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Benthopelagic megafauna assemblages of the Rio Grande Rise (SW Atlantic)

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ABSTRACT

The Rio Grande Rise (RGR) is a large and geomorphologically complex structure of the deep SW Atlantic Ocean. In 2013, the 600 – 1200 m deep plateau of the most prominent topographic component of the RGR (named Alpha) was explored during two dives of the manned submersible Shinkai 6500 (30°22′15″S – 36°02′02″W and 31°05′58″S – 34°02′40″W). Video profiles recorded during these dives were analyzed for description of benthopelagic megafauna (fish and crustaceans) assemblages, and quantitative assessment of structuring factors (depth, topography and habitat types). Fishes represented over 92% (462) of all benthopelagic megafauna, divided into 11 orders and 17 families. Over half of fish records were Macrouridae, Synaphobranchidae and Chaunacidae. Megafauna abundance varied at different spatial scales, being higher in shallower habitats (~600 m) dominated by branched suspension feeders (mostly sponges and cnidarians). Beta-diversity and community structure were related to habitat diversity. Because the RGR is vast and may comprise numerous distinctive habitats associated with depth, topography and water mass dynamics, fauna diversity may be high and patchy.

1. Introduction

Biodiversity patterns and ecological processes of seamounts, ridges and other topographic features of the deep ocean have been increasingly reported worldwide (Schlacher et al., 2010; Ramirez-Llodra et al., 2010) but some major geographic gaps exist. One of them is the SW and tropical Atlantic where only a few seamounts and ridges (e.g. around St. Peter's and St. Paul's islets and the Vitoria-Trindade seamount chain) have been studied (Lavrado and Ignacio, 2006; O'Hara et al., 2010; Pinheiro et al., 2015; Nunes et al., 2016). Elsewhere in the SW Atlantic the knowledge of the deep-sea fauna is generally poor (Clark et al., 2010a; Perez et al., 2012). Recently, however, perspectives of deep-sea mineral exploration have motivated studies on the biodiversity of a prominent geological structure known as the Rio Grande Rise (RGR) (Perez et al., 2012; Kitazato et al., 2017; Hajdu et al., 2017; Cardoso et al., 2017).

This massive structure extends for nearly 480,000 km^2, halfway between the South American continental margin and the Mid-Atlantic ridge, comprising three contiguous areas that elevate 1.5 – 3.5 km above the seafloor and a complex of surrounding seamounts. Its geological origin is associated with intense basalt flow produced by volcanism at the Mid-Atlantic ridge 89–78 million years ago (O'Connor and Duncan, 1990; Ussami et al., 2012). As the South Atlantic expanded, the basaltic plateau was separated and spread between South America and Africa, forming two "sister" topographic features, the Walvis Ridge and the Rio Grande Rise. Subsequent geological events shaped the RGR to its present geomorphology and substrate type configuration (Fig. 1), including: thermal subsidence, new volcanism in the Eocene Period (30–50 ma) that raised again the structures above sea level, erosion and shallow water sedimentation, and new subsidence to current depths (Ussami et al., 2012).

Throughout their geological formation, the RGR and Walvis Ridge have affected circulation patterns of the deep-water masses of the Atlantic, the North Atlantic Deep Water and the Antarctic Bottom Water (Morozov et al., 2010; Pérez-Días and Eagles, 2017), and may have had an important role in deep-sea faunal connectivity (Perez et al., 2012). Biological data on the RGR, however, has been historically scarce and limited to ichthyological reports produced during Russian fishing explorations in the 1960s through 1980s (reviewed by Clark et al., 2007 and Perez et al., 2012). These reports highlighted faunal similarities between the RGR and the Walvis Ridge, mostly associated with the dominance of subtropical-temperate species that occur circumglobally in the southern hemisphere (Parin et al., 1995). In recent years, however, the need to improve the understanding on biological and

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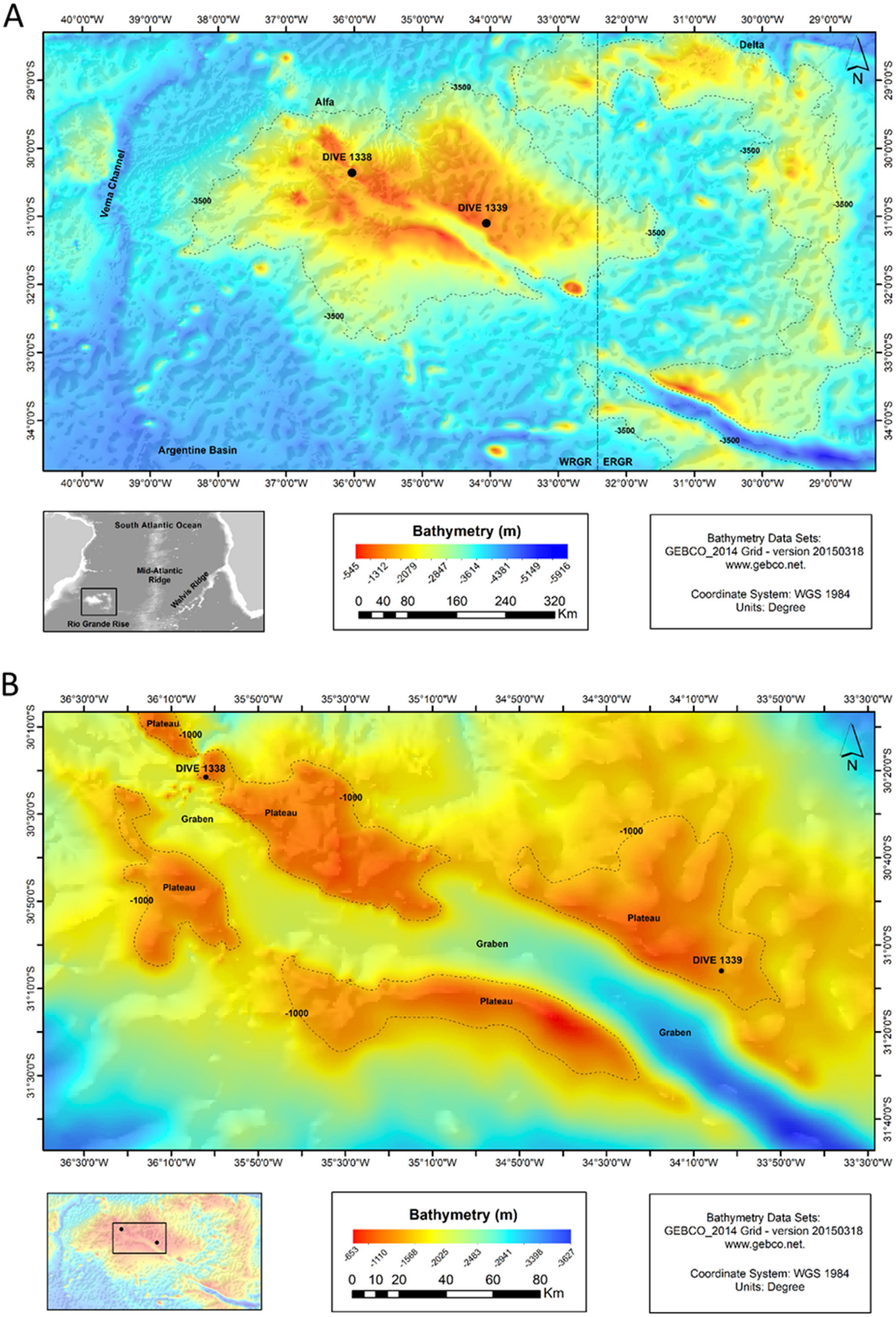

Fig. 1. Rio Grande Rise bathymetry map with location of two dives conducted by the submersible Shinkai 6500 in 2013 during the 'Iatá- Piúna' expedition (1338 and 1339). (A) General view of Alpha, (B) detail of Alpha's plateau. WRGR, Western Rio Grande Rise; ERGR, Eastern Rio Grande Rise.

ecological patterns of the RGR has become critical as exploration of Cobalt-rich Ferromanganese crusts in the area will increase in the near future (Hein et al., 2013) and will demand substantial ecological baseline knowledge (ISA, 2007; SPC, 2013).

Despite the outstanding differences from typical seamounts in terms of origin, geomorphology and size (Wessel, 2007), the main shallows that form the RGR may likewise (a) expose extensive benthic environments to important depth-correlated gradients (e.g. temperature, dissolved oxygen, POC flux; Speer and Zenk, 1993); (b) interpose deep oceanic flow, amplifying currents around their flanks and forming local uplifting circulation regimes (Murray and Reason, 1999; White et al., 2007); and (c) maintain environmental conditions that favor the incidence of hard-substrate habitats and select for distinctive megafauna assemblages, dominated by a variety of benthic suspension feeders (e.g. cold-water corals and sponges) and associated fauna (Samadi et al., 2007; Rogers et al., 2007 and others). In that regard, these shallows might well function as exceptionally large seamounts (or ridges) and justify the consideration of structural and functional properties of seamounts as a conceptual background against which RGR ecological data can be compared.

These ecological properties have been reviewed by Schlacher et al. (2010) in light of accumulating scientific evidence, which often failed to support the validity of most ‘paradigms’ previously established about seamounts as being hotspots of biodiversity and endemicity, isolated from other deep habitats and highly productive in comparison with the surrounding ocean (Rowden et al., 2010). Alternatively they highlighted the importance of expanding seamount studies in the sense of better representing their size and habitat diversity, and the full variety of conditions they may be exposed to including factors related to latitude, distance from continental margins, surface productivity patterns, deep current regimes and others (Stocks and Hart, 2007; Schlacher et al., 2010). Also considerable habitat and environmental conditions variability may exist within the area of a single seamount potentially increasing heterogeneity in the spatial structure of biological communities. This heterogeneity, however, has been little addressed in most seamount studies and remains a knowledge gap (Stocks and Hart, 2007; McClain et al., 2010. Rowden et al., 2010). The RGR not only lies in a particularly understudied suptropical area of the world ocean, but is also exceptionally large and geomorphologically complex (Geological Survey of Brazil, unpublished data), where habitat diversity may be a critical driver of biodiversity and community structure.

In 2013 the RGR was selected among the targets of the ‘Iatá-Piúna’ expedition proposed to explore deep (and extreme) environments of the SW Atlantic with the manned submersible Shinkai 6500 (Kitazato et al., 2017). Extensive video recording produced during two dives on selected sites of the summit of the RGR allowed unprecedented observations and quantification of habitats and megafauna diversity (Hajdu et al., 2017; Cardoso et al., 2017; Mastella, 2017). Fish and large, highly mobile, crustaceans were conspicuous components of recorded megafauna (here they are jointly termed ‘benthopelagic megafauna’). This study documents spatial, depth and habitat-specific variation of their assemblage structure and discusses it in the light of current concepts of seamount ecology.

2. Methods

The geomorphology of the Rio Grande Rise can be divided into an eastern and a western unit (Gamboa and Rabinowitz, 1984). The latter, here referred to as ‘Alpha’ (following the denomination currently used by the Geological Survey of Brazil - CPRM), is the largest plateau (~140,000 km^2 above the 4000 m isobath) characterized by gentle slopes, a flat 580 – 700 m deep summit and a conspicuous 300 km-long, 40 km-wide and 1.2 km deep trough (‘*graben*’) that crosses the structure's surface in a NW-SE direction (Fig. 1). The summit of Alpha was one of the targets of the ‘Iata-Piuna’ expedition in the SW Atlantic which included two dives of the submersible Shinkai 6500; one (Dive 1338) conducted on April 30 and the second (Dive 1339) on May 2, 2013.

Dive 1338 (30°22′15″S; 36°02′02″W) and Dive 1339 (31°05′58″S; 34°02′40″W) explored the northwestern and southeastern sectors of Alpha's summit, respectively (Fig. 1). Both dives involved approximately four hours of activities near the seafloor, including photo/video recording, geological and biological sampling. Except for one shrimp and one crab species (*Nematocarcinus parvus* and *Chaceon sanctaehelenae*, respectively), large mobile benthic and benthopelagic organisms (mostly fish) could not be captured by the submersible's sampling devices (e.g. slurp gun, manipulators) and therefore all records derive from the analysis of the high definition video (and photo) footage.

Shinkai 6500 operated two HD-TV color video cameras, both positioned at the bow, 1.7 m above the vehicle's bottom (Nakajima et al., 2014). Camera 1 angled obliquely 40° towards the seafloor and recorded continuously a fixed area ahead the bow of the submersible (horizontal aperture = 90°, vertical aperture = 57°). Footage produced by this camera was used for megafauna quantitative analysis. Camera 2 was mobile (pan – tilt) and was used for detailed observations and qualitative analysis of habitat features and megafauna species. Videos contained continuous information of date/time, depth (and altitude in meters) and the vehicle's heading (in degrees). Horizontal position (latitude, longitude) was estimated by SSBL (Super Short Base Line) method which required a transponder mounted on the submersible and an array of transducers on the hull of the RV Yokosuka. In this method the position is estimated by both phase lag, measured from angles of received sound waves, and distance, calculated from their travelling period.

Camera 1 video analysis initiated at the point of landing on the seafloor and included (a) habitat description and (b) benthopelagic megafauna recording. The first process involved recording the substrate type and coverage in 2-min segments or whenever the habitat structure changed (see below). In a subsequent procedure, all encounters with mobile megafauna organisms were recorded, including the number of organisms, time, depth and the presence (in the same image field) of benthic suspension feeders. During this procedure these organisms were classified in higher taxa (Class, Orders) and “morphotypes”, whose consistency were double checked by repeating the analyses of videos produced by both camera 1 and 2. When no morphotypes could be confidently assigned to a given organism after these repeated analysis, it accounted for higher taxa quantification only (e.g. ‘benthopelagic megafauna’, ‘fish’, ‘crustacean’). Some morphotype identification to family, genus and species level was possible through collaboration with deep sea fish and crustacean taxonomists.

Records of latitude and longitude were transformed into UTM (Universe Transverse Mercator) and used to estimate the linear distance covered by the submersible. In the videos, “moving ahead” time intervals were delimited and only these intervals were considered for megafauna quantitative analysis. Because observation opportunities are far more reliable in images of plane surfaces, quantitative data extracted from the steep ‘graben wall’ habitat (see below) were not considered comparable to the ones obtained in other habitats and therefore excluded from quantitative analysis.

2.1. Characterization of habitats and definition of depth strata

Seafloor characteristics were described along the video transect according to geomorphology, slope, substratum textures (e.g. bedrock, mud, mixed substrate) and “modifying” elements (e.g. currents, biological communities, sedimentation), following the classification system proposed by Greene et al. (1999) and Greene et al. (2007). Habitats were defined when a particular combination of these features were observed continuously along the dive transect. Habitats were delimited when these features changed abruptly (e.g. for more than 10 s of observations) characterizing the beginning of a new habitat. Identified habitats were also tentatively classified using the EUNIS classification system (www.eunis.eea.europa.eu).

Combined, both dives explored a depth range of 561 m (1233–672 m) which was divided into three strata of similar amplitude: 600 – 800 m, 800–1000 m, 1000–1200 m. These strata and the above-described habitats were defined as effect factors, and explored as hypothetic drivers of benthopelagic megafauna abundance, diversity and assemblage structure.

2.2. Data analysis

A descriptive analysis of benthopelagic megafauna diversity involved, initially, the estimation of morphotype richness (S) in each dive transect and habitat. That process involved the construction of morphotype accumulation curves for each transect and habitat, using ‘observation time’ as a measure of sampling effort. To examine how morphotype composition changed across different habitats along the submersible's track (morphotype ‘turnover’), Bray-Curtis similarities were calculated on presence/absence data, which measured change in composition rather than change in abundance of morphotypes (McClain et al., 2010). Shannon's diversity index (H’) and Pielou's evenness (J’) were calculated for each dive and habitat (except GW) considering the total number of individuals of each morphotype counted during “moving ahead” time intervals.

The following quantitative analysis involved sectioning the video profiles in 80 m-long segments where morphotypes could be identified. From the 61 segments available in total, 37 segments (~50%) were selected through a random draw. This draw was conducted separately for each habitat, except SCR (Dive 1338) where there were only three segments available, all of them included in the analysis (Table 1). The random selection of segments was conducted twice, one for abundance and another for diversity analysis. That was necessary because some of the 80 m segments had no morphotypes differentiated (only overall megafauna abundance) and these could not be included in the diversity (community) analysis (see below).

In both cases, the response variable was defined as the number or organisms counted within 80 m of linear observation. The choice of estimating densities of total megafauna or specific morphotypes was considered but overruled, because dive transects lacked regular/ constant parameters (e.g. linear tracks, constant altitude and speed), as required for sound estimates of the area covered by continuous video images (e.g. Trenkel et al., 2004a, 2004b).

Variability of all benthopelagic organisms and fish abundance was tested for the effect of dive sites and habitats (depth strata was not tested because Dive 1339 had only one stratum). Because habitats were not equally represented in each dive, an Analysis of Variance was performed where factor “habitat” was nested in factor “dive” (Zar, 2010). This implied defining two null hypothesis ($\alpha = 0.05$); (1) H_0: benthopelagic fauna (or only fish) abundance did not differ between dive sites, and (2) H_0: benthopelagic fauna (or only fish) abundance did not differ among habitats within each dive site. Morphotype abundance data was log-transformed to achieve normality requirements.

Diversity patterns were explored using community analysis techniques (Clarke and Warwick, 2001). A resemblance matrix was initially built, where pairwise similarities of morphotype composition of all 37 segments were expressed by the Bray-Curtis index calculated on root-transformed values of morphotype abundance. Analysis of Similarities (ANOSIM) was then applied to test for the effect of dive sites, habitats and depth strata in morphotype composition. Similar to the abundance analysis, factors ‘habitats’ and ‘depth strata’ were initially nested to factor ‘dive site’ (2-way nested ANOSIM). Because the effect of ‘dive sites’ was not found to be significant, all samples were pooled and one-way ANOSIM designs were performed separately for the effect of ‘habitats’ and ‘depth strata’, followed by pairwise tests (Clarke and Warwick, 2001). Finally, a Non-metric Multidimensional Scaling (MDS) ordination technique was used to obtain a 2-dimension representation of morphotype composition similarities among all samples.

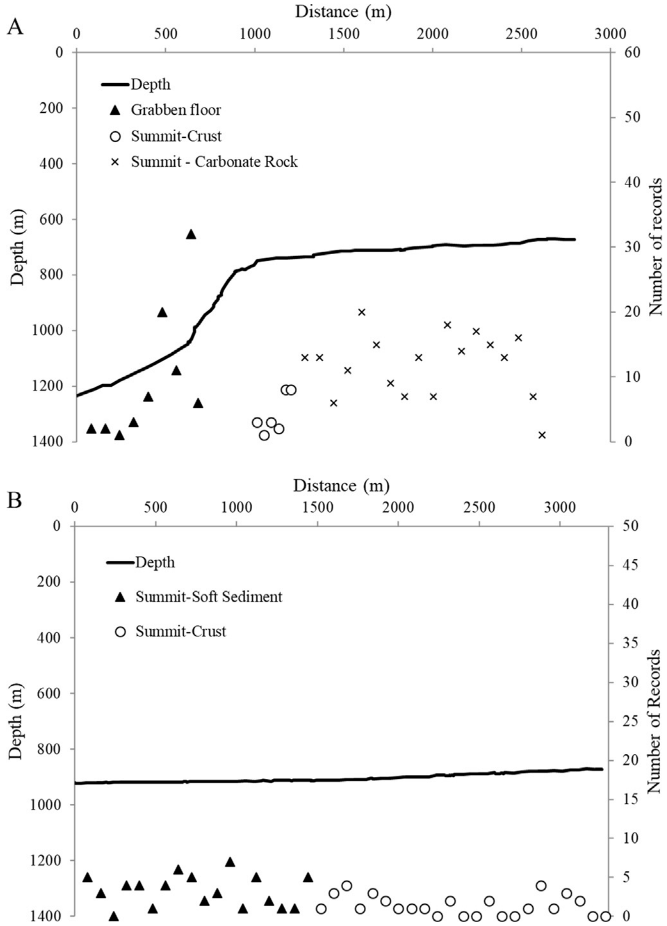

Fig. 2. Depth profiles (dark line) and number of records (symbols) of benthopelagic megafauna (fish and crustaceans) along the transects of two dives conducted in the Rio Grande Rise (SW Atlantic). Each symbol represents the sum of records counted in 80 m-long segments of continuous observation (moving forward). A. Dive 1338; B. Dive 1339.

Table 1
Benthic habitats differentiated along the transects of two deep sea dives conducted by the submersible Shinkai 6500 on the Rio Grande Rise (SW Atlantic). ‘Number of segments’ refers to the number of 80 m-long segments randomly chosen out of all segments available within each habitat (numbers between brackets).

Dive	Habitat		Dive time (min)	Moving ahead time (min)	Depth (m) (Start-End)	Distance (m)	Number of segments
1338	Graben – floor	GB	26.2	26.2	1233–1047	631.8	5 (8)
	Graben – wall	GW	139.6	41.3	1047–749	345.8	–
	Summit – crust	SCR	8.0	8.0	749–735	212.1	3 (3)
	Summit - carbonate rock	SCA	100.0	40.5	735–672	1042.1	10 (17)
1339	Summit - soft sediment	SSD	113.5	43.2	921–911	1388.4	9 (16)
	Summit - Plate-like crust	SCT	180.00	54.0	911–872	1870.9	10 (17)

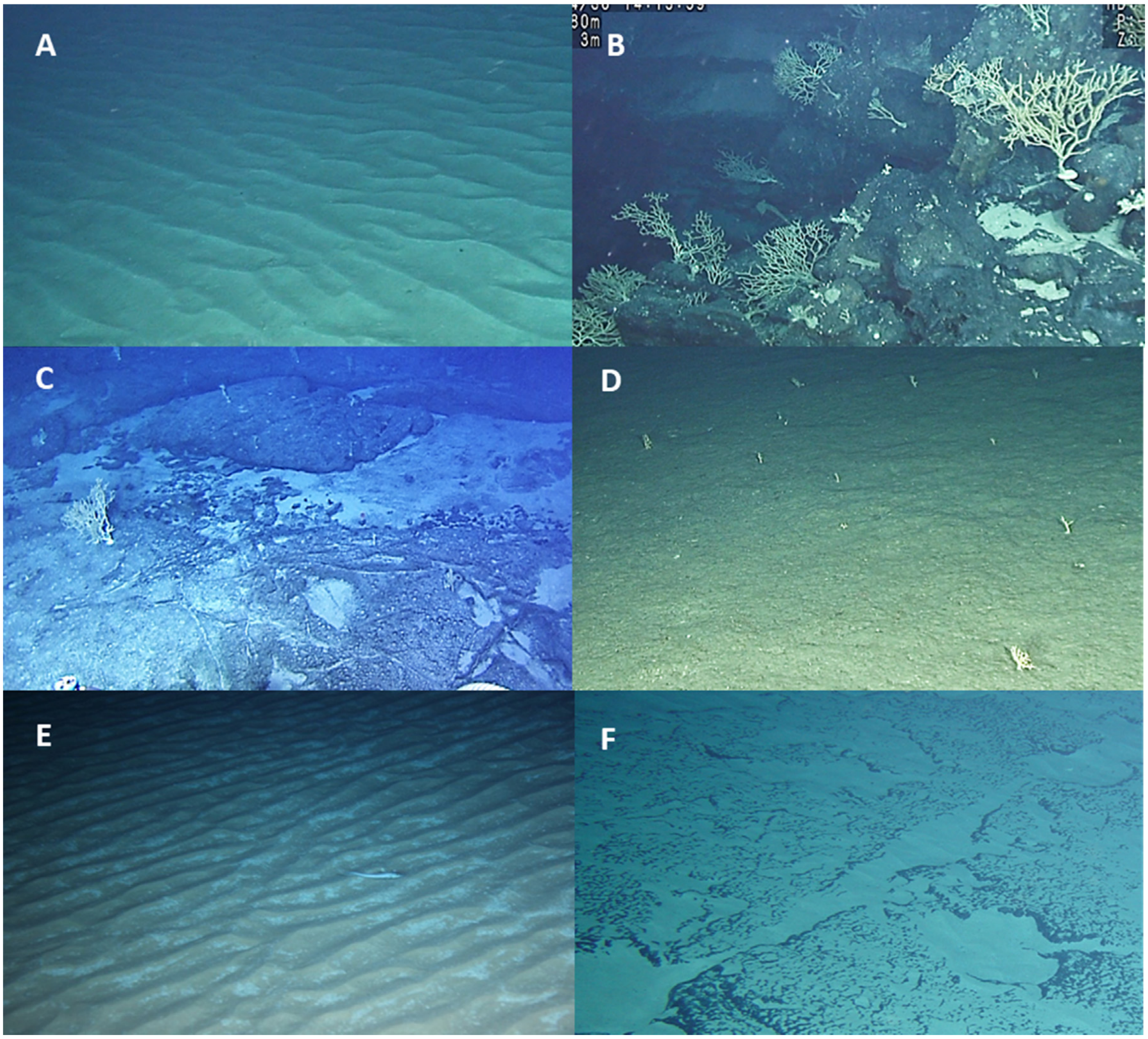

Fig. 3. Benthic habitats of the Rio Grande Rise (SW Atlantic). A – D, Dive 1338; E-F, Dive 1339. A, Graben floor (GB, depth 1233 m); B, Graben wall (GW, depth 880 m), note branched sponges (*Sarostegia oculata*); C, Summit – crust (SCR, depth 740 m); D, Summit – Carbonate Rock (SCA, depth 696 m); E, Summit - soft sediment (SSD, depth 920 m), note macrourid fish; F, Summit - Plate-like crust (SCT, depth 900 m).

3. Results

3.1. Habitat description and classification

Dive 1338 crossed four habitats differentiated by slope, substrate type and dominating benthic organisms (Table 1, Fig. 2, Fig. 3). The submersible started at the bottom of Alpha's graben at 1233 m depth. After a brief exploration of this area, it climbed the steep northern wall of the graben reaching a flat 650 – 750 m deep summit where exploration continued for nearly three hours (Fig. 3A-D). Biogenic sediments (mostly foraminifera and pteropod ooze) were present in three habitats. These sediments occurred (a) as a thick layer covering the entire scene and often with regular ripple marks (at the 'graben floor', GB, Fig. 3A), (b) thinly coating outcrops or filling crevices (mainly at the 'graben wall', GW, Fig. 3B), and (c) forming large pools amidst plate-like crusts ('summit – crust', SCR, Fig. 3C). The last and longest explored habitat ('Summit - carbonate rock', SCA) was flat, deprived of sediment, apparently exposed to strong current flux and formed by large pavements of carbonate rock (Fig. 3D).

Dive 1339 explored the 921–872 m deep summit of Alpha where two distinct habitats were found (Table 1, Fig. 2, Fig. 3). The first two hours of bottom exploration covered a flat habitat vastly dominated by a layer of soft sediments (of variable thickness) where ripple marks were present but often irregular or 'crossed' ('Summit - soft sediment', SSD, Fig. 3E). Outcrops became increasingly frequent and gradually changed the seascape to one dominated by a mixed hard - soft bottom habitat made up of plate-like crusts intermingled by sediment pools ('Summit - Plate-like crust', SCT, Fig. 3F).

Habitats were classified (Table 2) considering criteria defined for three different spatial scales: 'mesohabitats' (tens of meters to 1 km), 'macrohabitats' (one to 10 m) and 'microhabitats' (centimeters) (Greene et al., 1999, 2007). These criteria differentiated most habitats, except SCR and SCT, which were very similar (Fig. 3C and F). The EUNIS classification system did not provide such spatial scale distinction and therefore all habitats considered fell in the same 'large-scale' categories (e.g. A: Marine Habitats, A6: Deep-sea bed, A6.7: Raised features of the deep-sea bed, A6.72: Seamounts, knolls and banks, A6.722: Summit communities of seamount, knoll or bank within the mesopelagic zone, i.e. interacting with diurnally migrating plankton).

3.2. Abundance

Overall, benthopelagic organisms were more abundantly observed in Dive 1338 (median 12 inds./80 m) than in Dive 1339 (median 2 inds./80 m) (Fig. 4) and this difference was found to be highly significant ($p \leq 0.001$; Table 3). Within each dive, abundance (either of benthopelagic fauna or only fish) was not homogeneous among habitats ($p = 0.02$), and it was particularly high in SCA where 11–16 individuals

Table 2
Description of benthic habitats of the Rio Grande Rise according with the classification system proposed by Greene et al. (1999).

Habitat	Class(Meso – Macrohabitat)	Subclass(Macro- Microhabitats)	Modifiers
GB (Fig. 3A)	Bedform – Sediment waves	● Slope: Sloping (∼16°) ● Texture: Mud (carbonate ooze)	● Undulated surface - Ripples (> 10 cm in amplitude); thick to thin (< 5 cm) sediment layer covering bedrock ● Solitary stone corals (gen. *Caryophyllia*) and other scattered suspension feeders
GW (Fig. 3B)	Scarp - Wall	● Slope: Steeply sloping (∼46°) ● Texture: Rough bedrock surface (igneous)	● Irregular bottom ● Fe-Mn crust cover ● Thin sediment covering or small sediment packs accumulated in cracks and crevices ● Little or no covering of encrusting organisms ● Moderate to large concentrations of hexactinellid sponges (mostly *Sarostegia oculata*), other suspension feeders and associated fauna
SCR (Fig. 3C)	Exposure - outcrops	● Slope: Flat (∼4°) ● Texture: Rough or plate-like bedrock surface mixed with soft sediment	● Irregular bottom, pavements ● Fe-Mn crust cover ● Thin sediment covering (< 1 cm) or large sediment packs (pools) accumulated in spaces between bedrock pavements ● Little or no covering of encrusting organisms ● Moderate concentrations of stone corals, hexactinellid sponges (mostly *Sarostegia oculata*), other suspension feeders and associated fauna
SCA (Fig. 3D)	Flat	● Slope: Flat (∼4°) ● Texture: Smooth bedrock surface	● Regular bottom, pavement ● Carbonate rock ● Influenced by intense current flow; no sediment covering ● Moderate concentration of small hexactinellid sponges, corals and other suspension feeders and associated benthic fauna
SSD (Fig. 3E)	Bedform – Sediment waves	● Slope: Flat (∼0.4°) ● Texture: Mud (carbonate ooze) and sand	● Undulated surface - Ripples (> 10 cm in amplitude); thick to thin (< 5 cm) sediment layer covering bedrock ● Benthic fauna rarely observed
SCT (Fig. 3F)	Exposure - outcrops	● Slope: Flat (∼1°) ● Texture: Plate-like bedrock mixed with soft sediment	● Irregular bottom, pavements, boulders ● Fe-Mn crust cover ● Dusting sediment cover (< 1 cm) or large sediment packs (pools) accumulated in spaces between bedrock pavements ● Little or no covering of encrusting organisms ● Sparse concentrations of corals and hexactinellid sponges

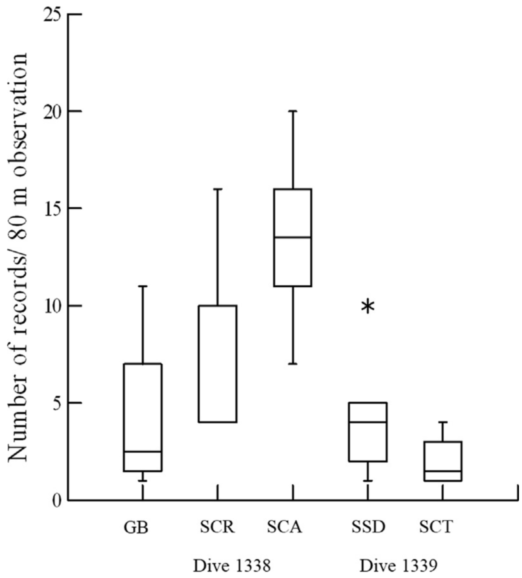

Fig. 4. Relative abundance of benthopelagic megafauna (fish and crustaceans) observed during two deep sea dives (1338, 1339) conducted on the Rio Grande Rise (SW Atlantic). Box plot represent distribution of the number of observed organisms in 80 m segments randomly sampled from each habitat (GB, Graben floor; SCR, summit-crust; SCA, summit carbonate rock; SSD, summit – soft sediment; SCT, summit plate-like crust). Horizontal lines of the boxes represent 75 (upper), median (middle) and 25 (lower) percentiles (box = interquartile range). Vertical bars represent data within 1.5 × the interquartile range. Asterisk is an outlier.

Table 3
Two-Way (Nested) ANOVA testing the hypothesis of no significant difference in the Log-transformed abundance of benthopelagic megafauna (fish and crustaceans) observed in the video profiles of two deep sea dives conducted on the Rio Grande Rise (SW Atlantic), and of habitats differentiated in each dive.

Variable: Log of Number of benthopelagic organisms in 80 m observation					
Factor: Dive sites, Habitats (nested in Dive sites)					
Source	SS	df	MS	F-ratio	p
DIVE	11.147	1	11.147	20.478	< 0.001
HABITATS(DIVE)	5.727	3	1.109	3.507	0.026
Error	17.419	32	0.544		
Variable: Log of Number of benthopelagic fish in 80 m observation					
Factor: Dive sites, Habitats (nested in Dive sites)					
Source	SS	df	MS	F-ratio	p
DIVE	10.207	1	10.207	20.362	< 0.001
HABITATS(DIVE)	5.604	3	1.868	3.726	0.021
Error	15.540	31	0.501		

Table 4
Diversity indices of benthopelagic megafauna (fish and crustaceans) observed in video profiles obtained during two deep sea dives conducted on the Rio Grande Rise (SW Atlantic). In the bottom line (Habitat features) numbers represent the proportion of megafauna records where suspension feeders were also visible.

	1338					1339		
	GB	GW	SCR	SCA	All	SSD	SCT	All
Diversity								
Richness (S)	11	13	6	10	28	12	12	17
Diversity (H')	2.11	–	1.43	1.45	2.13	2.15	2.21	2.38
Evenness (J')	0.88	–	0.80	0.63	0.67	0.86	0.89	0.84
Habitat features								
Records with Susp. Feeders	0.19	0.86	0.76	0.90	0.73	0.03	0.19	0.10

Table 5

Classification of benthopelagic megafauna taxa observed in video profiles obtained during two deep sea dives conducted on the Rio Grande Rise (SW Atlantic).

Class	Order	Family	Morphotype	Taxa
Elasmobranchii	Squaliformes	Etmopteridae	Etmo1	*Centroscyllium* sp.
			Etmo2	Unid.
Actinopterygii	Notacanthiformes	Halosauridae	Hallo1	*Aldrovandia* sp.
			Hallo2	*Halosaurus* sp.
	Anguilliformes	Nettastomatidae	Netta1	*Nettastoma* sp.
		Synaphobranchidae	Angui2	Unid.
			Synap3	*Synaphobranchus* sp.
			Synap4	*Synaphobranchus* sp.
			Synap5	*Synaphobranchus* sp.
			Synap6	*Synaphobranchus* sp.
			Synap7	*Synaphobranchus* sp.
	Osmeriformes	Alepocephalidae	Alepo1	Unid.
	Stomiiformes	Sternoptychidae	Sterno1	Unid.
	Aulopiformes	Ipnopidae	Ipno1	*Bathypterois* sp.
	Gadiformes	Moridae	Mori1	*Lepidion* sp.
		Macrouridae	Macr1	*Malacocephalus okamurai*
			Macr2	*Gadomus* sp.
			Macr3	*Coelorinchus* sp.
			Macr4	Unid.
			Macr5	Unid.
			Macr6	Unid.
		Lotidae	Loti1	*Gaidropsarus* sp.
	Ophidiiformes	Ophidiidae	Ophi1	*Spectrunculus* sp.
	Lophiiformes	Chaunacidae	Chau1	*Chaunax* sp.
	Beryciformes	Trachichthyidae	Trac1	*Hoplostethus* sp.
		Berycidae	Bery1	*Beryx splendens*
	Zeiformes	Oreosomatidae	Oreo1	*Oreosoma* cf. *atlanticum*
	Scorpaeniformes	Sebastidae	Seba1	*Helicolenus* sp.
			Seba2	*Trachyscorpia* sp.
		Peristediidae	Peri1	Unid.
Malacostraca	Decapoda	Palinuridae	Paln1	*Projasus parkeri*
		Geryonidae	Chac1	*Chaceon sanctaehelenae*
		Lithodidae	Lith1	*Neolithodes* sp.
		Nematocarcinidae	Nema1	*Nematocarcinus parvus*
		Polychelidae	Poly1	Unid.
	'Shrimp-like'	Unid.	Shrp1	Unid
		Unid.	Shrp2	Unid.
		Unid.	Shrp3	Unid.

per 80 m segments were encountered (Fig. 4). Considerable variation was observed, however, at smaller spatial scales in both dives (Fig. 2). In dive 1338, records of benthopelagic fauna were frequently associated with the presence of suspension feeders and habitats dominated by hard substrates (with limited presence of sediments) (73% of records) (Table 4). In dive 1339, that association was found in only 10% of fish/crustacean records.

3.3. Diversity

A total of 38 morphotypes was differentiated in the video analysis, 30 fishes and 8 crustaceans (Table 5). The video profile of dive 1338 accumulated a higher number of morphotypes during the observation time (29) than dive 1339 (17) (Fig. 5). However, this pattern was mainly a result of the higher number of habitats explored in the former dive, and the elevated morphotype turnover (see below), than the effect of increased diversity in any particular habitat. In fact, all habitats explored for more than one hour exhibited similar morphotype accumulation curves (Fig. 5).

When morphotype abundance was taken into consideration no substantial difference in diversity (H') between dives were evident (Table 4). Habitat SCR and SCA were the least diverse (H' = 1.4). SCA was also the most uneven (J' = 0.6) as a result of the effect of two dominant fishes, *Chaunax* and *Malacocephalus* (see below).

3.4. Assemblage structure

Fish represented over 92% (n = 462) of all benthopelagic megafauna recorded during the two deep sea dives in the Rio Grande Rise (total 501). Nearly 10% of fish records could not be assigned to any lower taxa. The remaining records were divided into 11 orders and 17 families (Table 5). Gadiformes and Anguilliformes aggregated nearly half of fish records in both dives, whereas Lophiiformes was also numerically important in dive 1338 (Fig. 6). The latter comprised one abundant morphotype, a toadfish, genus *Chaunax*. Rattails (Family Macrouridae) comprised most gadiform morphotypes, three of them particularly common in the video profiles: *Malacocephalus okamurai* (Macr1), *Gadomus* sp. (Macr2) and *Coelorinchus* sp. (Macr3) (Table 5). Most eels were identified in the Genus *Synaphobranchus* and at least two species seem to be present, *S. affinis* and *S. calvus*. Common seamount fish species were also frequently recorded, including alfonsinos (*Beryx splendens*), oreos (*Oreosoma cf. atlanticum*) and slickheads (Alepocephalidae). Chondrichthyes was represented by two small sharks of the Family Etmopteridae, one of them identified in the Genus *Centroscyllium*.

Large mobile crustaceans were much less common (or less visible) in the analyzed videos, comprising 7.2% of all megafauna records. Two swimming shrimp morphotypes were relatively frequent in the deepest areas (GB) explored by dive 1338 (Shrp1, Shrp2), but their identification even to order level was uncertain (Table 5). All other morphotypes were large decapods including commercial species *Chaceon sanctaehelenae* (Chac1) and *Projasus parkeri* (Paln1). *Nematocarcinus*(Nema1) was observed in association with large sponges and fly-trap anemonae, and was effectively sampled by the vehicle's slurp gun.

Approximately 2/3 of the 38 morphotypes were observed in one dive only and half of them only seen in one particular habitat (Table 6). Common occurrences across dive sites and in two or more habitats were limited to 10 and 15 morphotypes, respectively. The macrourid *M.*

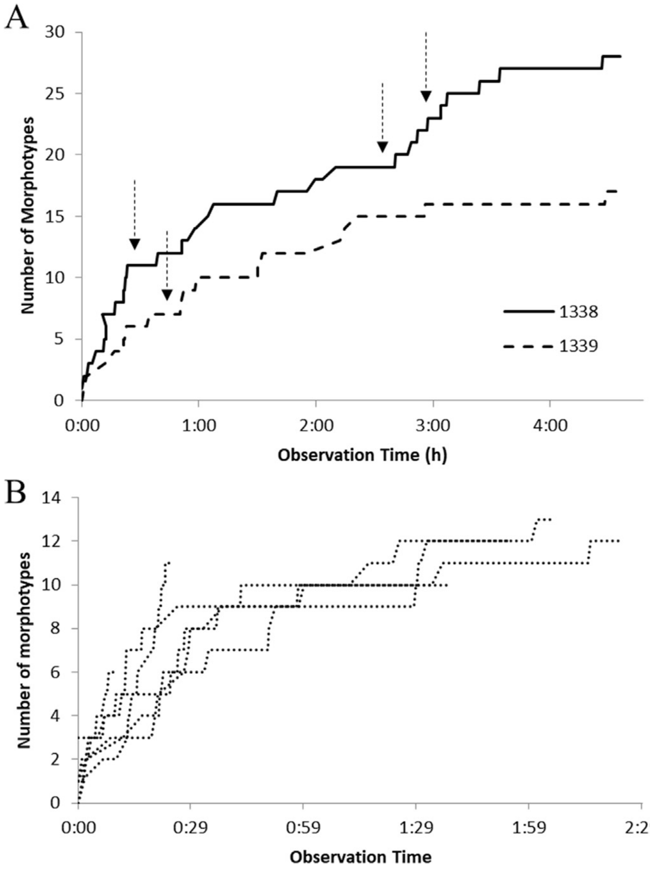

Fig. 5. Benthopelagic fish and crustacean morphotypes accumulation curve during two deep sea dives conducted on the Rio Grande Rise (SW Atlantic). A, Dive 1338 is compared with Dive 1339. Arrows indicate habitat transitions. B, curves represent individual habitats explored in dives 1339 and 1338.

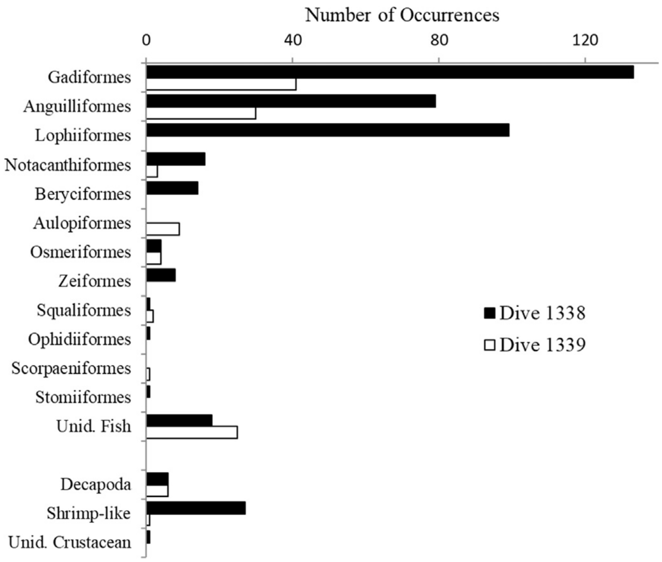

Fig. 6. Number of occurrences of benthopelagic megafauna major groups (mostly Orders) in video profiles derived from two deep sea dives conducted on the Rio Grande Rise (SW Atlantic).

Table 6

Numeric proportion of morphotypes recorded in the video profiles of Dives 1338 and 1339 conducted on the Rio Grande Rise (SW Atlantic). Numbers are percentages of the total number of fish counted within each habitat explored along the dive transects: GB, graben bottom; GW, graben wall; SCR, summit-crust; SCA, summit – carbonate rock; SSD, summit – soft sediment; SCT, summit plate-like crust. The line indicated by the term 'turnover' shows the change (in percentage) in morphotype composition from one habitat to another.

	Dive 1338				Dive 1339	
Morphotype	GB	GW	SCR	SCA	SSD	SCT
Mori1	0.00	0.00	0.00	0.00	0.00	7.14
Peri1	0.00	0.00	0.00	0.00	0.00	3.57
Etmo1	0.00	0.00	0.00	0.00	0.00	7.14
Litho1	0.00	0.00	0.00	0.00	0.00	3.57
Poly1	0.00	0.00	0.00	0.00	2.00	3.57
Nema1	0.00	0.00	0.00	0.00	2.00	3.57
Ipno1	0.00	0.00	0.00	0.00	18.00	0.00
Gery1	0.00	0.00	0.00	0.84	2.00	0.00
Bery1	0.00	0.00	0.00	4.64	0.00	0.00
Synap6	0.00	0.00	0.00	0.42	22.00	25.00
Loti1	0.00	0.00	0.00	1.27	0.00	0.00
Paln1	0.00	0.00	0.00	1.69	0.00	0.00
Netta1	0.00	0.00	0.00	11.81	0.00	0.00
Etmo2	0.00	0.00	4.76	0.00	0.00	0.00
Macr1	0.00	0.00	42.86	37.13	12.00	17.86
Chau1	0.00	1.96	28.57	38.82	0.00	0.00
Macr5	0.00	1.96	4.76	1.27	0.00	0.00
Oreo1	0.00	9.80	14.29	0.00	0.00	0.00
Synap4	0.00	3.92	4.76	0.00	12.00	3.57
Synap5	0.00	50.98	0.00	0.00	0.00	3.57
Macr4	0.00	1.96	0.00	0.00	0.00	0.00
Sterno1	0.00	1.96	0.00	0.00	0.00	0.00
Synap3	0.00	1.96	0.00	0.00	0.00	0.00
Macr6	0.00	5.88	0.00	2.11	0.00	0.00
Alepo1	3.23	3.92	0.00	0.00	8.00	0.00
Hallo1	14.52	3.92	0.00	0.00	2.00	0.00
Angui2	3.23	0.00	0.00	0.00	0.00	0.00
Trach1	4.84	0.00	0.00	0.00	0.00	0.00
Ophi1	1.61	0.00	0.00	0.00	0.00	0.00
Hallo2	4.84	3.93	0.00	0.00	4.00	0.00
Macr3	1.61	0.00	0.00	0.00	14.00	14.29
Macr2	19.35	0.00	0.00	0.00	2.00	7.14
Synap7	19.35	0.00	0.00	0.00	0.00	0.00
Shrp1	12.90	0.00	0.00	0.00	0.00	0.00
Shrp2	14.52	1.96	0.00	0.00	0.00	0.00
Turnover		60.0%	60.0%	62.5%		41.7%

okamurai (Macr1) and one eel (Synap4) were exceptions to this pattern occurring in both dive sites and four different habitats. Overall, habitats were characterized by the occurrence of distinctive groups of morphotypes, with the exception of SCR (Dive 1338) and SSD (Dive 1339) where exclusive morphotypes were rare (Table 6). Morphotype composition changed 60.0 – 62.5% between adjacent habitats (Table 6) in dive 1338, and the most distant habitats (GB – SCA) shared no common species. Habitats in dive 1339 changed in morphotype composition by 41.7%.

Fish and crustacean assemblages morphotype composition did not differ significantly between dive sites (Two-way ANOSIM nested design, $p > 0.5$). Significant variation was found, however, among habitats and depth strata (Table 7). In the former case, pairwise comparisons demonstrated that habitats of Dive 1339 (SSD and SCT) were similar in morphotype composition ($p = 0.195$), and did not differ from habitat SCR in Dive 1338 (SCR x SSD, $p = 0.595$; SCR x SCT, $p = 0.358$). All other habitat comparisons indicated significant differences in morphotype composition (Table 7).

MDS ordination successfully grouped samples in accordance with habitats and depth strata (2-D Stress = 0.04, Fig. 7). Transect segments of Dive 1339 were closely positioned in the 2-D space without a clear differentiation of habitats within this dive. One SCT segment, however, dissociated from this group (far right in the plot). Only one fish was recorded in this segment, *Gadomus* sp. (Macr2), which was only registered in GB segments. Samples of Dive 1338 were distributed in two main groups, one comprising the deep GB samples, and another the shallow SCA samples. The three emerging groups were generally coherent with the three depth strata (Fig. 7).

Table 7
One Way ANOSIM testing the hypothesis of no significant difference in benthopelagic megafauna community composition among habitats and depth strata in two areas of the Rio Grande Rise (SW Atlantic).

FACTOR: Habitats

Global Test: R = 0.530
p = .001

Comparison group	R	Total Permutations	Permutations ≥ R	p
GB x SCR	0.692	56	1	0.018
GB x SCA	0.927	999	1	0.002
GB x SSD	0.553	999	0	0.001
GB x SCT	0.397	792	1	0.001
SCR x SCA	0.761	286	2	0.007
SCR x SSD	−0.049	220	131	0.595
SCR x SCT	0.060	120	43	0.358
SCA x SSD	0.720	999	0	0.001
SCA x SCT	0.713	999	0	0.001
SSD x SCT	0.080	999	194	0.195

FACTOR: Depth Strata
Global Test: R = 0.495
p = .001

Comparison group	R	Total Permutations	Permutations > R	p
(< 800 m) x (800–1000 m)	0.399	999	0	0.001
(< 800 m) x (> 1000 m)	0.955	999	0	0.001
(800–1000 m) x (> 1000 m)	0.429	999	0	0.001

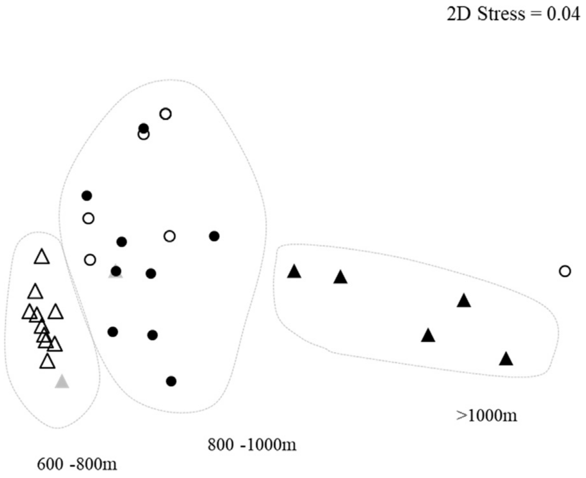

Fig. 7. Ordination (non-metric multidimensional scaling) comparing benthopelagic megafauna assemblage structure in dives 1338 (triangles) and 1339 (circles) on the Rio Grande Rise (SW Atlantic). Habitats defined in each dive are represented by symbols: Graben floor (black triangles); summit-crust/sediment (gray triangles); summit-carbonate rock (white triangles); summit- soft sediment (black circles); summit – crust/sediment (white circles). Dashed lines delimit most samples within three depth strata.

4. Discussion

Habitats and megafauna diversity were documented from deep sea dive observations on the plateau of the largest topographic component of the Rio Grande Rise. Dive trajectories explored summit areas near the edge of the graben scarp whose substrate was generally formed by plate-like crusts and patches of sediment of variable sizes (e.g. SCR and SCT). They also explored areas of the plateau, more distant from the graben, which were shallower (~600 m), formed by carbonate rock pavements, and deeper (~800–900 m), covered by thick sediments, in the northwestern and southeastern extremes of Alpha, respectively. Throughout observations of the video profiles, two main patterns emerged, both relevant to the characterization of the ecology of Alpha: (a) megafauna abundance may vary substantially in different spatial scales, and (b) megafauna community structure may be strongly associated with habitat type, changing rapidly from habitat to habitat.

Benthopelagic megafauna (mostly fish) abundance was higher in shallower areas and habitats where current regimes are presumably more intense, as evidenced by the scarcity of sediments and the recurrent incidence of branched sponges and other benthic suspension feeders. In general, these features characterized the area explored at the northwestern margin of Alpha and, within this area, the habitats of the summit (SCA) and graben edge (SCR) (Hajdu et al., 2017). In contrast, a considerable accumulation of sediments and the low incidence of suspension feeders, observed in the deeper summit of the southeastern area, would suggest a less dynamic environment where fishes were far less abundant (Mastella, 2017). Seamount fish have been principally reported to feed on pelagic prey in the water column, often made available by advection or vertical migrations (Porteiro and Sutton, 2007). Thus, resident seamount fish productivity has been related to imported and retained pelagic productivity, which in principle could explain higher fish abundance on the shallower areas of RGR plateau (~600 m depth).

The association of fish abundance with current flow, on the other hand, is not straightforward (Morato and Clark, 2007; Consalvey et al., 2010) but potentially intermediated by the hypothetical role of suspension feeders in coupling pelagic and benthic productivity (Pitcher and Bulman, 2007). *S. oculata* and other large sponges were dominant suspension feeders forming a ‘sponge garden’ in the explored area of the northwest RGR (Hajdu et al., 2017). *Chaunax* and macrourids were often seen in the vicinity of these sponges, while shrimps (e.g. *Nematocarcinus parvus*), lobsters (e.g. *Projasus parkeri*), eels (e.g. *Nettastoma* and *Synaphobranchus*) and the rockling *Gaidropsarus*, were observed interacting directly with them, probably feeding on small prey and detritus found on the sponge's wall and osculum (Cardoso et al., 2017; Perez et al., unpublished data). Exposition to currents, in association with depth and substrate types, may drive local environmental conditions and have an effect on fish abundance spatial variability on the plateau of the RGR.

Deep-sea sponge concentrations may also enhance diversity of epibenthic megafauna (Beazley et al., 2013) but such an effect was not evidenced in the RGR benthopelagic fauna associations. However, it is important to notice that the SCA habitat exhibited the most uneven morphotype composition, basically due to the observed dominance of *Chaunax* and *Malacocephalus*. If these areas are enriched by the greater proximity with surface waters and a highly energetic current regime, such a habitat could favor a few specialist fish species, as demonstrated for other groups of fauna in the deep sea (Rex and Etter, 2010).

Depth played an important role in characterizing assemblages of benthopelagic fauna of the RGR plateau areas, in accordance with ecological patterns demonstrated for continental margins, mid-ocean ridges and seamounts around the world (Carney, 2005; Leathwick et al., 2006; Bergstad et al., 2008; Lundsten et al., 2009; Anderson et al., 2013). Yet depth alone did not explain the observed community structure variability, and particularly the elevated taxa turnover (beta-diversity), strongly related with habitat heterogeneity. In general, species turnover in the bathyal region (200 – 4000 m) tends to be rapid but continuous (Carney, 2005). Drastic changes, however, may be driven by changes in food supply and sedimentary regime, as determined by strong bottom currents, and major topographic features (Rex and Etter, 2010). These factors essentially defined the different habitats explored along the two dives, whose ecological effects were stronger in the dive 1338 that covered a wider topographic profile and abrupt habitat transitions. Beta-diversity patterns tend to reflect habitat heterogeneity in the deep-sea (Anderson et al., 2013; Rex and Etter, 2010). The RGR may be characterized by a wide diversity of habitats as an outcome of its complex geological history and the associated environmental processes (eg. current regimes, sedimentation, and cobalt crust formation). In that sense it can be hypothesized that such historical process could have established a potential for selecting specialized fish and crustacean assemblages, which may lead to a greater biodiversity and community heterogeneity than that expected for smaller and more regular oceanic seamounts (Stocks and Hart, 2007). A similar hypothesis was proposed to explain the reduced diversity of fish species over seamounts (small with no sediment cover) off New Zealand in relation to adjacent slope areas (large and with both hard bottom and sedimented areas) (Tracey et al., 2010).

Fish diversity was relatively high in the explored areas of the RGR plateau. Assuming that all established morphotypes were individual species, total richness (30 morphotypes – 17 families) observed along a 5.4 km submersible transit length paralleled that reported, for example, in three seamounts in the NE Pacific (36 species – 19 families) explored during 10 – 15 km long dives (Lundsten et al., 2009). However, a series of 30 bottom trawls conducted on Alpha´s plateau (580 – 1830 m) during Russian fishing surveys in 1974, 1988 and 1999 (Parin et al., 1995) recorded a nearly two-fold fish species richness (65 species) distributed in 27 families. Differences between species composition of trawl catches and video observations have been reported elsewhere and generally attributed to fish behavior, sampling gear structure and operation patterns, and environmental conditions (Cailliet et al., 1999; Stoner et al., 2008; McIntyre et al., 2015). However, it is worth noting that families Macrouridae and Synaphobranchidae were among the most diverse in both RGR studies, but not Alepocephalidae, scarcely observed in the video profiles. This, in part, may be explained by differential behavior of fish species and reaction to a moving underwater vehicle, which may oscillate from neutral (no response), avoidance and attraction (Stoner et al., 2008). For example, in slope areas of the Bay of Biscay, Alepocephalids tended to concentrate 2 – 3 m above the seafloor, being mostly undetected by ROV cameras, yet vulnerable to commercial trawl nets, which produced important catches. On the other hand, Synaphobranchid eels were often found to be attracted by the ROV lights and abundantly recorded in video transects (Trenkel et al., 2004a).

Fish assemblages on seamounts are likely to be similar to those recorded from the continental slope, particularly in terms of presence-absence of species (Clark et al., 2010b). On the other hand, important variability in fish community composition has been found between seamounts even on relatively small spatial scales (Tracey et al., 2012). Assessing similarities between fish assemblages from the RGR and the Brazilian continental slope and adjacent seamounts and ridges, particularly the 'sister' Walvis Ridge and the Mid-Atlantic Ridge, seems critical to address fauna connectivity issues, highly relevant in the context of future mineral exploration. Such comparisons require extensive benthopelagic megafauna surveys in these areas, using comparable sampling methods and designs.

5. Conclusion

Megafauna abundance and community structure variability and patterns were related to depth and benthic habitats character and distributions in the plateau of the Rio Grande Rise. Because this topographic feature is large and may comprise many different habitats associated with depth, topography and water mass dynamics, fauna diversity may be high and patchy, as determined by habitat-specialized communities. Topography-induced current flow may be a driver of fauna abundance, in association with an important role of sponges in coupling pelagic and benthic productivity. These are critical elements to be further addressed in extended surveys over Alpha's plateau and other topographic features (e.g. mountain flanks and foot).

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