Estuarine, Coastal and Shelf Science 305 (2024) 108847

Contents lists available at ScienceDirect

Estuarine, Coastal and Shelf Science

journal homepage: www.elsevier.com/locate/ecss

Megahabitats shape fish distribution patterns on the Amazon coast

Alexandre Pires Marceniuk[a,b,1,*], Bruno Eleres Soares[c,1], Rodrigo Antunes Caires[d], Alfredo Carvalho-Filho[e], Ronaldo Barthem[f], Sergio Ricardo Floeter[g], Ricardo de Souza Rosa[a], Alex Garcia Cavalleiro de Macedo Klautau[h], Israel Hidenburgo Aniceto Cintra[i], Matheus Marcos Rotundo[j], Lucas T. Nunes[g,k]

[a] *Programa de Pós-Graduação em Ciências Biológicas, Universidade Federal da Paraíba, Brazil*
[b] *Programa de Pós-Graduacao em Ecologia e Conservação da Universidade Estadual da Paraíba, Brazil*
[c] *Institute of Environmental Change & Society, University of Regina, Canada*
[d] *Laboratório de Diversidade, Ecologia e Distribuição de Peixes, Instituto Oceanográfico da Universidade de São Paulo, Brazil*
[e] *Fish Bizz Ltd, Brazil*
[f] *Museu Paraense Emílio Goeldi, Brazil*
[g] *Marine Macroecology and Biogeography Laboratory, Departamento de Ecologia e Zoologia, Universidade Federal de Santa Catarina, Brazil*
[h] *Centro Nacional de Pesquisa e Conservação da Biodiversidade Marinha do Norte*
[i] *Universidade Federal Rural da Amazônia, Brazil*
[j] *Acervo Zoológico da Universidade Santa Cecília, Brazil*
[k] *Departamento de Biotecnologia, Instituto de Estudos do Mar Almirante Paulo Moreira, Brazil*

ARTICLE INFO

Keywords:
Amazon river
Brazilian north coast
Actinopterygii
Elasmobranchii
Megahabitat

ABSTRACT

The Brazilian North Coast (BNC) encompasses the intersection of multiple oceanographic features such as strong currents, a large continental shelf under the influence of the Amazon River freshwater and sediment outflow, extensive muddy and sand bottom, as well as a mesophotic reef system. As a result, the BNC hosts a diverse fish fauna, consisting of estuarine and freshwater species, including species endemic to the region. These fish species are distributed across a mosaic of megahabitats within the region. Here, we present the first comprehensive effort to understand the distribution patterns of ray-finned fishes and cartilaginous fishes among these different megahabitats. On 1891 samples, we recorded 616 species from 147 families distributed across five distinct megahabitats. The Continental Slope megahabitat had the highest number of families and consisted primarily of pelagic species, indicating its close association with the open sea. The Sand and Mud megahabitats exhibited high species richness and shared similar generalist fish families in terms of habitat use. The Amazon Plume megahabitat was characterized by freshwater and marine euryhaline species, emphasizing the influence of the Amazon River on the BNC's ecological dynamics. The Reef megahabitat had species closely associated with consolidated substrates and shared many species with the Sand megahabitat. This study offers valuable insights into fish species distribution and composition in the BNC, contributing to biodiversity assessments and conservation efforts in the region.

1. Introduction

Understanding species distribution patterns requires knowledge of how environmental features influence their ecology. Species' niche encompasses several biological and environmental dimensions, enabling them to persist and survive in specific spatial and temporal contexts (Hutchinson, 1957). A habitat gathers a series of characteristics that influence the spatial niche from which species obtain resources. Consequently, habitats play a crucial role in shaping local species diversity and composition (Bell et al., 1991). The size of habitats, and therefore their utilization by species, can vary from centimetres to kilometres, depending on the specific combination of biotic and abiotic variables in which species can find the particular resources they need, such as preferred foraging substrates, food, and shelter (Bell et al.,

* Corresponding author. Programa de Pós-Graduação em Ciências Biológicas, Universidade Federal da Paraíba, Brazil.
E-mail address: a_marceniuk@hotmail.com (A.P. Marceniuk).
[1] Equal authorship.

https://doi.org/10.1016/j.ecss.2024.108847
Received 7 September 2023; Received in revised form 11 June 2024; Accepted 13 June 2024
Available online 21 June 2024
0272-7714/

1991). The availability of these resources will determine species occurrence over an ecological/evolutionary time (Bell et al., 1991).

Megahabitat is a classification of habitat that ranges in size from kilometres to tens of kilometres (Greene et al., 1999). The megahabitat in the Amazon River mouth is based on the physical sedimentary structures that define distinct facies of strata formed during at least the last 100 years (Kuehl et al., 1986, 1996). The number of megahabitats varies with the authors, ranging from five (Kuehl et al., 1986), eight (Lavagnino et al., 2020) or nine (Araujo et al., 2021), depending on the area analysed and the grouping techniques applied. These megahabitats vary in several environmental characteristics related to habitat use by fishes, such as salinity (Soares et al., 2021), turbidity (Marceniuk et al., 2023), and substratum (Marceniuk et al., 2019).

The Brazilian North coast stretches over 575.103 km^2 on the northern continental shelf of Brazil, from the Oiapoque River to the Parnaíba River (Ekau and Knoppers, 1999). Within these boundaries, the Amazonian Continental Shelf stands out as the widest among the shelves along the Brazilian continental margin, with depths reaching up to 200 m (Neto et al., 2009). The substantial influx of freshwater and sediment from the Amazon River enables the formation of a plume that influences the offshore salinity over an extensive area of approximately 2 × 106 km^2 (Araujo et al., 2017) and the deposition of shallow and extensive mud in front of the Amazon River mouth (Varona et al., 2019; Molinas et al., 2020), with salinity near the substrate ranging from 0.05 to 36 ppm (Soares et al., 2021; Marceniuk et al., 2023).

This remarkable region, marked by brackish water and muddy coast, is home to distinctive marine ichthyofauna, consisting of species from both the Caribbean and Brazilian provinces, including marine species, as well as freshwater and estuarine species from the Amazon River mouth (Marceniuk et al., 2021). Initially, this region was delimited based on the distribution patterns of the freshwater subfamily Aspredininae (Myers, 1960; Dagosta and Pinna, 2019), and now it is classified in the North Brazil Shelf Large Marine Ecosystem, one of the 66 large marine ecosystems (LMEs) of the world (Isaac and Ferrari, 2017). Some studies recognize this region as a biogeographical barrier for reef fish species from the Great Caribbean and Brazilian Marine biogeographic provinces (Rocha, 2003; Floeter et al., 2008; Araujo et al., 2022).

Here we present the first effort to understand the distribution patterns of Actinopterygii and Elasmobranchii fishes among these different megahabitats on the Brazilian north coast. For this, we ask: Do megahabitats harbour distinct species or family-level compositions? We expect that more specialist species, in terms of habitat use, will be restricted to one or a few megahabitats, while other more generalist species/families will be broadly distributed in the BNC regardless of the megahabitats.

2. Material and methods

2.1. Study area

The Brazilian North Coast (Fig. 1) encompasses a biogeographical area of approximately 575,103 km^2 within the North Brazil Shelf Large Marine Ecosystem, which falls under the jurisdiction of the Brazil Exclusive Economic Zone. This region shares common environmental

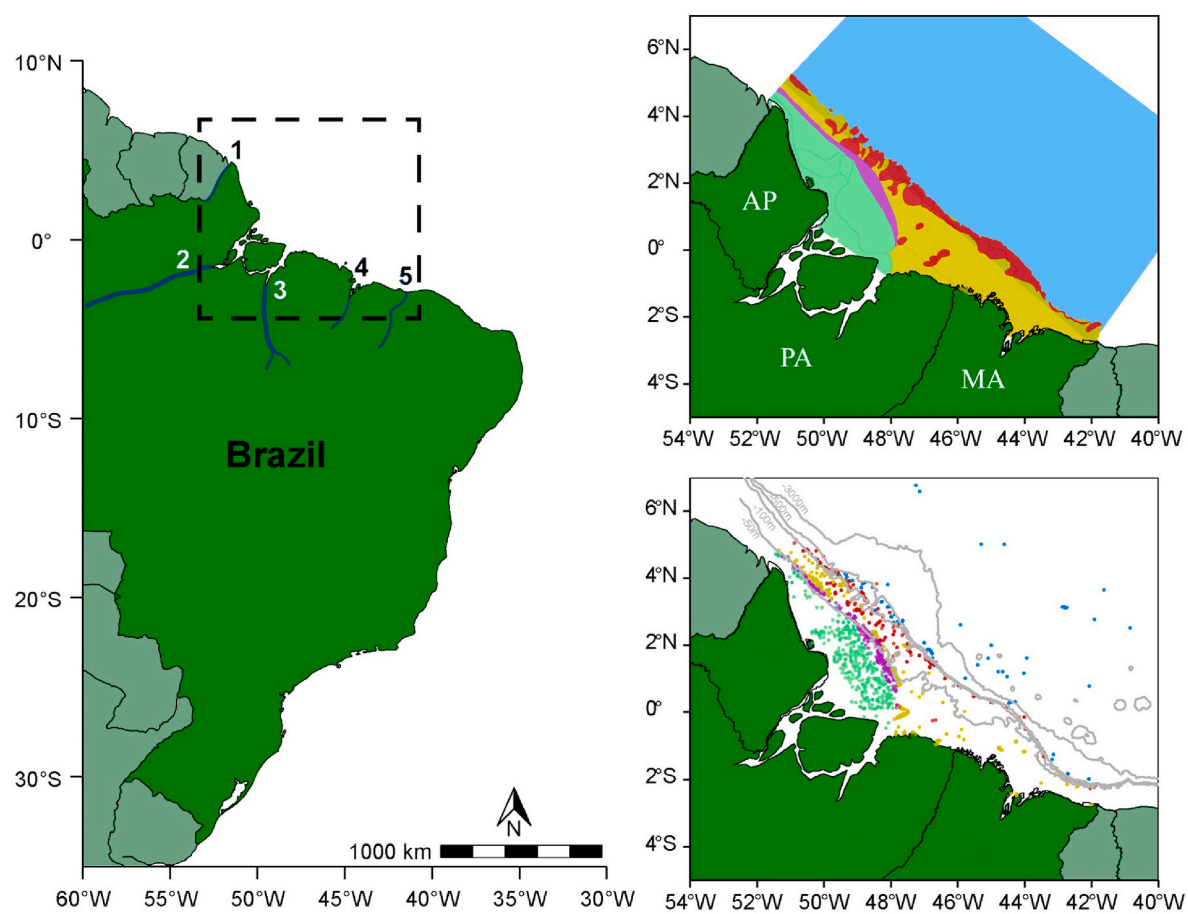

Fig. 1. Brazilian North Coast (dark green) showing the five sampled megahabitats, Amazon Plume (green), Sand (yellow), Mud (purple), Reef and Rhodolith (red) and Continental Slope (blue) (a) and, depiction of records per megahabitat scored in this work (b). AP, Amapá state, MA, Maranhão state and PA, Pará state. 1) Oiapoque river; 2) Amazon river; 3) Pará river (Tocantins and Araguaia rivers); 4) Mearim river; 5) Parnaíba river. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

characteristics with the area influenced by the plumes of the Amazon and Orinoco rivers (Ekau and Knoppers, 1999). The BNC is strongly influenced by the Amazon River, the largest in the world, which discharges between 80,000 and 250,000 m^3/s of freshwater (Curtrin, 1986) and carries up to 1.4 million tons of sediment annually into the ocean (Degen et al., 1991; Meade et al., 1985). River discharge forms a surface plume of low salinity (<35) and high concentration of suspended material and nutrients flows into the Western Tropical North Atlantic and is carried northwestward along the Amazonian Continental Shelf by the North Brazil Current (NBC; Araujo et al., 2017; Varona et al., 2019). The seasonal displacement of the salt wedge along the mouth of the Amazon forms a salinity gradient environment, with the surface under the influence of freshwater and the bottom under the influence of salt water. This mixing zone moves according to the flow of the Amazon River and allows freshwater and marine stenohaline species to occur in the same area at different depths or times of the year (Barthem and Schwassmann, 1994; Jaeger and Nittrouer, 1995; Marceniuk et al., 2023). These environmental conditions influence the oceanographic processes and consequently determine organisms' composition and distribution in the BNC (Goulding et al., 2003; Barthem et al., 2004; Nittrouer and Demaster, 1986; Costa and Figueiredo, 1998).

The coastal environments have high biological productivity with considerable biomass, which is exploited intensively by local fisheries (Isaac and Barthem, 1995, Sanyo Techno Marine, 1998; Isaac and Ferrari, 2017). The pelagic environment is considered oligotrophic, with a relatively shallow eutrophic zone, which is maintained by nutrients derived from the transportation of benthic organic material into shallow coastal sectors, and through the discharge of rivers and estuaries, which enrich the local waters (Teixeira and Gaeta, 1991).

The inner shelf presents isolated deposits of fluvial sand in areas of the Amazon and Pará rivers' mouths. The highly turbid discharge of the Amazon River may extend around 500 km north-western (Curtrin, 1986). The muddy bottom adjacent to the mouth of the Amazon River is composed mainly of fine sand (silt), while the north-western shelf is rich in clay (Kowsman and Costa, 1979; Coutinho, 1996). The Amazon canyon—adjacent to the mouth of the Amazon River—is formed by the accumulation of sediments from the Amazon River and extends beyond the limits of the Exclusive Economic Zone. The sunlight penetration on the mid continental shelf is modulated by an interplay between the Amazon River plume and the more transparent waters of the North Brazil Current (Francini-Filho et al., 2018).

The external portion of the Amazon continental shelf is irregular, with numerous gullies and canyons, and breaks at depths between 80 and 120 m (Barreto and Summerhayes, 1975; Neto et al., 2009; Lavagnino et al., 2020), devoid of sediments. At depths between 60 and 120 m, three carbonate facies can be found, formed by molluscs, benthic foraminifers, and algae typical of shallow coastal zones, in addition to biogenic sands (Oliveira et al., 2004; Oliveira et al., 2007; Barreto and Summerhayes, 1975; Kuehl et al., 1982; Kuehl et al., 1986). On the external shelf, the complex mesophotic reef system of the Great Amazon Reef System (GARS) covers an area of 9500 km^2 between 70 m and 220 m deep (Moura et al., 2016). It is constructed primarily by calcareous algae, sponges, and scleractinian corals (Francini-Filho et al., 2018), presenting a high diversity of organisms, such as algae, rhodolite, sponges, and corals (Cordeiro et al., 2015).

2.2. Database

We gathered occurrence data for Actinopterygii and Elasmobranchii living on depths ranging from 0 to 120m on the continental and insular shelf; and below 120m deep after the continental shelf break. We used four databases in the construction of our database: **(1)** 4173 records from the Japan International Cooperation Agency (JICA), sampled between the years 1996–1997 (Sanyo Techno Marine, 1998); **(2)** 1284 records from the Brazilian National Program for the Assessment of the Sustainable Potential of Natural Resources in the Exclusive Economic Zone (REVIZEE Score-North Program), 1996–2001; **(3)** 2860 records from industrial fisheries monitoring, conducted by the Centro Nacional de Pesquisa e Conservação da Biodiversidade Marinha do Norte (ICMBio/CEPNOR) 2017–2022; **(4)** 2211 records from FishNet database (http://www.fishnet2.net), 1959–2022.

Different fishing gears were used in each monitoring program: paired trawling (Piramutaba industrial fishing CEPNOR and JICA); double-otter-trawl (industrial shrimp CEPNOR and exploratory fishing REVIZEE); red snapper and lobster trap (industrial fishing of red snapper and lobster fisheries CEPNOR and exploratory fishing REVIZEE); fishing hooks (industrial fishing red snapper CEPNOR and exploratory fishing REVIZEE); otter-trawl net for demersal fishes (industrial fishing of *Macrodon ancylodon* CEPNOR); and bottom nets (industrial fishery of lobster, CEPNOR).

2.3. Megahabitats

For this study, we used five megahabitats (Fig. 1), based on the delimitations provided by Araujo et al. (2021). These megahabitats serve as ecological proxies for the historical process of sedimentation and resuspension of seabed layers at the mouth of the Amazon River, which occurred at least 100 years ago (Kuehl et al., 1986, 1996). For example, areas with fine-grained mud bottoms are found in regions heavily influenced by the discharge of the Amazon River, where seasonal shifts of the salt wedge and intense sediment coagulation processes are more prevalent (Nittrouer and Demaster, 1986). Conversely, reef bottoms are characteristic of regions with minimal influence from the Amazon River discharge (Francini-Filho et al., 2018). We grouped some megahabitats due to their similar structural characteristics and/or low sampling effort that could hamper data analysis, such as the megahabitats "Reef and Rhodolith" and "Rhodolith, Bryolith and other carbonate gravel", which were grouped into "Reef and Rhodolith".

1) **Amazon Plume (AMP)** – between 3 and 76m, this area has unconsolidated substratum and is under a strong influence of the seasonal Amazon River discharge, thus displaying a seasonal shift of the salt wedge, high sedimentation, and high-water turbidity. We gathered a total of 4255 records in this megahabitat using a double-otter-trawl net and paired trawling. From the total, 114 were retrieved from the REVIZEE project, 3865 from the JICA project, 157 from the fishery monitoring by CEPNOR, and 119 from zoological collections. AMP corresponds to the megahabitats: "Nearshore Mud", "Interbedded Mud and Sand", "Faintly Laminated Mud" and "Proximal Shelf Sand Silt" defined by Araujo et al. (2021).
2) **Sand (SND)** – between 1 and 112m, this area is predominantly marine, due to the low influence of the Amazon River discharge, and the bottom is dominated by relict sands with sparse submerged carbonate patches—such as the Parcel de Manuel Luís—under a low influence of the Amazon plume. We gathered a total of 1966 records using fishing hooks, red snapper and lobster traps and otter-trawl nets for demersal fishes. From the total, 286 were retrieved from the REVIZEE project, 955 from fishing monitoring by CEPNOR and 725 from zoological collections.
3) **Mud (MUD)** – between 16 and 92m, this area has some influence of the Amazon River discharge on the surface, but the bottom is predominantly marine and is composed of unconsolidated sediments. We gathered a total of 2165 records using a red snapper and lobster traps, double-otter-trawl nets, and trawling nets. From the total, we retrieved 232 from the REVIZEE project, 360 from the JICA project, 888 from fishery monitoring by CEPNOR and 685 from zoological collections. MUD corresponds to megahabitat "Mottled Mud" defined by Araujo et al. (2021).
4) **Reef and Rhodolith (RER)** – between 80 to 120m, the environment at the bottom of this area is marine and composed of rhodolith beds and biogenic reefs. We gathered a total of 1499 records using a red snapper and lobster trap, fishing hooks, trawling nets, and bottom

nets. From the total, 514 were retrieved from the REVIZEE project, 871 from fishing monitoring by CEPNOR and 114 from Zoological Collections. RER corresponds to megahabitats "Reef and Rhodolith" and "Rhodolith, Bryolith and other Carbonate Gravel" from Araújo et al. (2021).

5) **Continental Slope (CSL)** – oceanic environment defines the area outside of the continental shelf breaks, from 105 to 4397m. We gathered 643 records using red-snapper and lobster traps, and trawling nets. From the total, we retrieved 138 from the REVIZEE project and 505 from Zoological Collections.

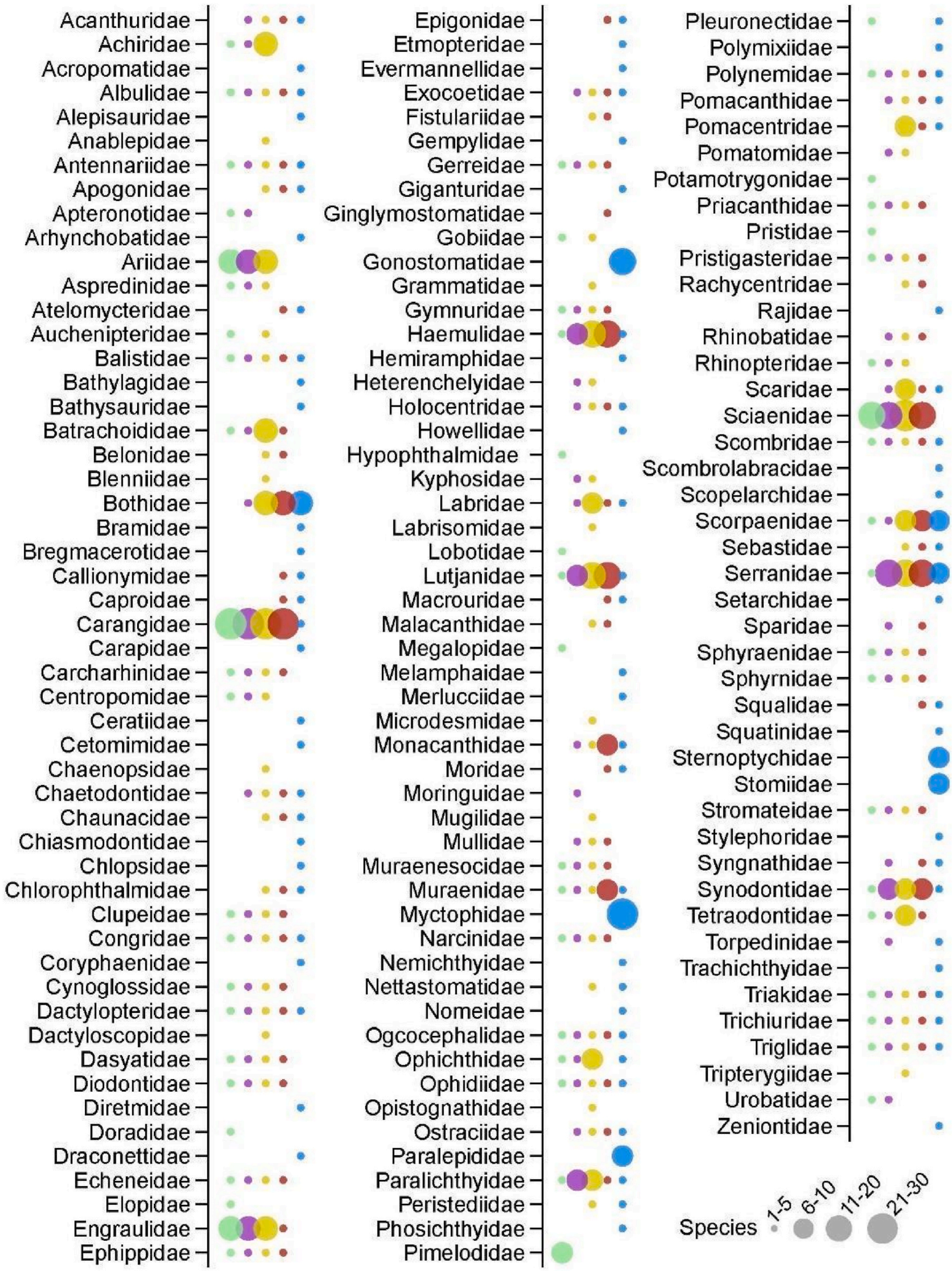

Fig. 2. Distribution of fish families across the five sampled megahabitats: Amazon Plume (green), Mud (purple), Sand (yellow), Reef and Rhodolith (red), and Continental Slope (blue). Circles size are related to the total number of species on each family in a megahabitat. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

2.4. Data analysis

A sample was defined as the combination between latitude and longitude points on which fish specimens were sampled. We attributed to each sample a megahabitat based on substratum composition (adapted from Greene et al., 2007; Lavagnino et al., 2020; Araujo et al., 2021). Due to variations in sampling effort (see Database section), we firstly converted the community matrix to a presence/absence. This adjustment accounted for potential discrepancies in species abundance resulting from the use of different fishing gears among megahabitats. Furthermore, to standardize our data and mitigate the effects of unequal sampling efforts, we employed rarefaction analysis. This analysis is widely used in ecological studies to standardize samples to the same size, thereby allowing for meaningful comparisons across different sampling efforts (Gotelli and Colwell, 2001; Magurran and McGill, 2011). Rarefaction thus provided a more balanced representation of species occurrences across different megahabitats, which is crucial for posterior accurate ecological analyses (Gotelli and Colwell, 2001).

In our study, to perform this rarefaction analysis, we used the "sample_n" function to randomly select 50 individual samples (equivalent to half of the smallest sampling effort) on each megahabitat and calculated the average occurrence for the 616 fish species. This process was iterated 1000 times for each megahabitat, resulting in a community matrix of species mean occurrences (5000 observations; CMO). This method was essential for reducing data dispersion and enhancing the explanatory power of our analyses, thereby enabling a more comprehensive description of observed patterns (Sanders, 1968; Magurran and McGill, 2011; Antão et al., 2020; Silva et al., 2023). Furthermore, to validate these procedures and ensure they did not alter species occurrence, we conducted three comparative analyses. We performed a boxplot (Fig. S1), a principal coordinate analysis, and a permutational multivariate analysis of variance (both using Bray-Curtis dissimilarity, Fig. S2) to compare the original data with the CMO matrix.

To identify similarities among megahabitats for both fish species and families we applied the Bray-Curtis dissimilarity on the CMO to perform a principal coordinate analysis (PCoA) with subsequent permutational multivariate analyses of variance (PERMANOVA; 999 permutations) to test the null-hypothesis of megahabitat being different in terms of species and family's composition. We then used the “betadisper” function, followed by analyses of variance (ANOVA), to test data dispersion among groups. We used the function “envfit” to calculate PCoA vectors for species and families (dependent variables). This function returned a r^2 and p value for each species and family, over 999 permutations. We used the families scores, calculated by the envifit function, to run a cluster analysis by using Canberra as the distance method and Ward.D2 as the agglomeration method. We calculated the mean occurrences on the CMO to obtain the similarities in species and family composition among megahabitats, for this, we used the Bray-Curtis Index. All analyses were performed on R software version 4.1.2 (R Core Team, 2021).

3. Results

We utilised 1891 samples in which we recorded a total of 616 fish species (Fig. S3) belonging to 147 families (Fig. 2), of which 564 species and 128 families are Actinopterygii and 52 species and 19 families are Elasmobranchii. Most families presented between 1 and 5 species in all megahabitats, with the exception of CSL in which most species occur exclusively in this megahabitat (Fig. 2).

We observed strong and significative differences among megahabitats considering the composition of both species (PERMANOVA: $F = 4334.2$, $R^2 = 0.78$, $p = 0.001$) and families ($F = 7702.1$, $R^2 = 0.86$, $p = 0.001$; Fig. 3). The megahabitats with the highest dissimilarity were the Amazon Plume and the Continental Slope. On the other hand, the Sand and Mud megahabitats exhibited a close relationship in terms of species and family composition. The Reef megahabitat showed a higher similarity to the Sand megahabitat (Fig. 3).

The Continental Slope (CSL) megahabitat had the highest number of families, accounting for approximately 60% of the total (**Table 1**). Within CSL, 27.2% of the families were exclusive to this megahabitat, including species from families such as Acropomatidae, Chlorophthalmidae, Diretmidae, Epigonidae, Gempylidae, Macrouridae, and Moridae (Fig. 4). On the other hand, the Amazon Plume (AMP) megahabitat had the lowest number of species (25.5%) and families (40.2%). Only eight families occurred exclusively in this megahabitat, comprising freshwater species from families like Apteronotidae, Auchenipteridae, Doradidae, Pimelodidae, and Potamotrygonidae, as well as coastal marine/estuarine families such as Achiridae, Ariidae, Centropomidae, Elopidae, and Lobotidae (Fig. 4). The Sand (SND) megahabitat exhibited the highest species richness, with 319 species, of which 12.3% were exclusive to this habitat (**Table 1**). The Reef (RER) megahabitat predominantly comprised fish species associated with consolidated substrates such as rocky and biogenic reefs. Families like Acanthuridae,

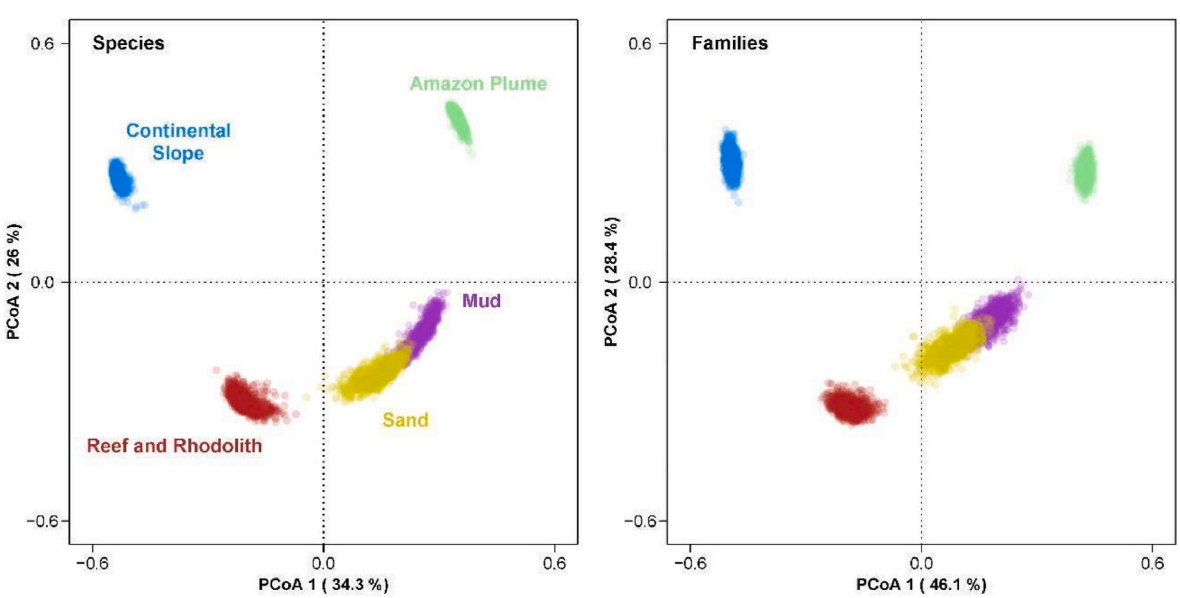

Fig. 3. Principal coordinate analysis (PCoA), showing ordination of samples according to CMO matrices for species and families. Colours represent the megahabitats. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 1
Sampling effort on the five sampled megahabitat (N); Absolute number of Species and Families recorded for each megahabitat; and Exclusive species and families occurring in each megahabitat, percentages considering the 616 species and 147 families.

Megahabitat	N	Species	Families	Exc. spp	Exc. families
Amazon Plume (AMP)	376	157 (25.5%)	59 (40.2%)	37 (6%)	8 (5.4%)
Sand (SND)	381	319 (51.8%)	84 (57.1%)	76 (12.3%)	10 (6.8%)
Mud (MUD)	411	223 (36.2%)	67 (45.6%)	16 (2.6%)	1 (0.7%)
Reef and Rhodolith (RER)	614	223 (36.2%)	71 (48.3%)	30 (4.9%)	1 (0.7%)
Continental Slope (CSL)	109	248 (40.3%)	88 (59.9%)	169 (27.4%)	40 (27.2%)

Chaetodontidae, Holocentridae, Labridae (including subfamily Scarinae), and Pomacentridae were commonly found in this megahabitat (Fig. 4). Both the Mud (MUD) and RER megahabitats had the lowest species and family richness, as well as the lowest number of exclusive species and families (Table 1).

The Amazon Plume (AMP) and Continental Slope (CSL) megahabitats exhibited the lowest similarity, sharing only 1.1% of species and 4.8% of families (Fig. 3). The AMP megahabitat shared several freshwater species (e.g., Auchenipteridae, Pimelodidae) and more euryhaline species (e.g., Ariidae, Achiridae, Centropomidae) with the Mud (MUD) and Sand (SND) megahabitats. In contrast, the MUD and SND megahabitats showed a high degree of overlap and similarity in composition, sharing 67.6% of species and 80.2% of families (Table 2). This similarity is reflected in the sample dispersion, as these megahabitats appear almost undifferentiated in the analysis (Fig. 3). The Reef and Rhodolith (RER) megahabitats demonstrated the highest similarity with the Sand megahabitat, sharing 33% of species and 51% of families (Table 2).

The CSL megahabitat primarily consisted of species and families

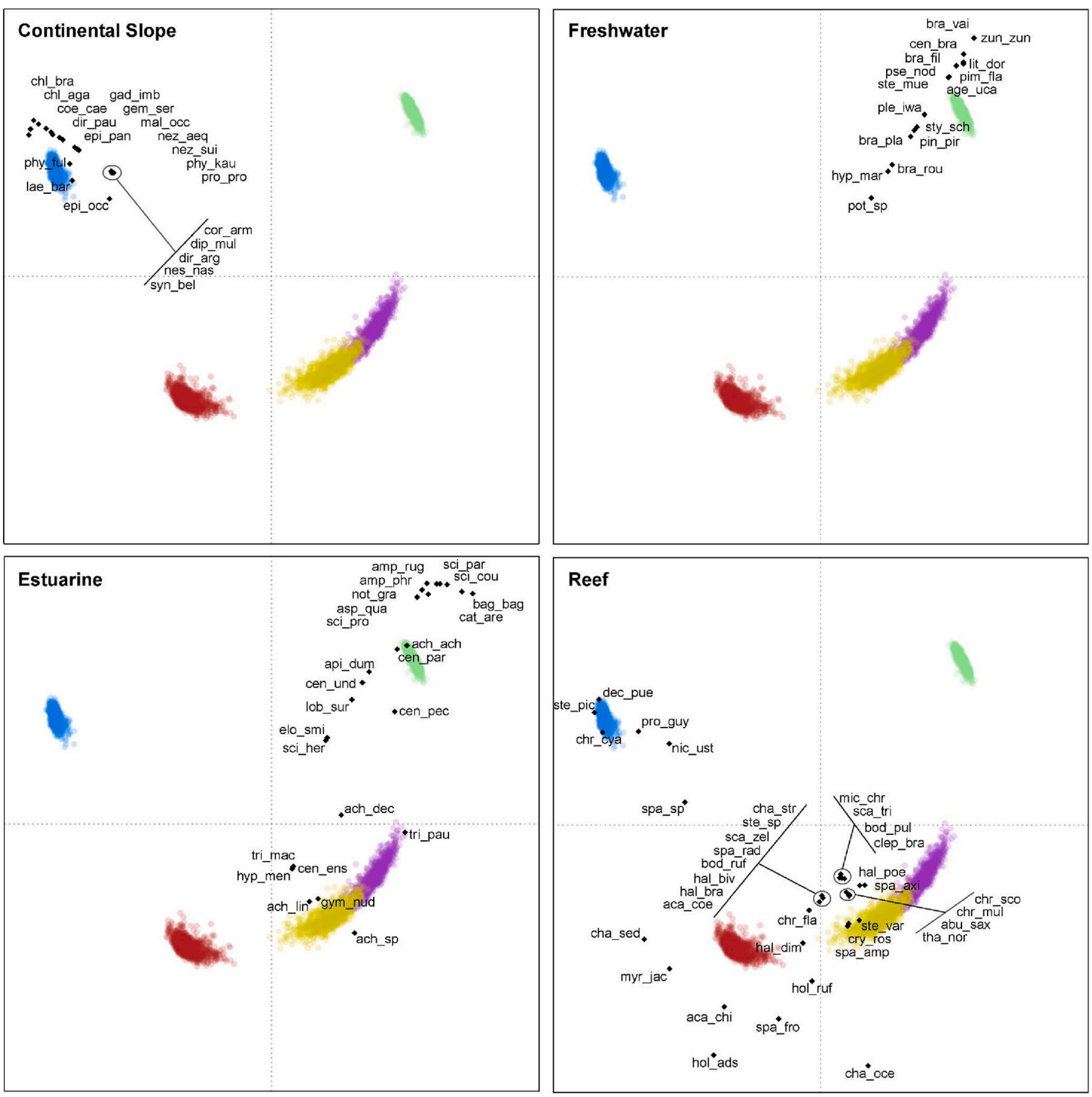

Fig. 4. The Principal Coordinate Analysis (PCoA) depicts the distribution of specific species in relation to their close association with distinct habitats. Pelagic species, commonly found in the open ocean of the Continental Slope, belong to the families Acropomatidae, Chlorophthalmidae, Diretmidae, Epigonidae, and Macrouridae.

Table 2
Bray-Curtis similarity index for species and families' composition across megahabitats. The lower triangle (values in bold) represents the similarities values for species, while the upper triangle (italic) represents the families' similarities.

	AMP	SND	MUD	RER	CSL
Amazon Plume (AMP)	1	*0.349*	*0.444*	*0.133*	*0.048*
Sand (SND)	**0.199**	1	*0.802*	*0.510*	*0.241*
Mud (MUD)	**0.280**	**0.676**	1	*0.412*	*0.198*
Reef and Rhodolith (RER)	**0.033**	**0.330**	**0.215**	1	*0.245*
Continental Slope (CSL)	**0.011**	**0.098**	**0.064**	**0.116**	1

associated with deep-sea and pelagic habitats, such as Gempylidae, Gurgesiellidae, Moridae, and Myctophidae. Surprisingly, the families Apogonidae and Pomacentridae were also grouped within this megahabitat, despite being more commonly found in reef systems (Fig. 5). Similarly to the CSL, the AMP predominantly comprised families in which species exhibited specific habits. This megahabitat included freshwater species, such as Doradidae and Potamotrygonidae, as well as marine euryhaline families like Elopidae, Lobotidae, Megalopidae, and Pristidae (Fig. 5). The MUD and SND megahabitats showed no clear pattern in terms of family composition, primarily because the majority of the families found within these megahabitats are considered generalists when it comes to habitat use. This suggests that these megahabitats contain a transitional fauna that shares species with the RER megahabitat (Fig. 5).

Several fish families, such as Carangidae and Serranidae, displayed a more generalized habitat preference and were found in more than two megahabitats. The Carangidae family consisted of 26 species, primarily distributed across the SAND, MUD, and Reef megahabitats. Among these species, only *Oligoplites palometa* exhibited a strong association with a specific habitat, namely the AMP ($r^2 = 0.6$; Fig. 6). The Serranidae family comprised 27 species, with *Anthias asperilinguis* and

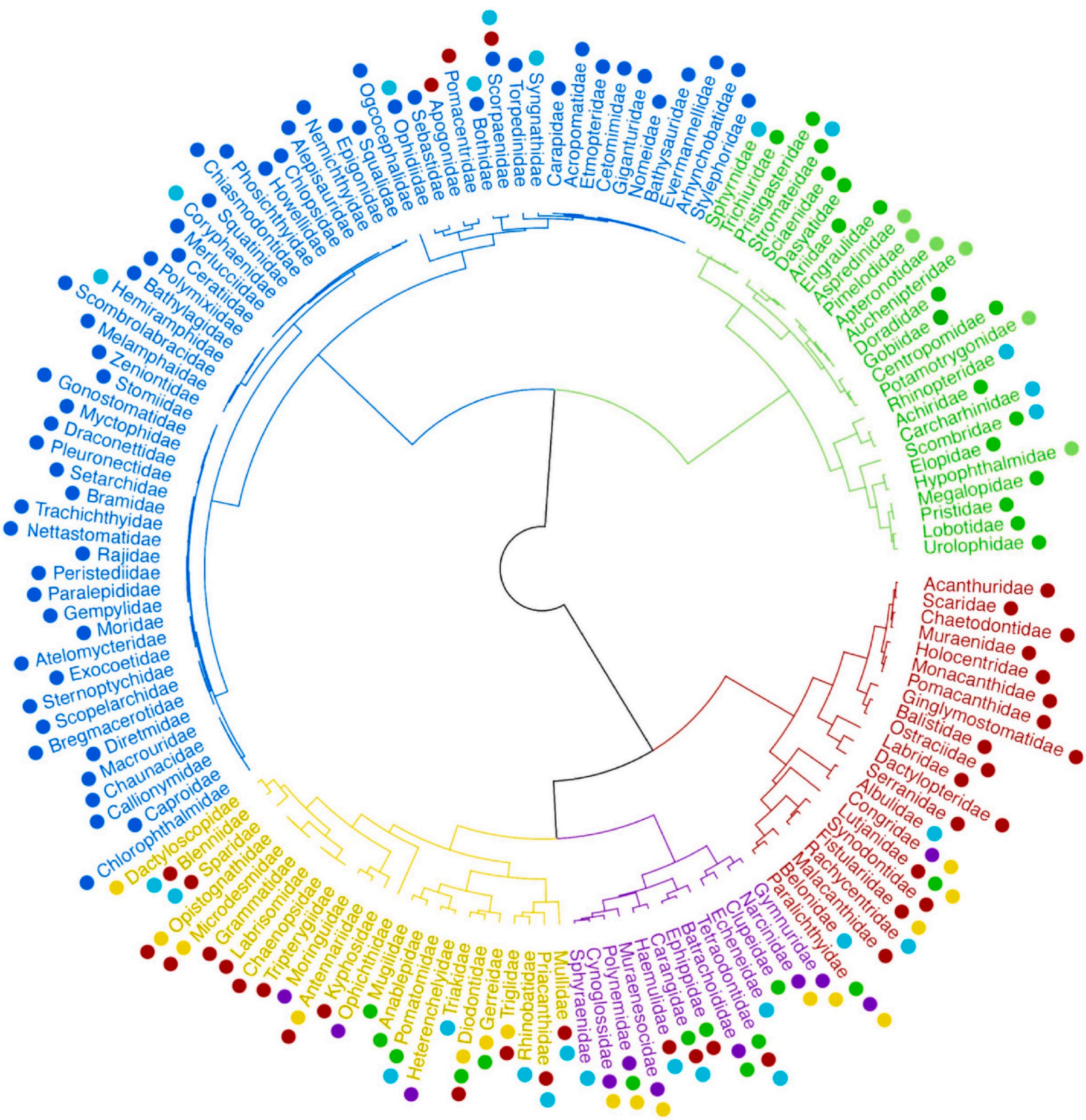

Fig. 5. Fish families clustering (Cophenetic = 0.88) based on PCoA ordination scores. Coloured circles represent species' major habits—based on literature data—found in each fish family: freshwater-related (light green), commonly euryhaline species (dark green), marine species commonly found outside the area of influence of the Amazon Plume (light blue), deep-sea-related species (dark blue), species which commonly use muddy substrates (purple), species which commonly use sandy substrates (yellow), species commonly associated to consolidate substrata (red). Dendogram lines and species' colours are related to the megahabitat (see Fig. 3). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

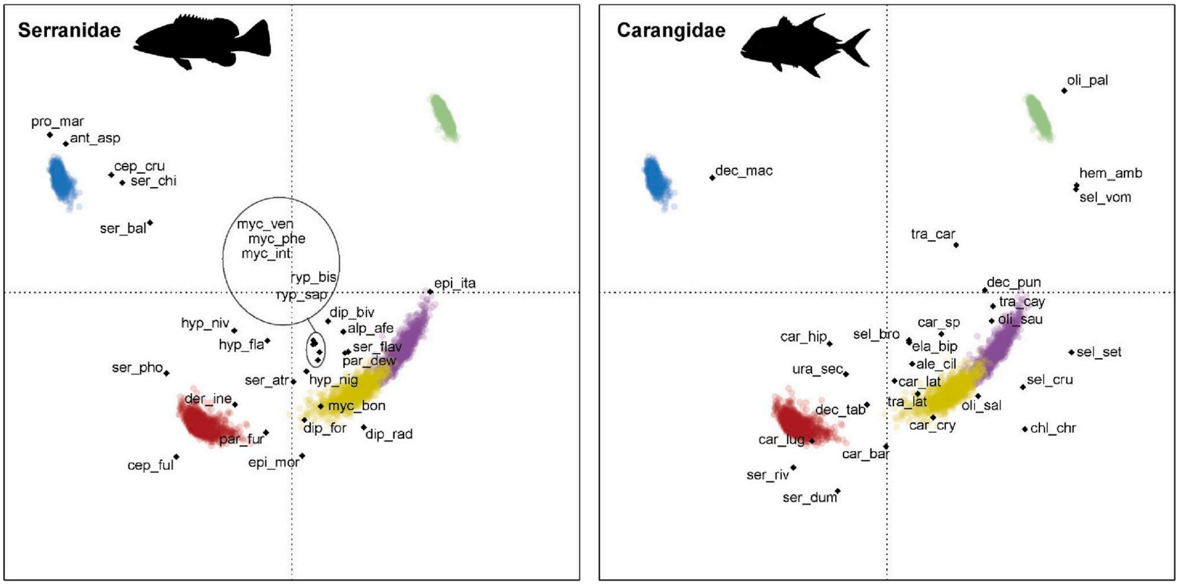

Fig. 6. Principal coordinate analysis (PCoA) showing distribution of two generalist families in terms of habitat usage. Serranidae and Carangidae species have species distributed on all five sampled megahabitats.

Pronotogrammus martinicensis being the only ones strongly associated with a specific megahabitat, namely the CSL ($r^2 = 0.57$ and 0.67, respectively; Fig. 6).

The spatial distribution of Elasmobranchii species and families was observed across all five megahabitats, with the Carcharhinidae, Dasyatidae, Gymnuridae, Narcinidae, and Sphyrnidae exhibiting a more generalized distribution encompassing all five megahabitats. However, a few families displayed a strong association with specific megahabitats. For instance, Arhynchobatidae, Rajidae, and Squatinidae were exclusively found in the CSL megahabitat, Ginglymostomatidae occurred solely in the RER megahabitat, and Potamotrygonidae and Pristidae were restricted to the AMP megahabitat (Fig. 7).

4. Discussion

The Brazilian North Coast present a diverse fish fauna which is significantly influenced by the mosaic of megahabitats on this region. This suggests fish species exhibit preferences for specific foraging substrates (Hobson and Chess, 1986) and/or are influenced by environmental factors. The discharge of freshwater from the Amazon River mouth, for example, seems to play a direct role in defining the megahabitats boundaries, especially that of the APM (Francini-Filho et al., 2018; Soares et al., 2021).

The Amazon Plume megahabitat confirms the existence of a barrier for non-euryhaline species, a condition corroborated by the presence of freshwater-related clades recorded up to ~40 m in depth, such as Apteronotidae, Auchenipteridae, Doradidae, Pimelodidae, and Potamotrygonidae, and euryhaline species often associated with estuarine regions, such as Achiridae, Ariidae, Centropomidae, Engraulidae, Elopidae, and Lobotidae. In addition, species dependent on consolidated substratum and/or non-euryhaline marine species, such as Synodontidae, Labriosomidae, Monacanthidae and Pomacentridae, were completely absent. This condition is reinforced by the Amazon Plume megahabitat presenting the lowest percentage of species and families,

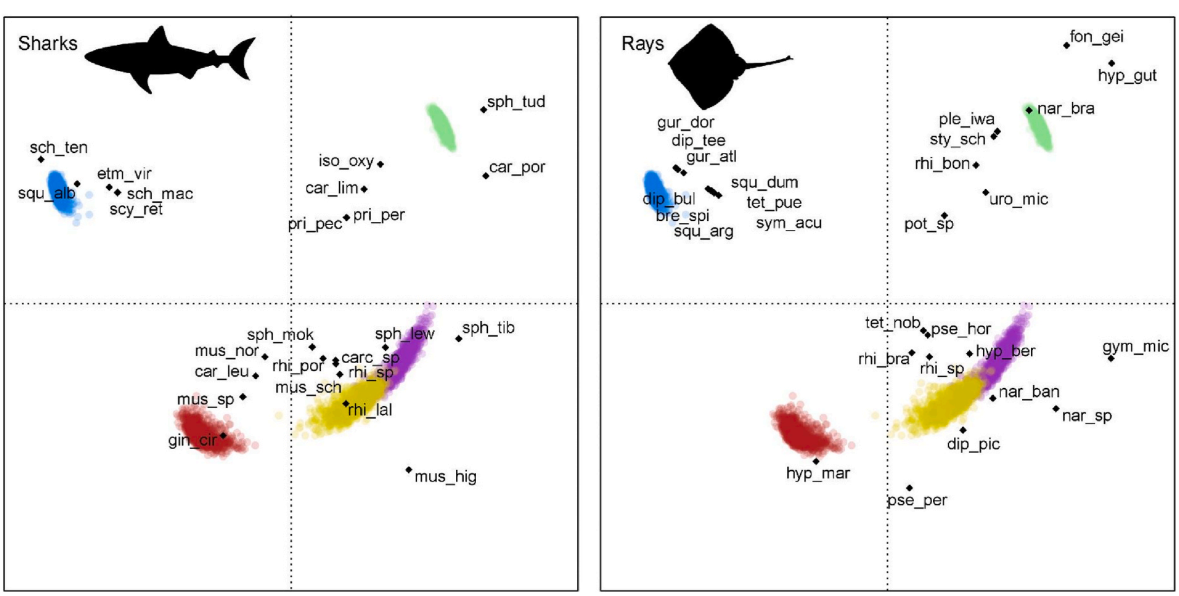

Fig. 7. Principal coordinate analysis (PCoA) showing distribution of Elasmobranchii species in the five megahabitats.

which shows the selective character of this environment.

The MUD and SND megahabitats are very similar in terms of ichthyofauna composition. This similarity in composition suggests a close relationship between these two habitats, potentially sharing similar ecological characteristics and providing suitable conditions for generalist fish species. These megahabitats show no clear pattern of family and species composition, which may also be associated with a transition fauna sharing species with the RER megahabitat and/or APM, as Carangidae, Haemulidae, Sciaenidae, Tetraodontidae. Our results suggest that the corridor connecting the Caribbean and Brazilian provinces are broader and not restricted to hard bottom areas, but also includes the MUD and SND megahabitats, which share part of the fauna with APM and RER. In fact, Carneiro et al. (2022) showed that extensive reef habitats (biogenic and geogenic) interconnect a large portion of the South America continental shelf between the Amazon reef system and the Eastern Brazilian reef system.

The ecological distribution of Elasmobranchii species is closely related to the ecomorphotypes defined by Compagno (1990), which broadly consider body shape, habitat, locomotion, and feeding behaviour as major traits related to their habitats. Several families with consistent ecomorphotypes demonstrate specific distributions within the megahabitats, reinforcing the overall patterns observed in this study. For instance, all documented species of Rajidae, Gurgesiellidae, and Arrhynchobatidae, which share the Rajobenthic ecomorphotype, were confined to the CSL megahabitat. Similarly, the nurse shark (Ginglymostomatidae) of the Probenthic ecomorphotype, was exclusively found in the RER megahabitat. Additionally, stingrays (Potamotrygonidae) and sawfishes (Pristidae) were exclusively present in the AMP megahabitat, aligning with Compagno (1990) Pristobenthic and Rajobenthic freshwater ecomorphotypes.

On the other hand, certain elasmobranch families with diverse ecomorphotypes, such as Dasyatidae, Carcharhinidae, and Sphyrnidae, have species occurring in all megahabitats across the continental shelf, indicating higher plasticity of species within these families, with no clear preferences for specific megahabitats. While there is a notable correspondence between the observed ecological distribution of elasmobranch species and Compagno (1990) ecomorphotype definitions, it is suggested that his classification system should be expanded to encompass Rajobenthic, Squatinobenthic, and Torpedobenthic.

Sixteen endemic species from the north coast of Brazil are strongly associated with APM and/or unconsolidated substrate, SND and MUD, with only four endemic species not associated with APM, *Cynoscion similis*, *Diplobatis picta* and *Lepophidium brevibarbe*, MUD SND and RER and *Schroederichthys tenuis*, RER and SL. Endemism in the area of influence of the Amazon Plume may be related to Proto-Caribbean changes and rearrangements of the hydrographic basins of the Amazon River (Hoorn et al., 2017; Shephard et al., 2010) and the establishment of the transcontinental Amazon river flow to the Atlantic Ocean during the middle to late Miocene, as demonstrated for the family with the highest number of endemic species, Ariidae with six species (Aguilera and Marceniuk, 2018).

Here we present the initial step towards comprehending species occurrence and distribution in the BNC, which is a significant endeavour given the region's importance, not only in terms of biodiversity but also as a transitional zone between provinces and for human utilization. By emphasizing the importance of megahabitats, we can subsequently explore variables that influence species preferences for specific megahabitats. Furthermore, by gaining a deeper understanding of habitat utilization, we can enhance the provision of information regarding the protection of specific areas.

CRediT authorship contribution statement

Alexandre Pires Marceniuk: Conceptualization. **Bruno Eleres Soares:** Writing – original draft, Conceptualization. **Rodrigo Antunes Caires:** Writing – review & editing, Data curation. **Alfredo Carvalho-Filho:** Writing – review & editing, Investigation, Data curation. **Ronaldo Barthem:** Writing – review & editing, Investigation, Data curation. **Sergio Ricardo Floeter:** Writing – review & editing, Conceptualization. **Ricardo de Souza Rosa:** Writing – original draft. **Alex Garcia Cavalleiro de Macedo Klautau:** Writing – review & editing, Resources, Data curation. **Israel Hidenburgo Aniceto Cintra:** Writing – review & editing, Data curation. **Matheus Marcos Rotundo:** Writing – original draft, Conceptualization. **Lucas T. Nunes:** Conceptualization.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Alexandre Pires Marceniuk reports financial support was provided by Protected Marine and Coastal Areas Project - GEF Mar. Alex Garcia Cavalleiro De Macedo Klautau reports a relationship with Federal Government of Brazil that includes: funding grants.

Data availability

The authors do not have permission to share data.

Acknowledgement

We thank Laís Araujo for kindly providing the megahabitats shapefiles and Protected Marine and Coastal Areas Project - GEF Mar of the Federal Government, responsible for supporting the collection of the specimens by Centro Nacional de Pesquisa e Conservação da Biodiversidade Marinha do Norte. A.P.M. is grateful for the postdoctoral fellowship at Universidade Federal da Paraiba (FAPESQ, Proc. 1262/2021), L.T.N. received a scholarship from Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq #151859/2022-1).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecss.2024.108847.

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