Numbered dots indicate positions of the ROV transects.

later) and subsequent FAO International Guidelines for the Management of High Seas Bottom Fisheries (Food and Agriculture Organization of the United Nations, 2009; Ardron et al., 2014).

The South Atlantic Ocean basin encompasses one third of the total number of seamounts higher than 1000 m in the Atlantic Ocean (estimated in 1435 seamounts in total, Yesson et al., 2011). Because the region has been historically overlooked in terms of deep-sea habitats and ecology (Perez et al., 2012), a limited number of seamounts in the South Atlantic have been explored and studied for biodiversity and ecological patterns (Clark et al., 2010a). Bottom fishing, however, has long taken place on seamounts of the SE Atlantic, under the management regime of the Southeast Atlantic Fisheries Organization (SEAFO) (Bensch et al., 2008). As part of this regime, seamount areas have been precautionarily closed to fishing, based on (a) topography and depth ranges where bottom fisheries and VMEs are likely to overlap, and (b) existing reports on the presence of VME indicator species in monitored catches. Comprehensive *in situ* descriptions of benthic ecosystems and data confirming VMEs distribution in the SE Atlantic, however, are generally scarce and greatly needed to support management measures (Bergstad et al., 2019a).

Data on habitats and biodiversity of this area were produced during Russian, Spanish and Namibian fishing surveys of the Valdivia and Ewing seamounts, where both pot fisheries for the deep-sea red crab (*Chaceon erytheiae*) and bottom trawl fisheries for pelagic armourhead (*Pseudopentaceros richardsoni*), splendid alfonsinos (*Beryx splendens*) and orange-roughy have historically taken place (McPherson, 1984, 1987; Zibrowius and Gili, 1990; Fedorov, 1991; Vinichenko and Kakora, 2008; Lopéz Abellán and Holtzhausen 2011; Durán Muñoz et al., 2012 and others). These seamounts (along with Wüst, Vema and Schmitt-Ott seamounts) were targets of a research cruise conducted in 2015 on board the RV Dr. Fridtjof Nansen, as part of an international effort to map and provide ecological descriptions of benthic environments of seamounts in the SEAFO Convention Area (Bergstad et al., 2019a and b; Gil and Ramil, 2021). This effort continued in 2019 in a subsequent cruise of the 'new' RV Dr. Fridtjof Nansen, this time focused on mapping and identifying VMEs on the southerly Discovery Rise seamounts (41–45°S, 3°W - 3°E), in areas both open and closed to longline fisheries targeting the Patagonian toothfish (*Dissostichus eleginoides*). As in 2015, this cruise produced unprecedented seafloor bathymetry mapping and video observations of benthic habitats and megafauna communities (Bull-Mortensen et al., 2019).

The Discovery Rise (41–45°S, 3°W - 3°E) is located at the southwestern border of the Cape Basin, comprising 12 large seamounts aligned in two 600 km-long sub-parallel ENE – WSW trending chains (Fig. 1). Because they are flat-topped (i.e. guyots), it is believed that these seamounts emerged as ocean island volcanoes 41-35 m.y. ago by intraplate magmatism, likely associated with the passage of the African Plate over a deep mantle plume (Discovery Plume), that eroded to sea level and subsided to 400–1500 m depths below surface (Le Roex et al., 2010; Werner and Hauff, 2014; Schwindrofska et al., 2016). These seamounts are influenced by the W – E flow the Antarctic Intermediate Water (AAIW, ~500–1000 m), the Upper Circumpolar Deep Water (UCDW, ~1000–1300 m) and the North Atlantic Deep Water (NADW, 1300–3500 m) (Emery and Meincke, 1986; Stramma and England, 1999; Arham et al., 2003; Morozov et al., 2010). The deepest sectors of the seamount flanks, below 3500 m, are influenced by the Antarctic Bottom Water (AABW) that flows from circumpolar waters into the Cape Basin through fractures in the Southwest Indian Ridge (Morozov et al., 2010; Ferreira and Kerr, 2017).

This study will characterize seafloor habitats (seascapes) and the observed fish and cephalopod fauna observed during a series of ROV transects conducted on selected seamounts of the Discovery Rise. These are conspicuous and mobile components of benthic and benthopelagic megafauna that concentrate permanently or temporarily at seamounts often taking advantage of surface-originated food sources and biogenic habitats, formed by cold water corals and sponges (Auster et al., 2005; Clark et al., 2007; Porteiro and Sutton, 2007; Morato and Clark, 2007; Campanella et al., 2021). Recent studies have revealed that depth, seafloor habitats, local circulation processes and distribution of suspension-feeding organisms may drive fish and cephalopod species distribution in South Atlantic topographic rises (i.e. Rio Grande Rise, São Paulo Ridge, Tristan da Cunha seamounts) (Perez et al., 2018, 2020; Campanella et al., 2021). These factors contribute to habitat diversity within a single topographic feature, potentially selecting for distinctive mesoscale megafauna assemblages and affecting overall seamount diversity (e.g. Ross and Quattrini, 2007; McClain et al., 2012; Baker et al., 2012; Victorero et al., 2018). Besides providing a descriptive analysis of benthic habitats and fish and cephalopod fauna, this study reports on the variation of fauna composition and diversity within and between seamounts and explore its associations with depth, geoforms (plateau vs, flanks), deep water masses and seascapes.

2. Methods

Between 24 January and February 24, 2019, selected seamounts of the Discovery Rise complex were explored during a research survey conducted on board the RV Dr. Fridtjof Nansen (Institute of Marine Research – IMR, Norway) as part of the EAF-Nansen Project "Supporting the application of the Ecosystem Approach to Fisheries Management considering climate and pollution impacts" (GCP/GLO/690/NOR). The survey followed from recommendations of the Southeast Atlantic Fisheries Organization (SEAFO) Scientific Committee to identify the occurrence and distribution of 'Vulnerable Marine Ecosystems' (VMEs) in sectors of sub-area D of SEAFO Convention Area, including areas closed to longline fishing (see details in Bull-Mortensen et al., 2019). The survey started at Shannon Seamount (42.99°S, 2.44°E) and continued northwards, at eastern and western regions of Tablemount Seamount (East region, 41.80°S, 1.95°E; West region, 41.74–42.18°S, 1.33–1.50°E) and the eastern and northern regions of the large Discovery Seamount (East region 41.88–41.98°S, 0.43–0.49°E; North region, 41.69–41.71°S, 0.058°E) (Fig. 1). The survey was completed at Heardman Seamount in the far south (45.38°S,0.42°E).

Bathymetric data was acquired at selected seamount regions and during pre-determined transects using a hull-mounted Kongsberg EM 302 multibeam echosounder. Nearly complete bathymetric maps were obtained for Shannon and Heardman Seamounts (see Bull-Mortensen et al., 2019). Seafloor was explored by HD video cameras during 20 transects conducted by the ROV contained in the Video-Assisted Multi Sampler (VAMS) system. This ROV-VAMS assemble moved along pre-determined transects to record seafloor images and landed on the seafloor for video exploration and sediment sampling using five hydraulically operated grabs (see Bull-Mortensen et al., 2019). During exploration the VAMS system moved at 0.3 knots on average (varying from 0.1 to 0.4 knots). Complete video transects were 57–150 min-long and followed 172–873 m-long quasi-linear paths (Table 1). Transect 8 was interrupted due to technical problems with the camera system, therefore is shorter than the other transects. Five other transects that exhibited camera failures and/or were limited in spatial coverage and observing time, were excluded from this study. Continuous information of date/time, depth (and altitude in meters) and the ROV heading (in degrees) were recorded by a logging system. ROV transects were set to qualitatively explore the occurrence of VME indicators (corals and sponges). Hence, the ROV did not maintain a constant altitude along the transects, and often approached/landed on the seafloor to obtain detailed images of benthic fauna. Because altitude defines the width of the ROV camera field of view (Jones et al., 2009), this operational procedure hampered the conversion of the linear distance covered by the ROV during a video transect into the observed area, consequently limiting the representation of fauna abundance/density. Temperature (°C), salinity (psu) and dissolved oxygen (ml/l) vertical profiles were obtained by a Seabird 911 CTD casts in the vicinity of each ROV-VAMS transect from the surface to near-bottom depths (maximum depth 1500

Table 1
Descriptive summary of ROV transects conducted in the Discovery Rise seamounts in January–February 2019, as part of the investigation on Vulnerable Marine Ecosystems in the convention area of the Southeast Atlantic Fisheries Organization (EAF-Nansen Programme). Temperature (Temp.), salinity and dissolved Oxygen are transect averages. AAIW, Antarctic Intermediate Water; UCDW, Upper Circumpolar Deep Water.

Transect	Seamount	Date	Initial Long Lat	Final Long Lat	Obs. time (min)	Distance (m)	Depth range (m)	Geoform	Temp. (°C)	Salinity (psu)	Diss. Oxygen (ml/l)	Dominant Water Mass
3	Shannon	31 Jan	2.4441 −42.9943	2.4518 −42.9929	142	509	595–605	plateau	4.48	34.19	5.54	AAIW
4	Shannon	01 Feb	2.4857 −42.9850	2.4825 −42.9826	131	628	1373–1545	flank	2.80	34.56	3.96	UCDW
5	Tablemount East	03 Feb	1.9499 −41.7914	1.9499 −41.7915	84	172	867–868	plateau	3.68	34.23	5.21	AAIW
6	Tablemount East	03 Feb	1.9545 −41.8138	1.9486 −41.8096	139	751	1095–1330	flank	2.96	34.44	4.23	UCDW
7	Tablemount West	04 Feb	1.5085 −42.1800	1.5085 −42.1800	101	304	1539–1540	plateau	2.80	34.59	4.03	UCDW
8	Tablemount West	05 Feb	1.4755 −42.0956	1.4754 −42.0956	32	56	956–956	plateau	3.21	34.28	4.88	AAIW-UCDW
10	Tablemount West	05 Feb	1.4756 −42.0956	1.4687 −42.0911	150	873	873–959	plateau	3.31	34.25	5.06	AAIW
11	Tablemount West	06 Feb	1.3686 −41.9381	1.3648 −41.9381	87	351	394–400	plateau	5.83	34.29	5.39	AAIW
12	Tablemount West	06 Feb	1.1815 −41.9381	1.1799 −42.0884	73	353	1397–1415	plateau	2.82	34.56	4.04	UCDW
14	Tablemount West	07 Feb	1.3348 −41.7426	1.3322 −41.7407	69	341	1015–1026	plateau	3.18	34.33	4.65	AAIW-UCDW
15	Discovery East	08 Feb	0.4349 −41.9856	0.4322 −41.9874	57	356	968–999	plateau	3.26	34.28	4.88	AAIW-UCDW
16	Discovery East	08 Feb	0.4940 −41.8879	0.4921 −41.8903	84	400	1394–1411	flank	2.83	34.55	4.04	UCDW
17	Discovery North	09 Feb	0.0593 −41.6874	0.0593 −41.6909	149	501	1730–1839	flank	2.70	34.69	4.17	UCDW
18	Discovery North	09 Feb	0.0585 −41.7172	0.0584 −41.7200	87	392	1331–1357	flank	2.87	34.52	4.06	UCDW
19	Heardman	15 Feb	0.4197 −45.3854	0.4226 −45.3834	116	540	1620–1639	plateau	2.50	34.60	4.10	UCDW

Table 2
Seascapes differentiated on the Discovery Rise seamounts, Southeast Atlantic, explored by ROV transects in January–February 2019.

Seascape	Bottom induration	Texture	Slope	Modifiers
Sediment flat SDF	Soft bottom, sediment cover	Uniform soft sediment (biogenic ooze)	Flat 2.2–2.5°	Sand waves, phytodetritus accumulated on sandwave troughs, *lebensspurren*
Sediment Flat - Scattered particles SDFSP	Soft bottom, sediment cover	Uniform soft sediment (biogenic ooze) interrupted by scattered particles (pebbles, cobbles, boulders, small outcrops)	Flat 2.2°	Sand waves, phytodetritus accumulated on sandwave troughs, *lebensspurren*, epifauna on loose particles
Sediment flat - dense particles SDFDP	Soft bottom, sediment cover	Soft sediment (biogenic ooze) interrupted by dense particles (pebbles, cobbles, small outcrops)	Flat 0.2–3.0°	Sand waves, phytodetritus accumulated on sandwave troughs, *lebensspurren*, epifauna on particles
Flank Bedrock FBK	Hard bottom,	Rough terrain formed by irregular outcrops and boulders interrupted by sediments accumulated in cracks, crevices and small ponds	Sloping 8.4–26.5°	Dusting (<1 cm) sediment cover on outcrops, sediment ponds between outcrops, epifauna on outcrops
Mixed substrate - sediment/ bedrock MSDBK	Mixed hard and soft bottom	Soft sediment predominates but is interrupted by bedrock buried or emerging in prominent plate-like and irregular outcrops	Flat to Sloping 0.0–11.6°	Thin (<5 cm) to thick (<5 cm) sediment layer covering outcrops, sediment ponds between outcrops, sand waves, *lebensspurren*, phytodetritus, epifauna on outcrops
Mixed substrate-bedrock/ sediment MBKSD	Mixed hard and soft bottom	Bedrock predominates in the form of plate-like and irregular outcrops, buried by sediment layers or interspersed by patches of sediment of various extents	Flat to Steeply Sloping 0.4–37.4°	Thin (<5 cm) to thick (<5 cm) sediment layer covering outcrops, sediment ponds between outcrops, sediments with sand waves, *lebensspurren*, phytodetritus, epifauna on outcrops
Organic Rubble Flat ORF	Mixed hard and soft bottom	Sediment surface covered by dense packs of large organic debris (rubble) including shells of brachiopodans and mollusks, coral skeletons and echinoid spines	Flat 0.1–2.7°	Dusting (<1 cm) sediment layer covering the rubble particles, epifauna on rubble particles
Mixed substrate-bedrock/ rubble MBKRB	Mixed hard and soft bottom	The same as MBKSD but outcrops interspersed by patches of organic rubble, including shells of brachiopodans and mollusks, coral skeletons and echinoid spines	Flat to Sloping 0.0–17.8°	Dusting (<1 cm) sediment layer covering the rubble particles, epifauna on rubble particles
Gravely flat GRVF	Hard bottom	Consolidated surface formed by granulated substrate - gravel, pebbles densely packed over sediment cover	Flat 0.4°	Dusting (<1 cm) sediment layer covering gravel particles, epifauna on rubble particles

m).

2.1. *Seascape characterization*

Each video profile was observed for the description of seafloor habitats (i.e. here referred to as ‘seascapes’). This process involved classifying seafloor images according with relevant features following Greene et al. (1999), Auster et al. (2005) and Greene et al. (2007), namely: (a) bottom induration (hard bottom, mixed hard and soft bottom, soft bottom), (b) substrate types (boulders, cobbles, pebbles, gravel, unconsolidated substrate varying from fine mud to coarse sand), slope (flat 0–5°, sloping 5–30°, steeply sloping 30–60°, vertical 60–90°, overhang >90°) and (c) habitat modifiers (physical - e.g., presence of current flow-derived sand waves; geological - e.g., dusting (<1 cm), thin (<5 cm) and thick (>5 cm) sediment cover on hard substrate; biological - e.g., presence of phytodetritus and *lebensspurren*). When mixed substrate types were observed, those covering more than 50% of the visible seafloor were considered ‘dominant’, whereas ‘secondary’ substrates were those covering between 30 and 50%. Seafloor classification was conducted in 2-min intervals. Seascape units were defined by one or more dominant substrate types regularly observed along a continuous segment of the seafloor and slope. Substrate types that contrasted with the dominant ones but did not persist long enough along the video track (e.g., a patch), were not considered a new seascape unit, but as part of the current seascape substrate variability. Descriptions of seascape units were complemented by habitat modifiers, and the overlaying water column properties (Table 2). These properties were also used to infer the influence of dominant water masses (following Emery and Meincke, 1986; Stramma and England, 1999; Arham et al., 2003; Morozov et al., 2010; Silveira et al., 2020 and others) and the calculation of mixing percentages (Mamayev, 1975).

2.2. *Fish and cephalopod observations*

Video profiles were observed continuously and paused when fishes or cephalopods were seen. Individuals were grouped into ‘morphological species’ (here called ‘morphotypes’) defined by shared characters and distinguishable from any other group of individuals (Durden et al., 2016). These morphotypes were named using codes (Table 3) and used as ‘Taxonomic Operational Units’ in the ecological community analyses (e.g. diversity indices, similarity/dissimilarity indices, beta diversity) (Brind’Amour et al., 2014). Because this method may group in the morphotypes more than one real species (e.g. cryptic species only distinguishable through very small characters not shown by the recorded images), it tends to underestimate diversity (Victorero et al., 2018). However, it is the most tractable methodology available for deep sea ecological studies using ROV images (Durden et al., 2016). Each morphotype was assumed to be one species and classified to the lowest taxonomic level possible based on visual assessment using taxonomic guides (e.g. Nesis, 1982; Cohen et al., 1990; Nielsen et al., 1999; Jereb and Roper, 2010; Jereb et al., 2014; Priede, 2017) and image catalogs available from different sources (e.g. OER’s Benthic Deepwater Animal Identification Guide -https://oceanexplorer.noaa.gov/okeanos/animal_guide/and others). These were tentative identifications (see

Table 3
Taxonomic classification of fishes and cephalopods observed in ROV transects conducted in the Discovery Rise (SE Atlantic). N, total number of individuals counted in the video transects.

Morphotype	Order	Family	Taxa ID	N
Class Cephalopoda				
ONK	Oegopsida	Onychoteuthidae	*Moroteuthopsis ingens*	6
HST		Histioteuthide	*Histioteuthis* cf. *atlantica*	1
OEGU		Indet	Oegopsida indet	3
OCTU	Octopoda	Octopodidae	Octopodida indet	2
OPT		Opistoteuthidae	*Opisthoteuthis* cf. *agassizii*	1
Class Actinopteri				
HDL	Chimaeriformes	Chimaeridae	*Hydrolagus* sp.	1
POLY	Notacanthiformes	Notacanthidae	*Polyacanthonotus* sp.	3
SNP1	Anguilliformes	Synaphobranchidae	Synaphobranchidae indet1	2
SNP2			Synaphobranchidae indet2	2
ORS	Zeiformes	Oreosomatidae	Oreosomatidae indet	1
COE1	Gadiformes	Macrouridae	*Coelorinchus* cf. *kaiyomaru*	12
MCR1			Macrouridae indet1	5
MCR2			Macrouridae indet2	1
MCR3			Macrouridae indet3	41
MCR4			Macrouridae indet4	1
MCR5			Macrouridae indet5	1
MCR6			Macrouridae indet6	1
MCR7			Macrouridae indet7	2
MCR8			Macrouridae indet8	1
COE2			*Coelorinchus* sp. *2*	1
CORY			*Coryphaenoides* sp.	2
CYN			*Cynomacrurus* cf. *piriei*	1
MCR10			Macrouridae indet10	4
MCR11			Macrouridae indet11	1
LPD		Moridae	*Lepidion* sp.	27
LMN			*Laemonema* sp.	116
ATR			*Antimora* cf. *rostrata*	3
GUT			*Guttigadus* sp.	92
TRP			*Tripterophycis* sp.	1
OPHI1	Ophidiiformes	Ophidiidae	Ophidiidae indet	1
CTX		Bythitidae	*Cataetyx* sp.	2
PRL	Perciformes	Liparidae	*Paraliparis* cf. *copei*	2
MLS		Zoarcidae	*Melanostigma* sp.	29
BRM	Scombriformes	Bramidae	*Brama* sp.	1
EPG	Acropomatiformes	Epigonidae	*Epigonus* cf. *telescopus*	3
ACTU1	Indet	Indet	Actinopterygii unid1	5
ACTU2	Indet	Indet	Actinopterygii unid2	1
				379

Table 3) used for seamount fauna characterization.

The consistency of morphotype characterization was repeatedly checked by comparing all available images and a final analysis of the video transects was conducted, which allowed for corrections and complementation of records. Each record included the time of visualization, the morphotype code and taxonomic classification, the number of individuals of the morphotype, and ROV transect information including geographic position (Latitude, Longitude) and depth. These records were formatted into a 'transect x morphotype' matrix which allowed exploratory analysis on fish and cephalopod distribution and diversity. Video profiles were grouped by seamount (or seamount region), geoform (plateau, flank) and by depth strata: 300–500 m, 500–1000 m, 1000–1300 m, 1300–1900 m. The depth boundaries of these strata followed from the vertical extent of deep water masses of the South Atlantic (South Atlantic Central Waters -SACW, AAIW, UCDW, NADW) (Arham et al., 2003; Silveira et al., 2020). In addition, the number of VME indicator taxa (as defined by SEAFO) in each ROV transect was recorded for comparative analyses (from Bull-Mortensen et al., 2019).

The total number of fishes and cephalopods, the number of morphotypes and number of VME indicator taxa within each ROV transect were recorded. Transect length (in meters) was estimated from total track records, excluding time periods when observation was difficult or ineffective (e.g., ROV altitude above 2 m, poor illumination, camera failures). Because sampling effort varied among transects, the number of counted individuals, number of distinguished morphotypes and of VME indicator taxa were divided by the total linear distance covered by the ROV transects (transect length) and also expressed in individuals and morphotypes per meter explored (Table S2). These distance-transformed and untransformed variables were tested for the effect of the total distance covered by the ROV transect (Table 4). Number of morphotypes per meter and number of VME taxa per meter were negatively affected by total distance ($p < 0.01$), in both cases, increasing the relative richness of shorter transects (Table 4). To avoid this effect, distance-transformed variables were not used in the following quantitative analyses.

Diversity patterns of transects were explored using Shannon's diversity and equitability indices and dominance curves. Total non-directional beta-diversity was estimated excluding morphotypes observed only once in the transects and using presence-absence data only. This choice followed from the impossibility of expressing reliably the density of fishes and cephalopods, given the difficulty to estimate the area covered by video transects where the ROV altitude, and the derived width of the video image, was not standardized (Jones et al., 2009). In addition, presence – absence approaches tend to provide informative results when distant and/or discontinuous regions are compared, as in the case of islands and seamounts exploration (Legendre, 2014). A dissimilarity matrix (matrix D) was built by computing the 'Jaccard' and 'Sørensen' dissimilarity indices between transects (Legendre and De Cáceres, 2013). A Principal Coordinate Analysis (PCoA) was used to ordinate ROV transects in a 2-D space and explore spatial patterns of similarities/dissimilarities among and within the explored seamounts. In addition, the total sum of squares (SS_{total}) was computed by summing the squared dissimilarities in the upper triangular portion of D, divided by the number of sites (n), and the total beta-diversity (BD_{total}) was calculated by dividing SS_{total} by n-1. BD_{total} was partitioned in local (transects) relative contributions (Local Contribution do Beta-Diversity, LCBD) following Legendre and De Cáceres (2013) and using the *beta.div* function of R package 'adespatial'. LCBD estimates were tested for significance by 999 random, independent permutations of the columns of D. Larger LCBDs characterized extraordinary sites i.e., with markedly different morphotype composition. Lastly, in order to explore dominant processes driving beta-diversity between ROV transect sites, both within and between seamounts, BD_{total} was further partitioned into 'species replacement' and 'species richness difference' by the *beta.div.comp* function using the Jaccard and Sørensen dissimilarity for presence-absence data (Legendre, 2014). Species replacement (or 'turnover') refers to the substitution of species along environmental gradients, as a function of individual species ecological tolerance. Alternatively, communities may differ in the number of species present due to local attributes, such as the diversity of niches available and others, in this case referred to as 'richness difference' (Legendre, 2014; Victorero et al., 2018). Estimating the relative role of these processes in defining BD_{total} of the Discovery Rise seamounts were expected to inform on the effect of potential environmental gradients across seamount spatial distribution vs. unique habitat configuration and other attributes of the different seamounts explored.

Table 4
Linear regression analysis testing the effect of transect distance, depth and presence of VME indicator taxa on the variation of the number of individuals (fishes and cephalopods) and the number of morphotypes recorded during ROV transects on the Discovery Rise seamounts (SE Atlantic). Numbers in bold represent significant effects ($p < 0.05$).

	slope	p	R^2
	Transect Distance (m)		
Individuals	−0.021	0.716	0.010
Individuals/m	<-0.001	0.392	0.057
Morphotypes	0.002	0.407	0.053
Morphotypes/m	<-0.001	**0.003**	0.499
VME ind.	0.008	0.064	0.240
VME ind./m	<-0.001	**0.010**	0.408
LCBD	<-0.001	0.836	0.003
	Depth (m)		
Individuals	−5.216	**0.025**	0.331
Morphotypes	−0.001	0.359	0.065
LCBD	<-0.001	0.417	0.051
E_H	<0.001	**0.036**	0.316
	VME Ind.		
Individuals	−5.300	0.108	0.187
Morphotypes	0.044	0.794	0.005
LCBD	<-0.001	0.123	0.173
E_H	0.022	0.135	0.176

3. Results

3.1. Explored seascapes

Explored transects were under the influence of two deep water masses of the South Atlantic, the Antarctic Intermediate Waters (AAIW) and the Upper Circumpolar Deep Waters (UCDW) (Table 1, Fig. S1). Mean transect temperature, salinity and dissolved oxygen ranged between 2.5 and 5.8°C, 34.19 and 34.69 psμ, and 3.96 and 5.54 ml/l, respectively (Table 1).

Nearly 60% of the total linear distance covered by these transects (3855 m) explored seamount plateau areas (10 transects, 394–1639 m-deep). These plateaus varied in depth, ranging from 600 m (Shannon), 800–1000 m (Tablemount E and W, Discovery E), 1000–1500 m (Tablemount W) and deeper than 1500 m (Heardman) (Table 1). On Tablemount West, however, transect 11 explored an exceptionally shallow summit hill (394–400 m). Because seamount flanks were deeper, steeper and less accessible due to rough terrain, only 5 transects (1095–1839 m-deep) were successfully conducted in these areas where nearly 2672 m were effectively explored.

The observed seafloor of both plateau and flank areas was covered chiefly by substrates of mixed textures (63.3% of the explored distance), where both outcrops or large rocky particles were distributed amongst (or partially covered by) variable patches of soft sediment (mostly biogenic ooze) (Fig. 2). Seafloor fully covered by soft sediments predominated in 28.6% of the distance explored by video transects, mostly

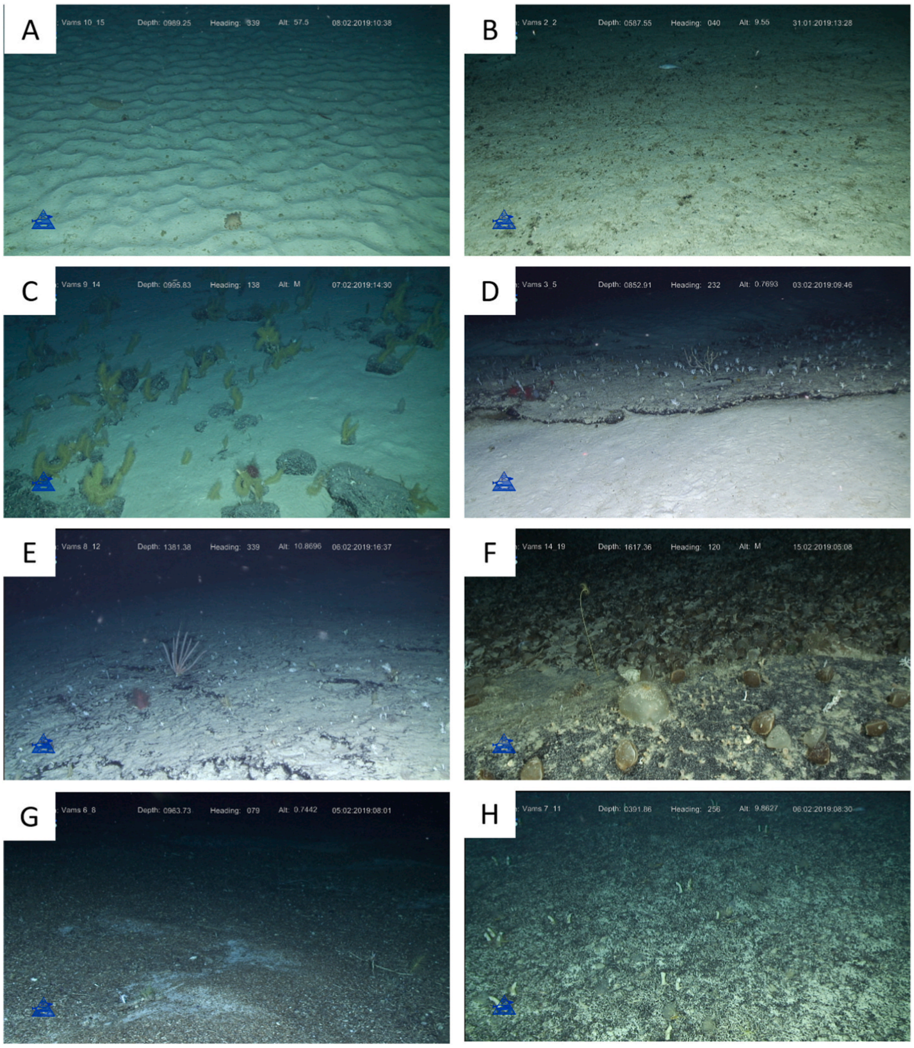

Fig. 2. Seascapes on plateau areas of the Discovery Rise seamounts (SE Atlantic). A, Sediment flat – SDF; B, Sediment Flat - Scattered particles – SDFSP; C, Sediment flat - dense particles – SDFDP; D, Mixed substrate - sediment/bedrock – MSDBK; E, Mixed substrate - bedrock/sediment – MBKSD; F, Mixed substrate - bedrock/rubble – MBKRB (brachiopodan shells); G, Organic rubble flat – ORF (stone corals, mollusk shells, echinoid spines); H, Gravely flat – GRVF.

over plateau areas. Rough bedrock (covering 7.8% of the covered distance) was the least common substrate, which predominated only over seamount flanks (Table S1). Adding to the seafloor texture, attributes, such as slope and physical and biological modifiers, allowed the distinction of nine seascapes (Table 2), five of them occurring on both plateau and flank transects, three exclusively on the plateaus and one exclusively on flanks (Table S1).

On plateau areas (Fig. 2), three seascapes were largely dominated by sediments with loose particles or small outcrops distributed (either sparsely or densely) over the seafloor (SDF, SDFSP, SDFDP, Fig. 2A, B, C). In these seascapes, sand waves formed by bottom currents were often observed with variable amounts of accumulated phytodetritus and animal markings (*lebensspurren*). Three plateau seascapes were characterized by mixed substrates where, either soft sediment (MSDBK) or bedrock (MBKSD) predominated, but were interrupted by contrasting textures; i.e., buried or emerging bedrock plates in MSDBK (Fig. 2D), or interspersed patches of sediment of various extents in MBKSD (Fig. 2E). One mixed substrate seascape was characterized by dense patches of coarse organic rubble (ORF) that included brachiopodan, cirripedian and mollusk shells, broken coral skeletons and echinoid spines (Fig. 2F and G). Lastly a very particular seascape was characterized on the shallowest Tablemount plateau area (390–400 m, transect 11) covered by densely packed gravel (GRV, Fig. 2H).

Seamount flanks (Fig. 3) also contained patches of organic rubble (ORF, Fig. 3C). This texture was also found accumulated amongst bedrock outcrops forming a mixed substrate seascape (MBKRB) (Fig. 3B). One seascape mostly defined by a substrate formed by irregular outcrops and boulders (FBK, Fig. 3A), was distinguished on the steep flanks.

3.2. *Cephalopod and fish fauna*

A total of 366 fishes and 13 cephalopods were seen along the 15 video transects analyzed (total time = 25.0 h). Fishes were grouped in 32 morphotypes. Thirty morphotypes were classified in 9 orders and 12 families (Table 3); two morphotypes could not be assigned to any taxon. Nearly 44% of all fish morphotypes (14) were included in the Macrouridae family. Family Moridae included 65.3% of all fish records (239), with two particularly abundant morphotypes classified as: *Laemonema* sp. (116) and *Guttigadus* sp. (92) (Fig. 4A and B). Morphotypes classified as Macrouridae indet. 3, *Melanostigma* sp., *Lepidion* sp. and *Coelorinchus* cf. *kayomaru* were also relatively abundant in the video transects (Fig. 4 C–F, Table 3). *Antimora* cf. *rostrata* and *Cynomacrurus* cf. *piriei* were the only large-sized morphotypes observed in the explored area (Fig. S2).

Five cephalopod morphotypes were differentiated in the videos, classified in two orders and four families. One morphotype could not be

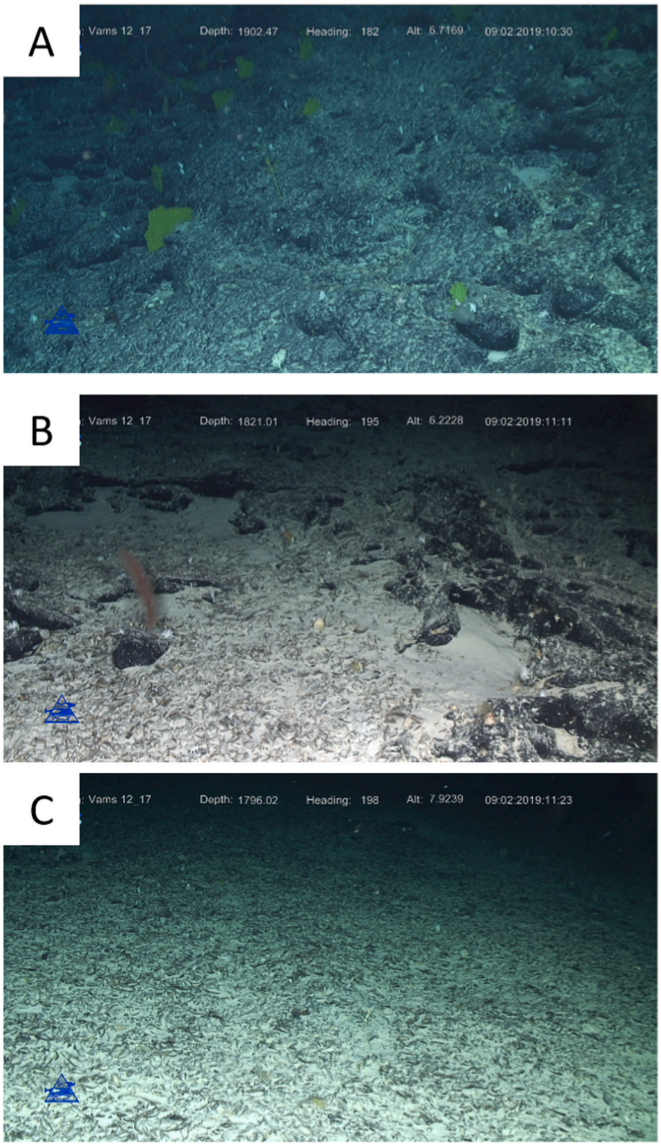

Fig. 3. Seascape on flank areas of the Discovery Rise seamounts (SE Atlantic). A, Flank bedrock – FBK; B, Mixed substrate - bedrock/rubble – MBKRB (cirripedian shells); C, Organic rubble flat- ORF (cirripedian shells).

assigned to family level. *Moroteuthopsis ingens* was the most abundant of them (6). Large specimens of the latter species were attracted by the ROV lights and two of them were accidently trapped in the ROV cage, allowing for a complete identification on deck. This species and *Opisthoteuhis* cf. *agassizi* are shown in Fig. 4G-H.

Considering the full distance covered by the ROV camera in 15 transects over all seamounts (6528 m), benthopelagic fish and cephalopods were observed at a mean rate of 25.3 individuals per transect, varying from 2 to 142 (SE = 10.7). Considerable variability in observation rates was observed among and within seamounts (Fig. 5, Table S2). Exceptionally high concentrations were recorded at Tablemount west transects 11 (142) and 14 (116). The former was conducted over the shallowest explored plateau (394–400 m) covered by the 'gravely flat' (GRVF) seascape (Fig. 6, Fig. 2H, Table S1). Transect 14 was conducted over a 1015–1026 m-deep area mostly covered by the 'Sediment flat - dense particles' (SDFDP) seascape (Figs. 6 and 2C, Table S1). These two sites were also under the influence of the AAIW and mixture zones with UCDW, with mean temperatures varying from 3.18 to 5.83°C, salinities 34.29 to 34.33 psµ and dissolved oxygen 4.65–5.39 ml/l (Fig. 7, Table 1). Fishes and cephalopods tended to be more frequently seen during transects conducted on seamount plateaus (mean = 33.9, SD = 50.8, Distance observed = 3855 m) than on flanks (mean = 6.4, SD = 5.9, Distance observed = 2672 m) (Fig. 5). This difference was also true when plateau transects 11 and 14 were not considered (Plateau mean = 10.1, SD = 7.1). The rate of fish and cephalopod observations in the ROV transects tended to decrease at greater depths (Table 4, $p = 0.025$), a trend also significant when the transects 11 and 14 were excluded ($p = 0.028$). Below 1300 m depths, under the influence of low temperatures and lower dissolved oxygen concentrations of the UCDW, observation rates were lowest (Fig. S1). Fish and cephalopod observation rates were not significantly affected by the number of reported VME taxa (Table 4, $p = 0.108$).

The number of morphotypes observed during one ROV transect varied from 1 to 8. On average, 5 morphotypes were observed per transect (±0.054 SE, N = 15), varying widely both between and within seamounts (Fig. 5). Observation rates were similar in transects conducted on seamount plateaus and flanks (mean ~ 5 morphotypes, SD ~ 2). Richest transects were observed on Tablemount seamount: 14 (8 morphotypes), 5, 6 and 12 (7 morphotypes) (Fig. 5). Of these, only transect 6 was conducted on a flank area. Particularly poor faunas were observed on Discovery seamount transect 17 (flank) and Tablemount seamount transects 7 and 8 (plateau). Plateau seascapes with mixed (MBKSD, MSDBK) or soft (SDF, SDFDP) substrates were associated with a higher number of morphotype observations (Fig. 6); lowest morphotype observations were associated with flank seascapes dominated by hard substrates and rubble (MBKRB and FBK), and gravel (GRVF) which covered the seafloor in transect 11 (see above). The number of morphotypes observed during the ROV transects was not affected by depth or the number of reported VME taxa (Table 4, $p = 0.359$ and 0.794, respectively). Morphotype observations were richer between 800 and 1500 m depths, and transect 11, conducted over the shallowest areas (see above), was particularly poor (Fig. 7).

Occurrence of morphotype sightings on various seamounts exhibited moderate levels of dominance (Fig. S3), which tended to increase at shallower depths (Fig. 7, Table 4, $p = 0.036$). This trend, however, is mostly driven by Tablemount seamount transects 11 and 14, where morphotype composition was highly uneven ($E_H = 0.43$ and 0.35, Fig. 7) due to concentrations of the morid cods *Laemonema* sp. and *Guttigadus* sp., respectively.

Jaccard and Sørensen species composition dissimilarities calculated between pairs of ROV transects were generally higher between transects conducted on different seamounts than between transects conducted on the same seamount (Wilcoxon non-parametric test, $p = 0.0002$) (Fig. 8). Also, dissimilarities between transects tended to be higher the greater the depth difference between them ($p < 0.001$), and this depth effect was also observed when only Tablemount, the most explored seamount, was considered ($p = 0.041$, Fig. 9). The 2-D spatial representation of the two first axes extracted using a Principal Coordinate Analysis (PCoA) (explaining jointly 28% of the total variance) partially aggregated transects conducted over the same seamount (Fig. 10). Deviations from this pattern seem to derive from morphotypes shared between: (a) Discovery and the adjacent Tablemount (transect 7), (b) Shannon and the northern Tablemount (transects 11 and 3), (c) Shannon and the southernmost Heardman (transects 4 and 19) (Fig. 10). The effect of depth in the ordination of transects in the 2-D space was less evident; transects within the 1300–1900 m depth stratum seemed partially separated from those within the 500–1000 m and 1000–1300 m, and the spatially isolated transects 3 and 11, were the shallowest ones (400–600 m depths).

Total non-directional beta-diversity calculated for ROV transects was 0.425 (Jaccard index) and 0.381 (Sørensen index), indicating that 57.5–61.9% of the recorded morphotypes were shared amongst ROV transects (maximum dissimilarity = 1.0). Tablemount and Discovery seamounts shared the highest number of morphotypes (7, Fig. S4). These are the least-distanced seamounts but were also the most explored ones. Contributions of each ROV transect to the total beta-diversity (LCBD) are represented in Fig. 7 (and Table S2), showing no clear association with

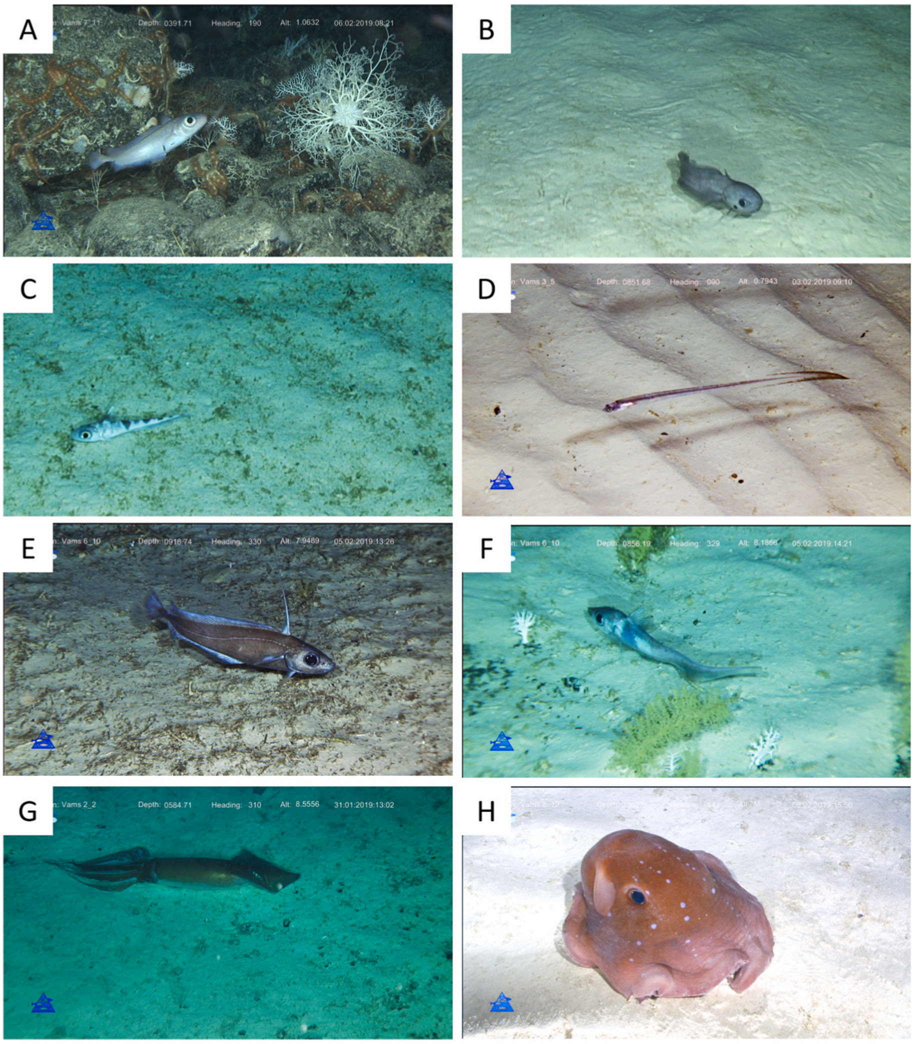

Fig. 4. Fishes and cephalopods observed in ROV transects conducted in the Discovery Rise seamounts (SE Atlantic). A, *Laemonema* sp. (LMN), B, *Guttigadus* sp. (GUT), C, Macrouridae indet. 3 (MCR3), D, *Melanostigma* sp. (MLS), E, *Lepidion* sp. (LPD), F, *Coelorinchus* cf. *kaiyomaru* (COE1), G, *Moroteuthopsis ingens* (ONK), H, *Opisthoteuthis* cf. *agassizii* (OPT).

depth variability (Table 4, p = 0.417). The only significant contribution to total beta-diversity was attributed to west Tablemount transect 11 (LCBD = 7.60–8.30%, p = 0.003). Non-significant but also high contributions were noted in Discovery seamount transects 17 (LCBD = 7.3–7.7%, p = 0.11–0.09), and 18 (LCBD = 7.2–7.5%, p = 0.18–0.14) (Fig. 7). Transect 11 corresponds to the previously mentioned shallowest site where only 4 morphotypes were recorded, two of them highly abundant, the morid *Laemonema* sp. (n = 112, Fig. 4A) and the macrurid indet. 3 (n = 27, Fig. 4C). Transects 17 and 18 were conducted on deep sites of the Discovery seamount northern flanks (1730–1839 m and 1331–1357 m, respectively) (Fig. 1), with only three rare morphotypes recorded altogether.

The species replacement component contributed with 66–67% of the total beta diversity, as estimated by Jaccard and Sørensen presence-absence dissimilarity indices, respectively, with species richness difference contributing with 33–34%. The relative importance of species replacement and species richness difference components between different seamounts and within the same seamount was explored (Fig. 8), suggesting that species replacement is more important between seamounts and species richness difference more important within seamounts (Wilcoxon non-parametric test, p = 0.035).

4. Discussion

All explored seamount areas in the Discovery Rise were under the influence of the East-West flowing AAIW, UCDW water masses and their interfaces at 900–1000 m depths. Seamount habitats influenced by AAIW were warmer (3.3–5.8°C) and more oxygenated (levels above 5.1–5.5 ml/l) than those under the influence of UCDW (2.5–2.8 °C; 4.0–4.2 ml/l). AAIW is characterized by a high-oxygen/low-salinity tongue found at 300 m depth at approximately 45°S, that descends northwards to 900 m at 30°S (Stramma and England, 1999), explaining its dominant influence over the 400–900 m-deep explored plateau areas. Flank areas in the 1000–1600 m depth range were under the influence of UCDW, which is characterized in the South Atlantic as a low-oxygen tongue lying between the oxygen maximums of AAIW and NADW, whose upper layer also flows eastward between 1300 and 2100 m (Stramma and England, 1999; Arham et al., 2003).

ROV observations revealed other important habitat variability in both plateau and flank areas of explored seamounts. These were all flat-topped single-summits, with 600–1600 m-deep plateaus covered by a combination of sediments and mixed textures that include variable extensions of exposed bedrock outcrops. These seascapes generally resembled those characterized in the 100–1000 m-deep plateau areas of Walvis Ridge seamounts (including Schmitt-Ott, Wüst and Vema,

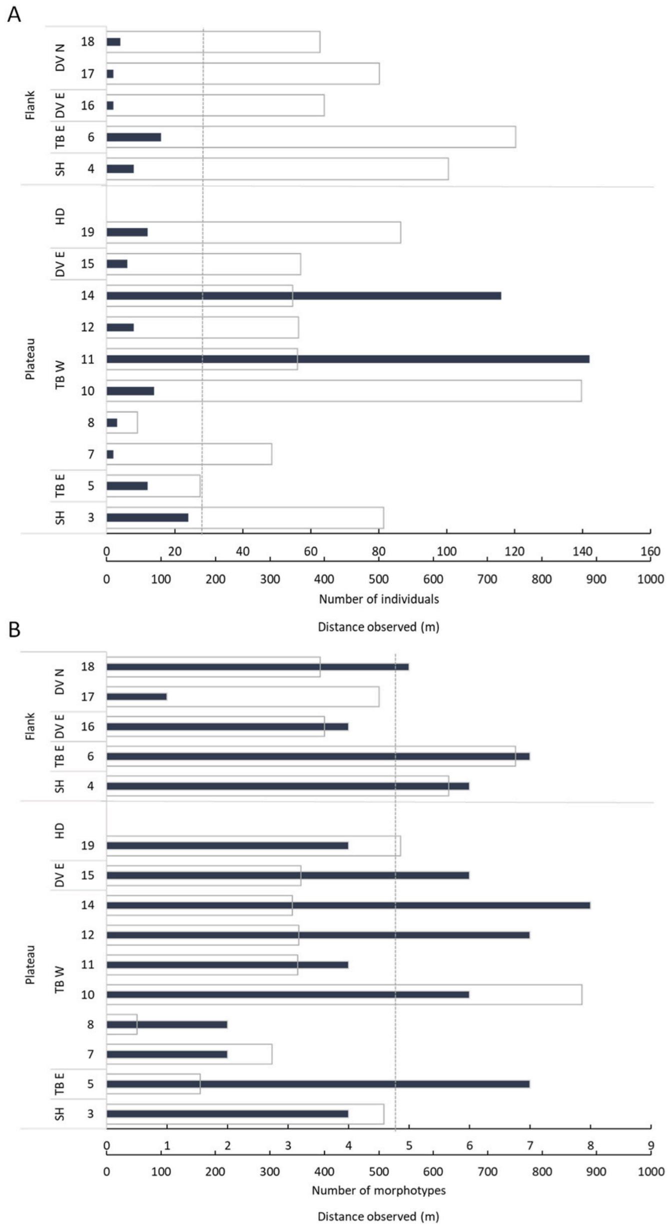

Fig. 5. Number of individuals (fishes and cephalopods) (A) and morphotypes (B) recorded during ROV transects conducted on flank and plateau areas of the Discovery Rise seamounts (SE Atlantic). Dark bars represent numbers of individuals and morphotypes, light bars represent the distance explored by video transects (in meters). Dashed lines indicate overall means of individuals and morphotypes. SH, Shannon; TB E, Tablemount East; TB W, Tablemount West; DV E, Discovery East; DV N, Discovery North; HD, Heardman.

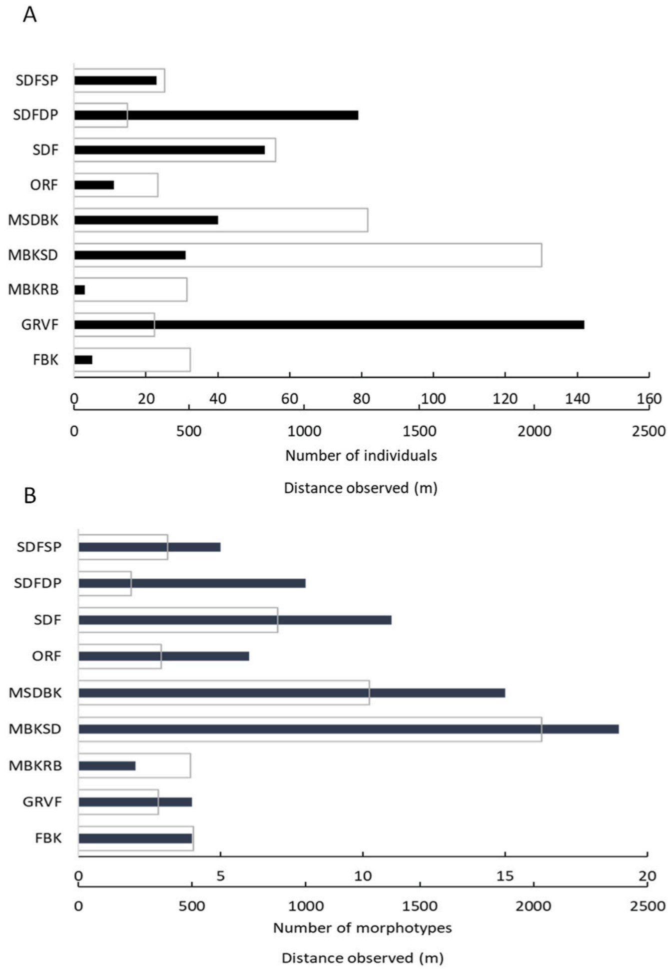

Fig. 6. Number of individuals (fishes and cephalopods) (A) and morphotypes (B) recorded along different seascapes defined during ROV transects conducted the Discovery Rise seamounts (SE Atlantic). Dark bars represent numbers of individuals and morphotypes, light bars represent the distance explored by video transects (in meters). Dashed lines indicate overall means of individuals and morphotypes. SDFSP, Sediment flat - scattered particles; SDFDP, Sediment flat - dense particles; SDF, Sediment flat; ORF, Organic Rubble Flat; MSDBK, Mixed substrate - sediment/bedrock; MBKSD, Mixed substrate - bedrock/sediment, MBKRB, Mixed substrate - bedrock/rubble; GRVF, Gravely flat; FBK, Flank bedrock.

Bergstad et al., 2019b), except that these seemed to contain a higher coverage of hard-substrate areas (mostly coral relicts). In part, this difference can be explained by the exploration strategy adopted in the Walvis Ridge, which prioritized positive features (knolls and hills) existing on the plateaus as ‘fishable’ areas (Bergstad et al., 2019b). In that sense, most seascapes characterized in the Discovery Rise seamount plateaus seemed comparable to those found in the areas referred in Bergstad et al. (2019b) as the ‘base’ of the plateau. These seascapes were also similar to those reported on the plateau of the SW Atlantic Rio Grande Rise main structure (known as ‘Alpha’, 600–1000 m depths), particularly with regards to areas covered by biogenic sediment and mixed sediment-bedrock seascapes (see Fig. 3C, E and 3F in Perez et al., 2018). It is suggested that the dynamic levels of sedimentation over the bedrock substrate (e.g., basaltic) of seamount plateaus may influence most habitat variability in these areas affecting megafauna diversity patterns (Clark et al., 2010a).

Ecological processes, however, may also play a role in the formation of seamount habitats, as evidenced by biogenic rubble deposits, a common texture observed in both Walvis Ridge and Discovery Rise seamounts. In the latter, rubble was chiefly formed by shells of mollusks, cirripedians and brachiopods, sea urchin spines, and skeleton debris of isidid corals (*Keratoisis*) (Fig. 3F, G, 4A, 4B) (Bull-Mortensen et al., 2019). In Schmitt-Ott, Wüst and Valdivia, rubble was dominated by fragments of stony corals (scleractinians) (Bergstad et al., 2019a). In these seamounts, live colonies of stony corals were reported in low densities, and it was implied that coral rubble (and consolidated carbonate outcrops and coral frameworks) were relics of benthic communities modified by past geological events (Bergstad et al., 2019a and b). In the Discovery Rise seamounts, no stony coral colonies were found. Considerable concentrations of live *Keratoisis* colonies (Isididae) and other sea fans and sea whips were found in several explored areas, along with cirripedians and brachiopods. It seems uncertain, however, whether organic rubble deposits have been formed by a recent supply of

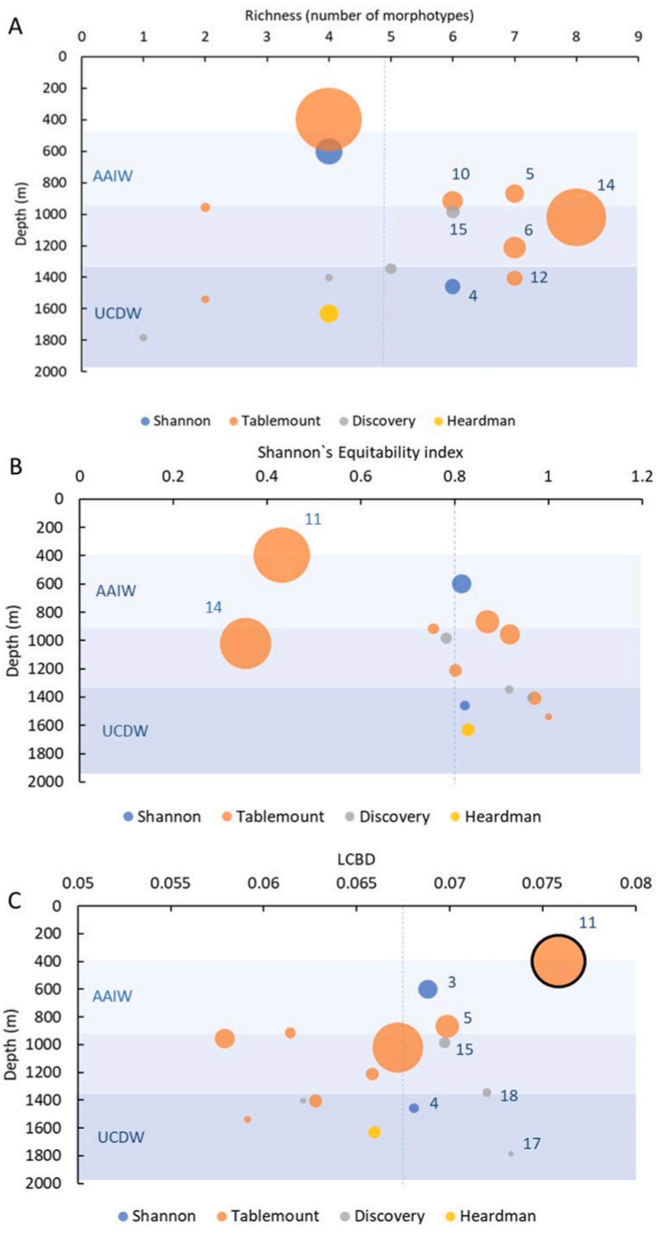

Fig. 7. Diversity patterns of fish and cephalopods observed during ROV transects on the Discovery Rise seamounts. A, richness, expressed in number of morphotypes; B, equitability, expressed by Shannon's equitability index; C, Local Contribution to Beta Diversity (LCBD). Indices variation are plotted against depth. Shaded areas indicate mean depth distribution the Antarctic Intermediate Water (AAIW), Upper Circumpolar Deep Water (UCDW) and mixture depths. Circle diameters are proportional to the number of individuals observed in each ROV transect. Numbers identify transects with values above average (dotted lines). In C, bold circle line indicates a transect where the estimated LCBD was significant ($p = 0.034$).

debris or by ancient communities and past geological events. The shallowest plateau area explored by ROV transect 11 (390–400 m), on west Tablemount seamount, revealed a considerably distinct seafloor texture formed by densely packed gravel and pebbles (Fig. 3H), which seemed to be under the influence of strong currents. This substrate differed from the reported deposits of organic debris and supported a distinctive megafauna diversity (see below).

Video observations revealed a benthopelagic megafauna dominated by small-sized teleost fishes where macrourids (rattails) were particularly well represented and morid cods included some abundant taxa (e.g. *Laemonema* sp., *Guttigadus* sp., *Lepidion* sp.). At least three cephalopod morphotypes identified as *M. ingens*, *H.* cf. *atlantica* and *O.* cf. *agassizii* are known to be seamount residents that dwell on or above flanks and summits (Clarke, 2007). Seamount-aggregating fish species (*sensu* Morato and Clark, 2007) were limited to single occurrences of an unidentified oreo dory and one black cardinalfish (*Epigonus* cf. *telescopus*). Patagonian toothfish, historically exploited by the long-line fishery particularly on the Discovery Rise seamounts (Area D, Southeast Atlantic Fisheries Organization, 2017a), was not observed in the video transects. This is a large-sized (up to 2.3 m-long) deep-water species of the Southern Ocean (45°-62°S) that tend to concentrate in small areas, yet possibly outside the field of vision of the ROV cameras, that were set to explore benthic organisms (e.g. VME indicators) on the seafloor. The species is known to perform 20–130 m daily vertical movements foraging both over the seafloor and in the mesopelagic (Collins et al., 2010). As a powerful predator and scavenger, it is promptly attracted by experimental baited cameras, but often discouraged to approach them due to the flashing lights of the cameras (Collins et al., 2006). It is possible that if there were individuals to be seen on the explored areas of the Discovery Rise, they may have avoided the proximity of the highly illuminated VAM system (Stoner et al., 2008).

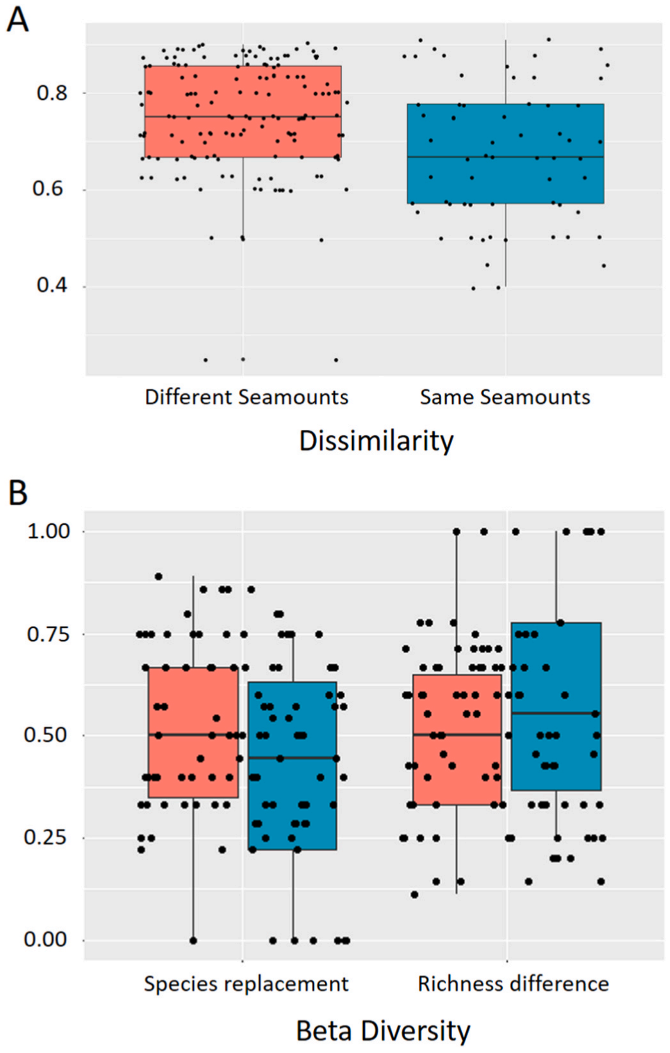

Fig. 8. Fish and cephalopod morphotype composition in ROV transects conducted on seamounts of the Discovery Rise (SE Atlantic). Pairwise presence-absence (A) Jaccard index dissimilarities, and (B) beta diversity components: 'Species Replacement' and 'Species Richness Difference'. Boxes represent distribution of values representing comparisons between transects located within the same seamount (blue boxes) and in different seamounts (red boxes).

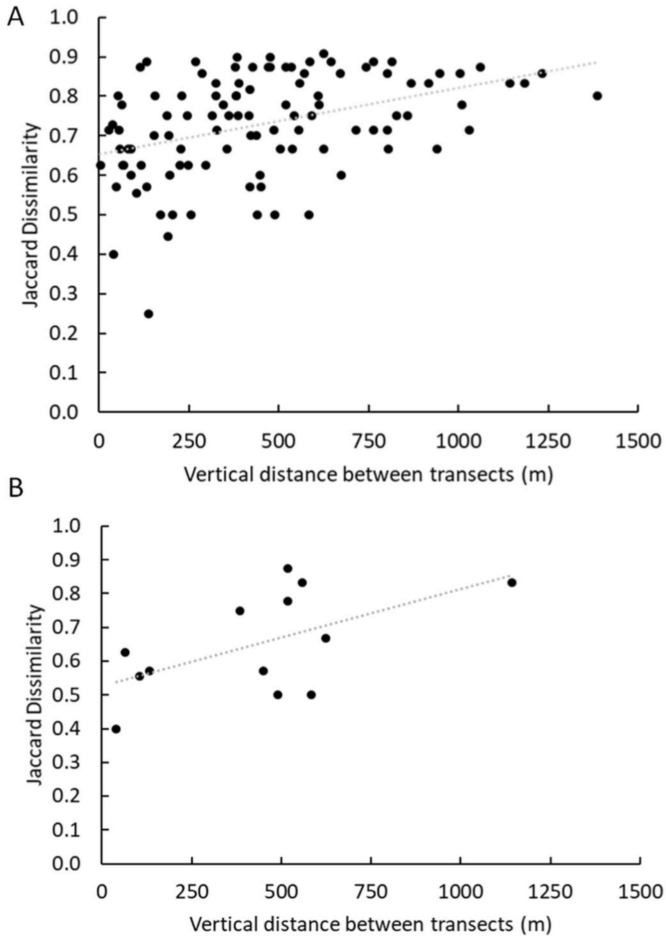

Fig. 9. Jaccard dissimilarities (Jd) calculated between ROV transects conducted on seamounts of the Discovery Rise (fish and cephalopod presence-absence data) expressed in relation to their absolute depth interval (Dd). A, All transects ($Jd = 0.653 + 0.0002Dd$; $p = <0{,}001$; $R^2 = 0.165$; $N = 105$); B, transects on Tablemount seamount ($Jd = 0.527 + 0.0003Dd$; $p = 0.041$; $R^2 = 0.327$; $N = 13$).

Other seamount-aggregating commercial species, including pelagic armourhead, splendid alfonsinos and orange-roughy were also absent from the Discovery Rise videos, but these were observed in several video transects produced at a similar depth range by the CAMPOD towed camera system in the Walvis Ridge (Valdivia and Ewing seamounts) and southerly seamounts (Wüst and Vema seamounts) (Bergstad et al., 2019a), including areas where historical catches have been reported (Southeast Atlantic Fisheries Organization, 2017b; c; d). It is possible that these species become scarce south of approximately 30°S, as indicated by SEAFO catch records, although their overall reported latitudinal ranges reach southern limits at 43–56°S (Priede, 2017 and others), which in the SE Atlantic would include the explored Discovery Rise seamounts.

Uncertainties in video-only taxa recognition prevent comprehensive comparisons between bathyal fish and cephalopod fauna studies in the South Atlantic. Considering the species that were positively identified in the Discovery Rise seamounts (and genera that have a restricted known geographic distribution) it was possible to conclude that the area is inhabited by: (a) Southern Ocean species reaching the northern limits of their distribution ranges, namely the macrourids *Cynomacrurus* cf. *piriei* and *Coelorinchus* cf. *kaiyomaru*, the morid cod *Guttigadus* sp. and the oegopsid squids *Moroteuthopsis ingens* and *Histioteuthis* cf. *atlantica* (Nesis, 1982; , Cohen et al., 1990; Cusseau, 1993; Meléndez and Markle, 1997; Vecchione et al., 2003; Jereb and Roper, 2010; Priede, 2017; Young and Vecchione, 2017) and, (b) species widely distributed in tropical, subtropical and temperate regions of the Atlantic Ocean possibly reaching the southern extremes of their distribution range in the Discovery Rise seamounts. These include the morid cods *Laemonema* sp. and *Antimora* cf. *rostrata*, *Paraliparis* cf. *copei*, *Epygonus* cf. *telescopus*, *Polyacanthonotus* sp., and the cirrate octopod *Opisthoteuthis* cf. *agassizii* (Villanueva et al., 2002; Haimovici et al., 2009; Jereb et al., 2014; Priede, 2017). Fish fauna reported in the Walvis Ridge, Wüst and Vema seamounts exploration in 2015 included 74 fish species (within 22 genera and 34 families), but the list mostly includes taxa recorded by bottom trawls conducted over selected plateau areas, limiting fish fauna comparisons between the two areas (Bergstad et al., 2019a; Food and Agriculture Organization of the United Nations, 2016). However, an analysis of the known distribution range of identified fish species suggests that nearly 1/3 of them occurred over tropical - subtropical regions of the Atlantic Ocean, whereas 10% were Southern Ocean species (Food and Agriculture Organization of the United Nations, 2016). Despite the

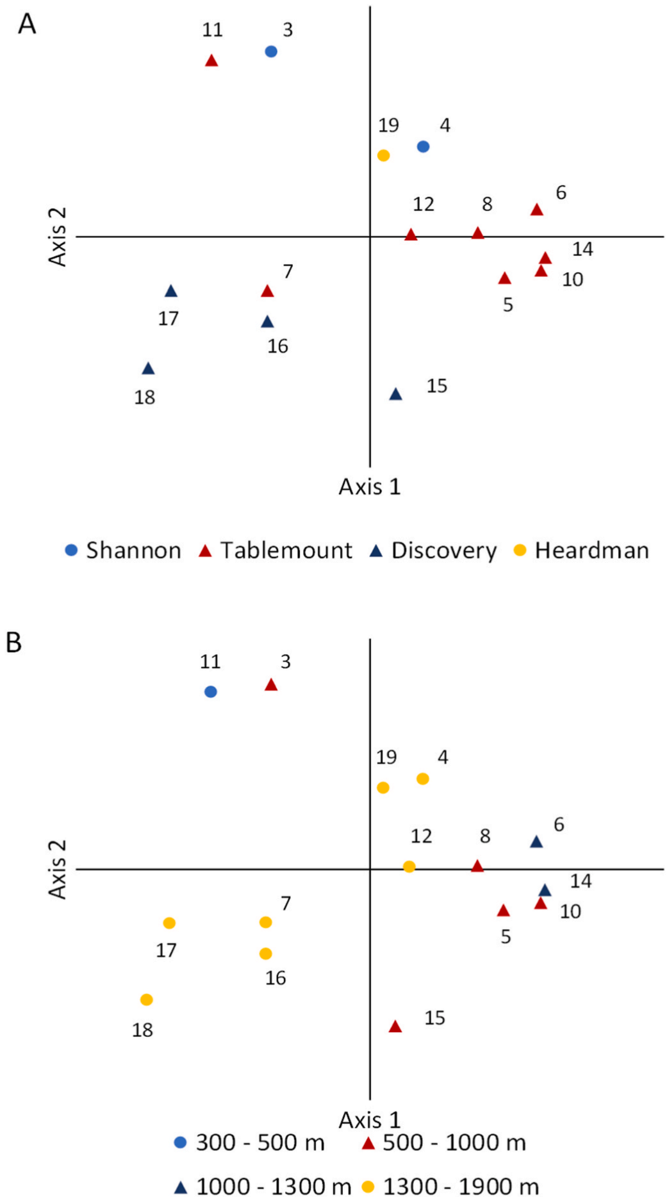

Fig. 10. Principal Coordinate Analysis ordination diagram of ROV transects conducted on seamounts of the Discovery Rise (fish and cephalopod presence-absence data). Colour symbols indicate seamounts (A) and depth strata (B). Numbers next to symbols indicate the ROV transects.

taxonomic limitations, it seems plausible to infer that fish and cephalopod fauna recorded at seamounts southward of 30°S (from SEAFO Divisions C to D) reflects an increasing influence of Sub-Antarctic/cold temperate regions that extend to the south of the Subtropical Confluence (35° - 45°S) (see De Broyer and Koubbi, 2014). This oceanographic front represents a boundary between oligotrophic surface waters of the Subtropical Gyre biogeochemical province of the South Atlantic to the north, and a highly productive South Subtropical Convergence Province to the south (Longhurst, 2007). This North-South contrast also determines a change in the amount energy transferred to deep water layers (i.e., through POC flux) and, in that sense, it has been regarded as a biogeographic boundary in mesopelagic (South Atlantic and Circumglobal Subtropical Front ecorregions, Sutton et al., 2017) and lower-bathyal (South Atlantic and Subantarctic provices, Watling et al., 2013) regions of the SE Atlantic. The Discovery Rise seamounts lie within this deep-water fauna transition zone, which adds ecological and economic importance to this area, e.g., the Patagonian toothfish has a circum-sub-Antarctic geographic distribution reaching, in the Atlantic, latitudes lower than 45°S only in the Patagonian Shelf and in the Discovery Rise seamounts where it is commercially exploited (Collins et al., 2010).

In addition, because bathyal regions of these seamounts are influenced by AAIW, UCDW and NADW, all transported by the W-E flowing South Atlantic Current (Fig. 1, Stramma and England, 1999), these seamounts could represent stepping stones for bathyal fauna W-E dispersion (e.g., Sánchez and Alvarez, 1988). Occurrences of *C.* cf. *piriei* and *C.* cf. *kaiomaru* at the Discovery Rise suggest that such connectivity may exist, in contrast to potential SW and SE regional seamount fauna identities, as observed in the North Atlantic and the South Pacific (Clark et al., 2010b). In fact, fish diversity observed in the Discovery Rise is considerably different from that observed, at comparable depths (600–1200 m), in the Rio Grande Rise, SW Atlantic (29° - 33°S) (Perez et al., 2018). A total of 30 fish morphotypes divided into 12 orders and 17 families, were observed along 5491 m-long video transects, exceeding by 3 orders and 5 families those observed in the Discovery Rise seamounts and sharing only 5 orders (Notacanthiformes, Anguilliformes, Zeiformes, Gadiformes, Ophidiiformes) and 5 families (Synaphobranchidae, Moridae, Macrouridae, Ophidiidae, Oreosomatidae). Video observations of the Rio Grande Rise seafloor included a higher diversity of Anguilliforms (families Nettastomidae and Synaphobranchidae) and a lower diversity of morid cods (only one morphotype in the genus *Lepidion*).

Seamount fauna diversity result from structuring factors operating at different spatial scales, spanning regional processes of dispersion and speciation to local selective effects of individual seamounts, depth and habitat configuration within seamounts (Lundsten et al., 2009; Clark et al., 2010b; McClain et al., 2012; Tracey et al., 2012; Victorero et al., 2018). The isolated effect of these factors on fish and cephalopod diversity in remote oceanic seamounts, however, can seldom be addressed by robust experimental studies owing to difficulties in conduct multiple samples in the irregular and deep seafloor (McClain et al., 2012). Fish and cephalopod observation data obtained in the Discovery Rise seamounts are considerably limited and affected by these difficulties; seamounts, depth strata and geoforms (plateaus x flanks) were unevenly explored by transects, and the qualitative sampling approach adopted to identify mostly corals and sponges may have disadvantaged the assessment of highly mobile components of seamount megafauna. In this regard, the observed diversity patterns were mostly exploratory, but suggested a substantial amount of variation in abundance, diversity and fauna composition both between and within the explored seamounts, in agreement with more comprehensive seamount fauna studies, (e.g. Clark et al., 2010b; Tracey et al., 2012 and others).

Fishes and cephalopods were observed in all the explored sites of the Discovery Rise. They were more frequently observed and more diverse in the large Tablemount seamount, which was also the most explored by video transects. Similarities of presence-absence fauna composition revealed some degree of seamount identity and video transect dissimilarities were higher between seamounts than within seamounts. Yet, there were also substantial sharing of morphotypes between seamounts, mostly between the least distanced Tablemount – Discovery seamounts, but also with the most remote and least explored Heardman seamount. One morphotype, the morid cod *Lepidion* sp. was recorded in all seamounts. Sampling limitations preclude a conclusive assessment of fish and cephalopod seamount exclusive and shared species. However, analyzed data suggests that this fauna is not homogeneous among seamounts and structured by the interaction of distinct drivers including, *inter alia*, distance among seamounts, seamount size, summit depth and habitats diversity, amount of influence of AAIW – UCDW, latitude and geographic position in relation to the Subtropical Confluence (Lundsten et al., 2009; Clark et al., 2010b; Tracey et al., 2012). Sorting out the influence of these drivers require more extensive and well-planned sampling in the area, but the prevalence of species replacement processes in the total beta-diversity may indicate that these drivers, individually or jointly, may establish environmental gradients selecting for individual seamount fish and cephalopod species (Victorero et al., 2018).

Depth negatively affected observation rates of fish and cephalopods, possibly reflecting the combined effect of a suite of depth-related factors including the geomorphology (plateau x flanks) and deep-water masses (and their physical and chemical properties) vertical distribution. These animals were more frequently seen on shallower plateau areas under the influence of warmer and more oxygenated AAIW. As high-level consumers, they may benefit from concentrating in seamount summit areas in order to take advantage of enhanced feeding opportunities, as determined by the proximity with surface-related food sources (e.g. vertically migrating zooplankton and mesopelagic fish, Colaço et al., 2013; Preciado et al., 2017) and increased water flow dynamics (e.g. increased zooplankton lateral advection) (Genin, 2004; Rogers, 2018). Depth of transects did not seem to affect richness, but it may have a role on morphotype composition as presence-absence dissimilarities between video transects increased with larger depth intervals between them, even in a single seamount. Such a pattern was demonstrated by more robust studies in several seamounts, including the Rosemary Bank seamount, NE Atlantic (Eerkes-Medrano et al., 2020), and the Davidson seamount, NE Pacific, where changes of 50% in fish assemblage composition were observed over ~1500 m depth intervals (McClain et al., 2012). Comparable changes were also reported for ~600 m depth intervals in the Rio Grande Rise area (Perez et al., 2018).

In these studies, depth variability was one of the factors that contributed to important within-seamount megafauna spatial heterogeneity, in combination with geomorphology and habitat diversity (Ross and Quattrini, 2007; McClain et al., 2012; Baker et al., 2012; Victorero et al., 2018; Eerkes-Medrano et al., 2020). In the Discovery Rise seamounts, spatial habitat heterogeneity may have accounted for the increased ‘species richness’ component of beta diversity within seamounts, which supports the existence of mesoscale fish assemblages (McClain et al., 2012). Tablemount seamount contained the most diverse sites, probably because it was also the most widely explored. In this seamount considerable fauna spatial variability was likely associated with habitat heterogeneity on the plateau and flank areas. In that regard, seven out of the nine seascapes defined in all explored areas were available in Tablemount plateau and flanks, including 90–100% of the seascapes containing the highest numbers of morphotypes (SDFDP, MSDBK, MSBKSD). These seascapes included variable coverages of soft and hard bottoms, which usually have been related to enhanced fish fauna diversity in different deep-sea regions (Auster et al., 2005; Ross and Quattrini, 2007; Perez et al., 2018).

In addition, spatial variability in fish and cephalopod fauna observations were greatly influenced by two sites, which contained exceptionally high aggregations of two dominant morid cods: *Laemonema* sp. at transect 11, the shallowest ‘gravely’ site explored (397 m) and *Guttigadus* sp. at transect 14, a site of intermediate depth (1020 m) covered mostly by soft sediments. The former contributed the most to the overall beta diversity calculated for all video transects, due to a species poor and distinct fauna, associated to a unique depth and seascape. Fish and large mobile invertebrate species may aggregate on seamount summits for feeding (see above) and reproductive purposes (Genin, 2004; Clarke, 2007; Morato and Clark, 2007; Porteiro and Sutton, 2007; Rogers, 2018). It is possible that a few opportunistic species may respond more quickly to feeding opportunities and become dominant in shallower plateaus (Levin et al., 2001; Victorero et al., 2018). This can be the case of *Laemonema* sp. and *Guttigadus* sp. at the Tablemount seamount plateau, but also of the toadfish *Chaunax pictus*, and the macrurid *Malacocephalus okamurai*, most abundant and dominant species at the shallowest 600 m-deep areas of the Rio Grande Rise plateau (Perez et al., 2018). None of these species (or congenerics) have been previously classified as 'seamount-aggregating" species (*sensu* Morato and Clark, 2007) but the reported distribution and abundance patterns on single seamounts imply that specific habitat configurations, not only lower depths (and perhaps reproductive season), may drive these aggregations.

Nesis (1993) and Clarke (2007) proposed that cephalopods may have distinct ecological associations with seamount habitats. *Moroteuthopsis ingens* belongs to a non-vertical migratory bathypelagic group (Nesis group 3) living near or over the flanks, potentially in regular contact with the seafloor, which would justify the scales covering the mantle (Clarke, 2007). In Shannon seamount a group of *M. ingens* were observed 'actively' attacking the ROV and sitting on the mostly sedimented seafloor. According to Nesis (1993) 'many species' of Histioteuthis are vertical diel migrators that can be advected by currents over the seamounts at night descending to the bottom in daylight (Group 4), and *O.* cf. *agassizii* is a lower bathyal species that live on or over the seafloor (Group 1c). This species was regarded as an indicator of a South Africa lower slope cephalopod assemblage (700–900 m) (Roeleveld et al., 1992) here also reported in adjacent oceanic seamounts.

The Discovery Rise seamount exploration in 2019 supplemented an international effort started in 2015 to map and describe benthic habitats in fishable areas of SE Atlantic seamounts, both within and outside closure areas established under the SEAFO management regime (Bergstad et al., 2019a and b). Seafloor mapping and description of benthic fauna diversity in selected areas were major objectives of this initiative addressed by Bull-Mortensen et al. (2019 and subsequent publications). In the present study general habitat configuration of some seamount areas was described and related with the observed patterns of diversity of fishes and cephalopods, adding-on to these studies and providing baseline information in contribution to the existing knowledge on the ecology of South Atlantic deep seamounts and ridges (e.g. Perez et al., 2018; Perez et al., 2020). Comprehensive analyses of biodiversity patterns and their main ecological drivers still depend on increased sampling efforts in such remote areas of the Atlantic.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Jose Angel Alvarez Perez reports travel was provided by Food and Agriculture Organization of the United Nations. Roberto Sarralde Vizuete reports travel was provided by Food and Agriculture Organization of the United Nations. Fransico Ramil reports travel was provided by Food and Agriculture Organization of the United Nations. Sara Castillo reports travel was provided by Food and Agriculture Organization of the United Nations. Jose Angel Alvarez Perez reports a relationship with Universidade do Vale do Itajaí that includes: employment. Francisco Ramil reports a relationship with University of Vigo that includes: employment. Roberto Sarralde Vizuete reports a relationship with Instituto Español de Oceanografía that includes: employment. Sara Castillo reports a relationship with University of Vigo that includes: funding grants.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.dsr.2022.103849.

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