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Rich and underreported: First integrated assessment of the diversity of mesopelagic fishes in the Southwestern Tropical Atlantic

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Mesopelagic fishes play critical ecological roles by sequestering carbon, recycling nutrients, and acting as a key trophic link between primary consumers and higher trophic levels. They are also an important food source for harvestable economically valuable fish stocks and a key link between shallow and deep-sea ecosystems. Despite their relevance, mesopelagic ecosystems are increasingly threatened by direct and indirect human activities while representing some of the largest and least understood environments on Earth. The composition, diversity, and other aspects of the most basic biological features of numerous mesopelagic groups of fishes are still poorly known. Here, we provide the first integrative study of the biodiversity of mesopelagic fishes of the southwestern Tropical Atlantic (SWTA), based on two expeditions in northeastern Brazil in 2015 and 2017. A full list of mesopelagic fishes of the region is provided, including rare species and new records for the Brazilian Exclusive Economic Zone and the indication of potentially new species in groups such as the Stomiiformes and Beryciformes. Key aspects of the diversity of mesopelagic fishes of the region were also assessed, considering different depth strata and diel periods. At least 200 species, 130 genera, 56 families, and 22 orders of the Teleostei and one shark (*Isistius brasiliensis*, Dalatiidae, Squaliformes) were recorded, including potentially eight new species (4%) and 50 (25%) new records for Brazilian waters. Five families accounted for 52% of the diversity, 88% of specimens collected, and 66% of the total biomass: Stomiidae (38 spp., 8% of specimens, 21% of biomass), Myctophidae (34 spp., 36%, 24%), Melamphaidae (11 spp., 2%, 7%), Sternoptychidae (9 spp., 26%, 10%), and Gonostomatidae (7 spp., 16%, 4%). During the day, richness and diversity were higher at lower mesopelagic depths (500–1000 m), with contributions of typically bathypelagic species likely associated with seamounts and oceanic islands. At night, richness and diversity increased at epipelagic depths, indicating the diel ascension of several species (e.g., myctophids and sternoptychids) that can endure temperature ranges of up to 25°C. Information on the geographic distribution of several rare species worldwide is also provided.

KEYWORDS

deep-sea, oceanic islands, seamounts, biodiversity, Brazil, Fernando de Noronha Ridge

Introduction

Mesopelagic fishes (200–1,000 m depth) are among the most abundant vertebrates in the biosphere (Gjøsaeter and Kawaguchi, 1980; Irigoien et al., 2014; Nelson et al., 2016). They often have a global distribution, vertical migratory behavior, and several adaptations to overcome challenges imposed by the deep-sea environment (Gjøsaeter and Kawaguchi, 1980; Sutton, 2013; Priede, 2017). Some of these adaptations include low metabolic rates, high tolerance to environmental changes, and complex visual and bioluminescence systems (Priede, 2017). Consequently, the mesopelagic zone holds one of the most diverse fish communities of the ocean, contributing to several ecosystem processes (Gjøsaeter and Kawaguchi, 1980; St. John et al., 2016). Mesopelagic fishes play critical roles by sequestering carbon, recycling nutrients, and acting as key trophic links between primary consumers and higher trophic levels (e.g., larger fishes, mammals, and seabirds) (e.g., Ariza et al., 2015; Cavan et al., 2019; Eduardo et al., 2020a; Eduardo et al., 2020b; Eduardo et al., 2021). They are also an important food source for harvestable fish stocks and a key link between shallow and deep-sea ecosystems (e.g., Cherel et al., 2010; Eduardo et al., 2020b; Eduardo et al., 2021).

Despite their importance, mesopelagic communities are increasingly threatened by climate change (Levin et al., 2019), plastic pollution (Ferreira et al., 2022; Justino et al., 2022), and exploitation of deep-sea resources (Hidalgo and Browman, 2019; Drazen et al., 2020). There is also a major lack of knowledge of the biology, ecology, distribution, and diversity of mesopelagic species, which are typically under-sampled and sparse in data (Glover et al., 2018; Hidalgo and Browman, 2019; Martin et al., 2020).

The southwestern Tropical Atlantic (SWTA) encompasses oceanic islands, underwater canyons, and several seamounts (Travassos et al., 1999; Tchamabi et al., 2017). This region holds distinct biodiversity and includes several Marine Protected Areas and Ecologically or Biologically Significant Marine Areas (EBSAs) that, by definition, are special places of fundamental importance for biodiversity and life cycles of marine species (CBD, 2014). Moreover, the SWTA includes different biogeographic provinces with contrasting thermodynamic features, current systems, and water-mass properties, leading to shifts in biodiversity and ecosystems (Bourlès et al., 1999; Pinheiro et al., 2018; Assunção et al., 2020; Costa da Silva et al., 2021; Dossa et al., 2021; Tosetto et al., 2021; Silva et al., 2022).

The first collection of deep-sea fishes in the SWTA was carried out by the HMS *Challenger* (1872–1876; Günther, 1887). Since then, mesopelagic fishes have been sporadically collected by different vessels, such as the RV *Akademik Kurchatov* (1971–1972; Parin et al., 1974), RV *Walther Herwig* (1966–1971; many authors), RV *Marion Dufresne* (1987; Séret and Andreata, 1992), RV *Atlântico Sul* (1996–1999; Figueiredo et al., 2002; Bernardes et al., 2005), RV *Thalassa* (1999–2000; Costa et al., 2007), RV *Astro Garoupa* (2003; Costa and Mincarone, 2010), RV *Gyre* (2008; Costa et al., 2015; Mincarone et al., 2017), and the RV *Luke Thomas* and RV *Seward Johnson* (2009, 2011; Lins Oliveira et al., 2015). Although these expeditions substantially contributed to understanding the diversity and ecology of several groups, they were sparse and focused mostly on demersal species (Melo et al., 2020). Only a few studies focused on the mesopelagic communities of the SWTA, with most of them being restricted to the composition and taxonomy of specific groups (e.g., Lima et al., 2011; Mincarone et al., 2014). Consequently, an integrative overview of the mesopelagic fish community of the region is still lacking, leaving a "dark hole" in our understanding of their diversity, ecology, and function in marine ecosystems.

Two recent expeditions focused on mesopelagic fauna were made aboard the RV *Antea*, as part of the project ABRACOS (Acoustics along the BRAzilian COaSt; Bertrand, 2015; Bertrand, 2017). For the first time, the mesopelagic zone of the SWTA was extensively surveyed, resulting in collections of thousands of deep-sea invertebrates and fishes. Based on these collections, various studies have been published addressing the diversity and ecology of several fish groups, such as Argentiniformes (Mincarone et al., 2021a), Aulopiformes (Mincarone et al., 2022), Myctophiformes (Eduardo et al., 2021), Beryciformes (Afonso et al., 2021), Stomiiformes (Eduardo et al., 2020a; Eduardo et al., 2020b; Villarins et al., 2022), Ceratioidei (Mincarone et al., 2021a), Caristiidae (Mincarone et al., 2019), Howelidae (Eduardo et al., 2019), and Trichiuridae (Eduardo et al., 2018). However, most of the results of these cruises remains unpublished. Here, we present an integrative study of the biodiversity of mesopelagic fishes from the SWTA. A full list of mesopelagic species collected during the ABRACOS expeditions, including a compilation of published new records and the indication of potentially new species, is provided. Key aspects of the mesopelagic fish diversity of the region were also addressed, considering different depth strata and diel periods.

Methodology

Study area

The study area comprised the northeastern Brazilian coast, from Rio Grande do Norte to Alagoas states (5°–9°S), and the seamounts and oceanic islands of the Fernando de Noronha Ridge, including the Rocas Atoll (3°52′S, 33°49′W) and the Fernando de Noronha Archipelago (3°50′S, 32°25′W) (Figure 1). The main oceanographic physico-chemical features

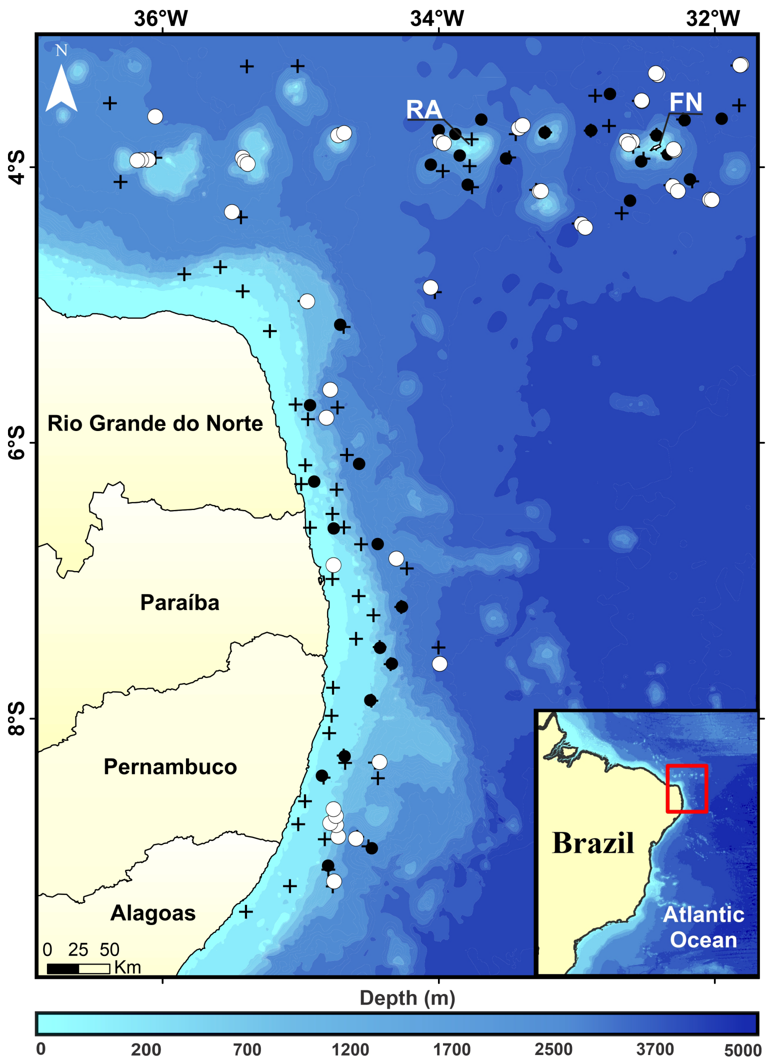

FIGURE 1
Study area with CTDO profile (cross) and trawl samples (dots). Black and white symbols for ABRACOS 1 and ABRACOS 2, respectively.

of the region were recently described by Assunção et al. (2020); Costa da Silva et al. (2021), and Dossa et al. (2021). Overall, the SWTA is considered oligotrophic. However, locally the banks and islands act as topographic obstacles to currents, driving subsurface enriched waters to the surface (Travassos et al., 1999; Tchamabi et al., 2017; Costa da Silva et al., 2021; Silva et al., 2022). This process increases primary production and enhances the mass and energy fluxes throughout the food web (Travassos et al., 1999; Tchamabi et al., 2017).

Data and specimen collection

Data and specimens were collected during the Acoustics along the BRAzilian COaSt (ABRACOS) surveys, carried out from 29 August to 21 September 2015 (AB1) and from 9 April to 10 May 2017 (AB2), aboard the French RV *Antea* (Bertrand, 2015; Bertrand, 2017). Temperature profiles were collected using a CTDO SeaBird911+. Mesopelagic fishes were collected day and night at 80 trawl stations by using mesopelagic (AB1; body mesh 30 mm, cod-end mesh 4 mm, size of the net mouth: 16.6 x 8.4 m; Bertrand, 2015) and micronekton (AB2; body mesh 40 mm, cod-end mesh 10 mm, size of the net mouth: 24 x 24 m; Bertrand, 2017) nets (Figure 1; Supplementary Material 1 and 2). Targeted depth ranged from 10 to 1,113 m and was defined by the presence of acoustic scattered layers or patches detected by a Simrad EK60 (Kongsberg Simrad AS) split-beam scientific echosounder, operating at 38, 70, 120, and 200 kHz. Except for the layers 200–300 and 700–800 at night, where no aggregation of organisms were observed through acoustics, all depth strata were sampled at least once (Supplementary Material 1). The net geometry was monitored using SCANMAR sensors, to give headline height, depth, and distance of wings and doors to ensure the net was fishing correctly. Based on SCANMAR the estimated opening area of the micronekton trawl was 120 m^2. For the mesopelagic trawl, however, the opening resembled an ellipse of 65 m^2. As the trawl was not fitted with an opening and closing mechanism, the collection of specimens during the lowering or hoisting of the net was reduced as much as possible by decreasing ship velocity and increasing winch speed. At the target depths, trawling activity lasted for about 30 minutes at 2–3 kt. Therefore, collection of specimens most likely occurred at target depths, which are indicated as capture depths in the species accounts.

Specimens were sorted to the lowest taxonomic level and frozen or, in the case of rare species or taxonomic uncertainty, fixed in 4% formalin and then preserved in a 70% alcohol solution (Eduardo et al., 2020a). In the laboratory, specimens were identified, measured (nearest 0.1 cm of standard length, SL), and weighed (nearest 0.01 g of total weight, TW). Excluding a few specimens of the Stomiidae, Sternoptychidae, and Myctophidae used for biological analyses (Eduardo et al., 2020a; Eduardo et al., 2020b; Eduardo et al., 2021), all specimens were deposited in the NPM – Fish Collection of the "Instituto de Biodiversidade e Sustentabilidade, Universidade Federal do Rio de Janeiro" (NUPEM/UFRJ). Taxonomic classification follows Nelson et al. (2016), with exceptions noted in Villarins et al. (2022) for the Stomiiformes.

Richness estimators and biodiversity indexes

We first computed a randomised species accumulation curve to assess whether the fish community was exhaustively sampled with the gears employed (Gotelli and Colwell, 2001). This enables calculating a mean number of species for a given number of samples within a 95% confidence interval. The Chao1 index, which extrapolates the total expected number of species in the area for a given sampling gear, was subsequently calculated (Magurran, 2004).

Other aspects of the biodiversity were assessed based on the sample-size-based rarefaction and extrapolation sampling curves, calculated for the species richness, Shannon diversity, and Simpson dominance, the three most widely used species diversity indexes (Magurran, 2004). For that, we used Hill's numbers, which integrate species richness and relative abundance to propose a more intuitive and statistically rigorous alternative to calculate diversity measures (Chao et al., 2014). Statistical significance was evaluated based on the confidence interval overlapping of the curves.

Sample-size-based rarefaction and extrapolation sampling curves (Hsieh et al., 2016) were also constructed to test for differences in diversity indexes when considering depth strata (epipelagic 0–200 m; upper mesopelagic 200–500 m; lower mesopelagic 500–1000 m) and the diel period (day and night). As the sampling strategy employed in the AB2 expedition was much more efficient in collecting mesopelagic fishes (see Discussion), comparisons using diversity indexes were only made for this survey. Statistical analyses and the calculation of diversity indices were performed using the software R version 4.0.3 through the packages "iNext" (Hsieh et al., 2016) and "vegan" (Oksanen et al., 2017). Fish larvae and species traditionally classified as epipelagic were excluded from the species list, and they were not considered for the diversity assessments. Specimens identified at the genus level only (small-sized and/or damaged specimens), which might represent more than one species, were also excluded from the analyses (Supplementary Material 3).

Results

Biodiversity

Considering our two surveys, 7,119 specimens of mesopelagic fishes, representing 200 species in 130 genera, 56 families, and 22 orders of the Teleostei and one shark (*Isistius brasiliensis*: Dalatiidae, Squaliformes), were collected and identified (Table 1). The species accumulation curve was steep,

TABLE 1 Species recorded, survey (S) (1: ABRACOS 1; 2: ABRACOS 2), number of specimens (N), frequency of occurrence to overall samples (FO %), standard length (SL, mean and range), total wet weight (TW, mean and range), collection locality (PE, Pernambuco; PB, Paraíba; RN, Rio Grande do Norte; FNR, Fernando de Noronha Ridge), depth range (based on the target depth of each trawl), temperature range (T), and new records in the Brazilian Exclusive Economic Zone (EEZ).

Species	S	N	FO%	SL (mm)	TW (g)	Locality	Depth (m)	T (°C)
SQUALIFORMES								
Dalatiidae								
Isistius brasiliensis (Quoy & Gaimard, 1824)	1	1	1.2	172 (TL)	20.0	PB	100	24.4
NOTACANTHIFORMES								
Halosauridae								
Aldrovandia sp.*	2	1	1.2	167	3.4	FNR	900	4.3
ANGUILLIFORMES								
Eurypharyngidae								
Eurypharynx pelecanoides Vaillant, 1882	2	13	4.9	287 (99–524)	6.5 (1.0–33.9)	FNR	780–900	4.3–4.7
Nemichthyidae								
Avocettina infans (Günther, 1878)	2	1	1.2	502	2.2	FNR	900	4.3
Labichthys carinatus Gill & Ryder, 1883	2	2	2.4	397 (227–568)	7.0 (0.5–13.5)	FNR-PE	680–720	4.9–5.2
Nemichthys scolopaceus Richardson, 1848	1	7	3.7	290 (235–330)	2.9 (2.0–4.7)	FNR	105–525	6.8–24.4
Serrivomeridae								
Serrivomer beanii Gill & Ryder, 1883	2	49	13.4	422 (60–592)	14.5 (0.5–65.4)	FNR-PB-PE-RN	90–900	4.3–25.1
Serrivomer lanceolatoides (Schmidt, 1916)	2	1	1.2	413	4.6	FNR	900	4.3
Stemonidium hypomelas Gilbert, 1905	2	2	2.4	256	6.2 (3.4–9.0)	FNR	800–900	4.3–4.7
ALEPOCEPHALIFORMES								
Platytroctidae								
Platytroctidae sp.*	2	1	1.2	55	0.8	FNR	610	5.6
Alepocephalidae								
Alepocephalidae sp.*	2	1	1.2	45	0.7	FNR	900	4.3
Photostylus pycnopterus Beebe, 1933[1]	2	2	2.4	85 (75–95)	4.1 (2.7–5.5)	FNR	800–900	4.3–4.7
ARGENTINIFORMES								
Opisthoproctidae								
Opisthoproctus soleatus Vaillant, 1888[2]	2	1	1.2	49	1.0	FNR	385	9.2
Rhynchohyalus natalensis (Gilchrist & von Bonde, 1924)[2]	2	1	1.2	109	12.3	FNR	800	4.7
Winteria telescopa Brauer, 1901	2	31	9.8	95 (51–118)	6.7 (1.3–10.6)	FNR-RN	440–900	4.3–8.5
Microstomatidae								
Xenophthalmichthys danae Regan, 1925[2]	2	2	2.4	87 (60–114)	3.2 (2.1–4.3)	FNR	385–505	7.0–9.2
Bathylagidae								
Dolicholagus longirostris (Maul, 1948)	2	8	7.3	79 (41–100)	3.3 (1.3–4.8)	FNR	430–900	4.3–8.5
Melanolagus bericoides (Borodin, 1929)	2	9	3.7	148 (128–167)	17.8 (11.7–25.8)	FNR	430–900	4.3–8.54
STOMIIFORMES								
Diplophidae								
Diplophos australis Ozawa, Oda & Ida, 1990	2	3	2.4	81 (71–99)	0.8 (0.5–1.3)	FNR	780–800	4.6–4.7
Diplophos taenia Günther, 1873	1-2	25	12.2	71 (42–129)	1.9 (0.6–4.3)	FNR-PB	25–800	4.7–28.8
Manducus maderensis (Johnson, 1890)	2	2	3.7	56 (42–65)	1.3 (0.7–1.4)	FNR	90–615	5.6–25.1
Triplophos hemingi (McArdle, 1901)[3]	2	1	1.2	196	13.5	FNR	800	4.7
Gonostomatidae								
Cyclothone spp.*	1-2	874	28.0	33 (12–45)	1.4 (0.2–7.4)	FNR-PB-PE-RN	350–1000	4.3–27.6
Gonostoma atlanticum Norman, 1930	1-2	67	18.3	51 (19–68)	1.8 (0.13–7.8)	FNR-PB-PE-RN	100–900	4.3–24.6
Gonostoma denudatum Rafinesque, 1810[3]	2	1	1.2	122	7.8	FNR	440	8.5
Margrethia obtusirostra Jespersen & Tåning, 1919	1	1	1.2	27	3.2	FNR	525	6.8
Sigmops bathyphilus (Vaillant, 1884)	2	1	1.2	155	17.3	FNR	800	4.7
Sigmops elongatus (Günther, 1878)	1-2	41	14.6	145 (45–250)	13.1 (0.5–26.8)	FNR-PB-PE-RN	100–1000	4.3–24.6

(Continued)

TABLE 1 Continued

Species	S	N	FO%	SL (mm)	TW (g)	Locality	Depth (m)	T (°C)
Zaphotias pedaliotus (Goode & Bean, 1896)	2	184	15.9	57 (37–81)	1.2 (0.5–4.7)	FNR-PB	130–900	4.3–22.1
Sternoptychidae								
Argyropelecus aculeatus Valenciennes, 1850	2	51	12.2	56 (30–82)	6.1 (0.8–20.9)	FNR-PB-PE-RN	100–900	4.3–24.6
Argyropelecus affinis Garman, 1899	2	439	14.6	52 (27–82)	2.7 (0.5–6.9)	FNR-PB-RN	30–800	4.6–28.7
Argyropelecus gigas Norman, 1930	2	9	2.4	86 (78–91)	14.2 (10.4–17.0)	FNR-RN	610–700	5.2–5.6
Argyropelecus hemigymnus Cocco, 1829	1-2	80	22.0	24 (8–36)	2.4 (0.2–4.9)	FNR-PE-RN	260–900	4.3–13.7
Argyropelecus sladeni Regan, 1908	2	27	11.0	57 (32–94)	4.1 (0.7–14.2)	FNR	30–800	4.6–28.7
Sternoptyx diaphana Hermann, 1781	2	1091	20.7	24 (11–43)	2.0 (0.4–4.9)	FNR-PB-PE-RN	65–900	4.3–26.5
Sternoptyx pseudobscura Baird, 1971	2	123	12.2	35 (13–59)	2.9 (0.5–9.9)	FNR-PB-PE	520–900	4.3–6.3
Sternoptyx pseudodiaphana Borodulina, 1977	2	3	2.4	49 (42–59)	6.9 (5.2–9.9)	FNR	800–900	4.4–4.7
Valenciennellus tripunctulatus (Esmark, 1871)	1-2	19	8.5	24 (23–32)	1.6 (1.0–2.3)	FNR-PE	360–1000	4.3–10.9
Phosichthyidae								
Ichthyococcus polli Blache, 1964	1-2	14	9.8	52 (41–72)	2.5 (1.1–8.4)	FNR-PB	385–900	4.3–9.2
Phosichthys argenteus Hutton, 1872	2	1	1.2	64	8.1	RN	630	5.6
Pollichthys mauli (Poll, 1953)	1	1	1.2	38	1.5	RN	75	25.7
Vinciguerria nimbaria (Jordan & Williams, 1895)	1-2	24	11.0	26 (17–49)	2.0 (0.4–6.5)	FNR-PB-PE-RN	50–780	4.6–26.6
Stomiidae								
Aristostomias grimaldii Zugmayer, 1913[3]	2	5	2.4	74 (65–86)	3.1 (1.8–5.0)	FNR	700–800	4.7–5.26
Aristostomias tittmanni Welsh, 1923	2	3	3.7	43 (32–76)	2.5 (2.0–3.5)	FNR-PB	30–800	4.6–28.7
Astronesthes atlantica Parin & Borodulina, 1996	1-2	3	3.7	38 (31–51)	1.2 (0.62–2.0)	FNR	90–525	6.8–25.1
Astronesthes gemmifer Goode & Bean, 1896	2	1	1.2	146	21.6	FNR	430	8.5
Astronesthes gudrunae Parin & Borodulina, 2002[3]	2	1	1.2	111	11.1	FNR	610	5.6
Astronesthes richardsoni (Poey, 1852)	2	7	6.1	71 (22–132)	5.7 (1.1–13.5)	FNR	25–780	4.6–28.8
Astronesthes similus Parr, 1927	1-2	10	3.7	43 (36–75)	2.9 (0.5–4.9)	FNR-PB	100–800	4.7–24.4
Bathophilus nigerrimus Giglioli, 1882[3]	2	2	2.4	89 (84–95)	6.1 (5.1–7.2)	FNR	90–610	5.6–25.1
Bathophilus pawneei Parr, 1927	2	4	3.7	66 (30–124)	3.2 (1.2–8.7)	FNR	65–440	8.5–26.5
Borostomias elucens (Brauer, 1906)[3]	2	55	8.5	168 (46–299)	48.2 (0.5–218.9)	FNR	610–900	4.3–5.6
Chauliodus sloani Bloch & Schneider, 1801	1-2	348	22.0	162 (55–270)	9.6 (0.3–53.9)	FNR-PB-PE-RN	430–900	4.3–8.5
Eustomias bibulbosus Parr, 1927[3]	2	1	1.2	87	0.6	PE	680	5.2
Eustomias braueri Zugmayer, 1911[3]	2	2	1.2	69 (56–82)	1.6(0.6–2.6)	PE	680	5.2
Eustomias brevibarbatus Parr, 1927	2	6	7.3	97 (85–128)	1.8 (0.5–4.6)	FNR	90–900	4.3–25.1
Eustomias enbarbatus Welsh, 1923	2	2	2.4	54 (54–55)	2.1 (2.1–2.1)	FNR-PE	680–780	4.6–5.2
Eustomias minimus Clarke, 1999[3]	2	1	1.2	69	3.2	FNR	780	4.6
Eustomias schmidti Regan & Trewavas, 1930[3]	2	1	1.2	68	4.9	FNR	780	4.6
Eustomias sp. 1**[3]	2	1	1.2	168	8.2	FNR	800	4.7
Eustomias sp. 2**[3]	2	1	1.2	120	2.3	FNR	430	8.5
Eustomias sp. 3**[3]	2	4	2.4	68 (49–78)	2.4 (1.6–2.8)	FNR	90–720	4.9–25.1
Eustomias sp. 4**[3]	2	1	1.2	122	2.1	FNR	800	4.7
Eustomias sp. 5**[3]	2	3	1.2	54 (28–98)	0.5 (0.4–0.6)	FNR	780	4.6
Grammatostomias dentatus Goode & Bean, 1896[3]	1	1	1.2	114	3.5	PE	1000	4.3
Grammatostomias ovatus Prokofiev, 2014[3]	1	1	1.2	67	1.5	PE	1000	4.3
Heterophotus ophistoma Regan & Trewavas, 1929	2	8	6.1	205 (96–253)	57.9 (0.7–107.6)	FNR	430–900	4.3–8.5
Leptostomias gladiator (Zugmayer, 1911)[3]	2	1	1.2	83	0.9	FNR	780	4.6
Malacosteus niger Ayres, 1848	2	46	9.8	107 (633–181)	8.3 (1.4–34.4)	FNR	610–900	4.3–5.6
Melanostomias bartonbeanis Parr, 1927[3]	1-2	2	2.4	117 (50–185)	10.9 (2.3–19.6)	FNR-PB	100–780	4.6–24.4
Melanostomias biseriatus Regan & Trewavas, 1930[3]	2	2	2.4	103 (29–177)	11.1 (4.9–17.2)	FNR-PE	610–680	5.6
Melanostomias tentaculatus (Regan & Trewavas, 1930)	1-2	5	4.9	162 (48–201)	15.7 (2.6–20.7)	FNR-PB-PE	430–1000	4.3–8.5
Melanostomias sp.**[3]	2	1	1.2	180	11.4	FNR	440	8.5

(Continued)

TABLE 1 Continued

Species	S	N	FO%	SL (mm)	TW (g)	Locality	Depth (m)	T (°C)
Pachystomias microdon (Günther, 1878)[3]	2	9	8.5	137 (39–181)	23.2 (2.3–42.5)	FNR	430–900	4.3–8.5
Photonectes achirus Regan & Trewavas, 1930[3]	2	3	2.4	56 (33–79)	3.4 (1.2–3.4)	PB-RN	100–800	4.7–24.6
Photostomias atrox (Alcock, 1890)	2	1	1.2	118	1.0	PE	680	5.2
Photostomias goodyeari Kenaley & Hartel, 2005[3]	2	1	1.2	64	0.7	FNR	720	4.9
Stomias danae Ege, 1933	2	1	1.2	95	1.8	PB	800	4.7
Stomias longibarbatus (Brauer, 1902)	2	5	6.1	281 (173–390)	9.7 (1.4–25.7)	FNR	260–800	4.7–13.7
Thysanactis dentex Regan & Trewavas, 1930	1-2	41	19.5	90 (43–150)	3.1 (0.5–10.6)	FNR-RN	90–900	4.3–25.1
ATELEOPODIFORMES								
Ateleopodidae								
Ateleopodidae sp.*	2	1	1.2	122	0.6	FNR	800	4.7
AULOPIFORMES								
Anotopteridae								
Anotopterus pharao Zugmayer, 1911	1	1	1.2	27	1.0	RN	20	26.7
Giganturidae								
Gigantura chuni Brauer, 1901[1]	2	3	2.4	111 (42–181)	19.4 (4.9–33.9)	FNR	610–800	4.7–5.6
Gigantura indica Brauer, 1901	1-2	31	22.0	102 (16–190)	3.9 (0.6–11.7)	FNR-PB-PE	50–900	4.3–27.6
Chlorophthalmidae								
Parasudis truculenta (Goode & Bean, 1896)	1	2	1.2	31 (30–33)	3.8 (3.2–4.5)	FNR	105	24.4
Notosudidae								
Ahliesaurus berryi Bertelsen, Krefft & Marshall, 1976[1]	2	1	1.2	198	17.8	FNR	800	4.7
Scopelosaurus smithii Bean, 1925	2	1	1.2	177	22.4	PE	680	4.5
Scopelarchidae								
Benthalbella infans Zugmayer, 1911[1]	1	1	1.2	57	4.0	RN	560	5.9
Rosenblattichthys hubbsi Johnson, 1974[1]	2	4	1.2	79 (40–100)	4.5 (0.5–6.9)	PB	800–800	4.7–4.7
Scopelarchoides danae Johnson, 1974[1]	2	1	1.2	80	2.3	FNR	780	4.6
Scopelarchus analis (Brauer, 1902)	1	2	2.4	103 (91–115)	7.9 (4.7–11.2)	FNR	510–525	6.0–6.8
Scopelarchus guentheri Alcock, 1896	2	8	6.0	79 (38–113)	4.9 (0.5–12.2)	FNR-PB-RN	385–900	4.3–9.2
Evermannellidae								
Odontostomops normalops (Parr, 1928)	2	4	3.7	134 (121–166)	11.9 (9.9–17.3)	FNR	610–900	4.3–5.6
Paralepididae								
Lestidiops affinis (Ege, 1930)	2	2	2.4	80 (58–102)	1.6 (1.6–1.7)	FNR	110–430	8.5–24.1
Lestrolepis intermedia (Poey, 1868)	2	1	1.2	–	5.7	FNR	90	25.1
Stemonosudis gracilis (Ege, 1933)	2	1	1.2	217	3.9	FNR	100	24.6
Stemonosudis intermedia (Ege, 1933)	1-2	4	3.7	130 (71–205)	1.1 (0.5–2.26)	FNR-PB	50–900	4.3–27.6
Stemonosudis siliquiventer Post, 1970	2	1	1.2	102		FNR	800	4.7
Alepisauridae								
Omosudis lowii Günther, 1887	2	10	7.3	82 (39–212)	7.2 (0.5–38.6)	FNR	385–900	4.3–9.2
MYCTOPHIFORMES								
Neoscopelidae								
Scopelengys tristis Alcock, 1890[1]	2	2	2.4	121 (98–145)	12.5 (5.34–19.71)	FNR	780–800	4.6–4.71
Myctophidae								
Benthosema suborbitale (Gilbert, 1913)	1-2	20	8.5	24 (13–31)	1.7 (0.21–3.3)	FNR-PB-RN	30–440	8.5–28.7
Bolinichthys distofax Johnson, 1975	2	85	11.0	62 (32–91)	6.4 (0.5–23.8)	FNR-PB-PE-RN	430–900	4.3–8.5
Bolinichthys photothorax (Parr, 1928)	1-2	55	13.4	53 (22–67)	5.8 (0.51–27.8)	FNR-PB	510–900	4.3–6.0
Bolinichthys supralateralis (Parr, 1928)	2	4	3.7	75 (50–92)	10.2 (6.6–16.3)	FNR	720–900	4.3–4.9
Ceratoscopelus warmingii (Lütken, 1892)	1-2	41	20.7	50 (18–74)	2.6 (0.5–6.2)	FNR-RN	30–900	4.3–28.7
Dasyscopelus asper (Richardson, 1845)	1-2	53	13.4	58 (14–75)	3.8 (0.9–7.1)	FNR-PE-RN	25–900	4.3–28.8
Dasyscopelus obtusirostre (Tåning, 1928)	1-2	17	9.8	66 (25–84)	5.0 (0.6–7.8)	FNR-PB-PE-RN	30–800	4.7–28.7

(Continued)

TABLE 1 Continued

Species	S	N	FO%	SL (mm)	TW (g)	Locality	Depth (m)	T (°C)
Dasyscopelus selenops (Tåning, 1928)	2	2	3.7	45 (27–59)	2.5 (2.2–2.8)	FNR-PE	430–900	4.3–8.5
Diaphus bertelseni Nafpaktitis, 1966	2	2	2.4	84 (74–94)	8.0 (6.8–9.3)	FNR-RN	100–385	9.2–24.7
Diaphus brachycephalus Tåning, 1928	1-2	470	29.3	38 (09–58)	1.5 (0.5–17)	FNR-PE-RN	30–1000	4.3–28.7
Diaphus dumerilii (Bleeker, 1856)	1-2	114	24.4	45 (26–59)	2.4 (0.5–11)	FNR-PB-PE-RN	65–900	4.3–26.5
Diaphus fragilis Tåning, 1928	1-2	147	24.4	49 (14–86)	2.6 (0.4–11.7)	FNR-PB-PE-RN	65–900	4.3–26.5
Diaphus garmani Gilbert, 1906	1-2	137	11.0	41 (25–51)	2.6 (0.5–9.9)	FNR-PE-RN	65–900	4.3–26.5
Diaphus lucidus (Goode & Bean, 1896)	2	43	11.0	76 (31–96)	5.3 (1.3–9.7)	FNR-PB-PE-RN	25–800	4.7–28.8
Diaphus mollis Tåning, 1928	1-2	52	20.7	48 (15–59)	1.9 (0.2–4.0)	FNR-RN	105–900	4.3–24.4
Diaphus perspicillatus (Ogilby, 1898)	1-2	279	20.7	49 (18–69)	2.1 (0.5–4.9)	FNR-PB-PE-RN	65–900	4.3–26.5
Diaphus problematicus Parr, 1928	1-2	4	3.7	69 (52–77)	4.1 (1.7–5.8)	FNR	430–720	4.9–8.5
Diaphus splendidus (Brauer, 1904)	1-2	241	18.3	53 (20–85)	2.3 (0.5–6.6)	FNR-PB-PE-RN	100–900	4.3–24.6
Diogenichthys atlanticus (Tåning, 1928)	1	9	3.7	18 (15–23)	0.5 (0.2–1.0)	FNR	60–525	6.0–26.6
Electrona risso (Cocco, 1829)	2	76	17.1	66 (50–81)	7.4 (3.2–12.4)	FNR-PB-RN	385–900	4.3–9.2
Hygophum hygomii (Lütken, 1892)	2	2	1.2	53 (52–54)	2.2 (1.9–2.4)	FNR	800	4.7
Hygophum macrochir (Günther, 1864)	1-2	28	8.5	50 (34–60)	1.9 (0.5–8.0)	FNR-PB	30–800	4.6–28.7
Hygophum reinhardtii (Lütken, 1892)	1-2	5	3.7	51 (24–76)	2.5 (1.2–6.8)	FNR	30–150	20.0–28.7
Hygophum taaningi Becker, 1965	1-2	108	12.2	51 (26–66)	1.9 (0.9–3.1)	FNR-RN	90–900	4.3–25.1
Lampadena luminosa (Garman, 1899)	1-2	29	4.9	28 (19–51)	2.2 (0.5–5.4)	FNR-PB-RN	100–900	4.3–24.6
Lampanyctus alatus Goode & Bean, 1896	2	2	1.2	37 (37–38)	3.5 (2.9–4.2)	FNR	430	8.5
Lampanyctus lineatus (Tåning, 1928)	1-2	5	4.9	137 (26–178)	19.0 (0.63–29.46)	FNR-PB	50–900	4.3–26.5
Lampanyctus festivus Tåning, 1928	2	4	1.2	87 (56–120)	6.8 (1.3–13.7)	FNR	900	4.3
Lampanyctus nobilis Tåning, 1928	1-2	285	29.3	19 (57–120)	2.6 (0.4–14)	FNR-PB-PE-RN	25–900	4.3–28.8
Lampanyctus tenuiformis (Brauer, 1906)	2	26	9.8	111 (44–149)	16.0 (0.7–46.4)	FNR-PE-RN	25–900	4.3–28.8
Lepidophanes guentheri (Goode & Bean, 1896)	1-2	219	29.3	48 (22–62)	3.6 (0.5–9.9)	FNR-PB-PE-RN	25–1000	4.3–28.8
Myctophum nitidulum Garman, 1899	1-2	12	11.0	59 (38–70)	3.6 (1.8–5.1)	FNR-PB-RN	30–800	4.7–28.7
Notoscopelus resplendens (Richardson, 1845)	2	2	2.4	75 (67–84)	3.1 (2.7–3.5)	FNR	430–780	4.6–8.54
Taaningichthys bathyphilus (Tåning, 1928)	2	10	4.9	62 (54–71)	1.7 (1.1–2.8)	FNR	720–900	4.3–4.98
LAMPRIFORMES								
Lophotidae								
Eumecichthys fiski (Günther, 1890)	2	1	1.2	1880	2190.0	FNR	780	4.6
Trachipteridae								
Desmodema polystictum (Ogilby, 1898)	2	1	1.2	74	1.0	FNR	800	4.7
Trachipterus sp. (Ramsay, 1881)	2	5	6.1	36 (18–55)	3.1 (0.1–7.0)	FNR-PE-RN	100–510	6.0–24.4
Zu cristatus (Bonelli, 1819)[1]	1-2	9	11.0	57 (10–89)	14.7 (0.1–93.1)	FNR-RN	20–720	4.9–26.7
STYLEPHORIFORMES								
Stylephoridae								
Stylephorus chordatus Shaw, 1791[1]	1-2	64	18.3	176 (59–279)	3.7 (0.5–11.0)	FNR-PB-RN	25–900	4.3–28.8
GADIFORMES								
Melanonidae								
Melanonus zugmayeri Norman, 1930	2	21	11.0	115 (64–265)	11.6 (1.0–11.9)	FNR	95–900	4.3–24.7
Macrouridae								
Bathygadus sp.*	2	2	1.2	76 (72–81)	1.3 (1.0–1.5)	FNR	900	4.3
Macrouroides inflaticeps Smith & Radcliffe, 1912	2	2	2.4	197 (179–215)	91.4 (67.4–115.4)	FNR	800–900	4.3–4.7
Bregmacerotidae								
Bregmaceros cf. *atlanticus* Goode & Bean, 1886	1-2	20	7.3	65 (32–85)	1.9 (0.5–4.4)	FNR-RN	90–800	4.7–25.1
TRACHICHTHYIFORMES								
Anoplogastridae								
Anoplogaster cornuta (Valenciennes, 1833)	2	4	3.7	100 (85–107)	31.2 (18.3–43.4)	FNR-RN	610–800	4.7–5.6

(Continued)

TABLE 1 Continued

Species	S	N	FO%	SL (mm)	TW (g)	Locality	Depth (m)	T (°C)
Diretmidae								
Diretmoides pauciradiatus (Woods, 1973)	1-2	23	8.5	26 (4–62)	3.4 (0.5–8.5)	FNR	85–900	4.3–25.4
Diretmus argenteus Johnson, 1864	2	116	13.4	53 (14–75)	8.1 (0.6–67.4)	FNR	430–900	4.3–8.5
Trachichthyidae								
Aulotrachichthys argyrophanus (Woods, 1961)	2	6	3.7	28 (24–34)	1.2 (0.7–1.5)	FNR	230–780	4.6–12.4
BERYCIFORMES								
Rondeletiidae								
Rondeletia loricata Abe & Hotta, 1963	1-2	3	3.7	55 (32–78)	4.8 (1.2–10.4)	FNR	525–900	4.3–6.8
Cetomimidae								
Cetomimus sp.*[4]	2	2	2.4	64 (39–65)	1.8 (1.5–2.1)	FNR-PE	680–780	4.6–5.2
Cetostoma regani Zugmayer, 1914	1-2	5	4.9	98 (81–114)	5.8 (1.6–18.4)	FNR	525–900	4.3–6.8
Ditropichthys storeri (Goode & Bean, 1895)[4]	2	1	1.2	49	1.5	FNR	610	5.6
Gyrinomimus bruuni Rofen, 1959[4]	2	2	1.2	63 (60–66)	8.6 (1.2–16.1)	FNR	900	4.3–4.3
Melamphaidae								
Melamphaes eulepis Ebeling, 1962[4]	2	10	4.9	43 (35–47)	20.3 (10.8–24.6)	FNR	430–900	4.3–8.5
Melamphaes leprus Ebeling, 1962[4]	2	1	1.2	80	14.0	FNR	430	8.5
Melamphaes longivelis Parr, 1933[4]	2	2	2.4	75 (74–75)	46.8 (8.0–85.7)	FNR	630–780	4.6–5.6
Melamphaes polylepis Ebeling, 1962	2	37	9.8	53 (36–70)	34.1 (2.0–60.0)	FNR-PE	610–900	4.3–5.6
Melamphaes typhlops (Lowe, 1843)	2	7	7.3	54 (37–71)	31.6 (1.0–60.8)	FNR-PE	430–900	4.3–8.5
Melamphaes sp.** [4]	2	1	1.2	62	43.9	FNR	900	4.3
Poromitra megalops (Lütken, 1878)	1-2	27	9.8	46 (25–59)	1.8 (0.5–4.2)	FNR-RN	525–900	4.3–6.8
Poromitra sp.**	1-2	28	11.0	85 (48–121)	10.6 (1.3–37.3)	FNR-PE-RN	45–1000	4.3–8.5
Scopeloberyx opercularis Zugmayer, 1911	2	1	1.2	32	3.9	FNR	780	4.6
Scopeloberyx opisthopterus (Parr, 1933)	2	4	3.7	29 (25–32)	2.7 (1.9–3.6)	FNR	720–900	4.7–4.9
Scopelogadus mizolepis (Günther, 1878)	1-2	19	9.8	54 (37–70)	9.8 (0.8–39.1)	FNR	430–900	4.3–8.5
OPHIDIIFORMES								
Bythitidae								
Bythitidae sp.*	2	2	2.4	87 (86–89)	2.7 (2.6–2.8)	FNR-PE	680–900	4.3–5.26
KURTIFORMES								
Apogonidae								
Paroncheilus affinis (Poey, 1875)	1	1	1.2	28	4.2	RN	75	25,6
PERCIFORMES								
Howellidae								
Bathysphyraenops simplex Parr, 1933[5]	1	3	3.7	65 (41–78)	7.5 (5.0–9.0)	FNR	525–900	4.3–6.8
Howella atlantica Post & Quéro, 1991	2	25	8.5	58 (52–69)	4.0 (2.6–6.5)	FNR-PE	680–900	4.3–5.2
Bramidae								
Brama brama (Bonaterre, 1788)	2	1	1.2	28	1.0	FNR	900	4.3
Brama caribbea Mead, 1972	1-2	64	15.9	25 (12–55)	2.0 (0.4–9.8)	FNR-PE-RN	58–900	4.3–26.6
Taractichthys longipinnis (Lowe, 1843)	2	1	1.2	32	1.3	PE	240	14.8
Caristiidae								
Paracaristius nudarcus Stevenson & Kenaley, 2011[6]	2	1	1.2	175	181	FNR	430	8.5
Platyberyx andriashevi (Kukuev, Parin & Trunov, 2012)[6]	2	3	2.4	68 (24–149)	31.2 (1.1–87.8)	FNR	230–800	4.7–12.4
Platyberyx paucus Stevenson & Kenaley, 2013[6]	2	3	3.7	95 (92–98)	33.4 (31.1–36.7)	FNR-RN	630–800	4.7–5.6
Platyberyx pietschi Stevenson & Kenaley, 2013[6]	2	1	1.2	74	9.2	RN	630	5.6
SCOMBROLABRACIFORMES								
Scombrolabracidae								
Scombrolabrax heterolepis Roule, 1921	2	1	1.2	76	6.1	FNR	900	4.3
SCOMBRIFORMES								

(Continued)

TABLE 1 Continued

Species	S	N	FO%	SL (mm)	TW (g)	Locality	Depth (m)	T (°C)
Gempylidae								
Gempylus serpens Cuvier, 1829	1-2	3	3.7	68 (44–112)	1.1 (0.9–1.3)	FNR	70–900	4.3–25.8
Lepidocybium flavobrunneum (Smith, 1843)	1	1	1.2	36	4.1	FNR	110	24.0
Nesiarchus nasutus Johnson, 1862	2	4	3.7	107 (85–145)	1.7 (0.7–2.8)	FNR	90–800	4.7–25.1
Promethichthys prometheus (Cuvier, 1832)	1	15	1.2	154 (112–191)	20.2 (15.0–34.0)	FNR	150	20.6
Nomeidae								
Cubiceps pauciradiatus Günther, 1872	2	10	7.3	91 (75–129)	13.2 (6.7–30.3)	FNR	65–720	4.9–26.5
Psenes cyanophrys Valenciennes, 1833	1-2	5	3.7	86 (14–133)	38.9 (8.9–70.2)	FNR	25–570	6.3–28.8
Trichiuridae								
Aphanopus intermedius Parin, 1983[7]	2	1	1.2	720	550	FNR	610	5.7
TRACHINIFORMES								
Chiasmodontidae								
Chiasmodon braueri Weber, 1913	2	2	1.2	82 (70–95)	2.9 (2.2–3.7)	FNR	900	4.3
Chiasmodon niger Johnson, 1864	2	1	1.2	90	7.9	FNR	800	4.7
Kali kerberti (Weber, 1913)	2	5	4.9	127 (69–170)	11.8 (1.1–29.3)	FNR	720–800	4.6–4.9
Pseudoscopelus cordilluminatus Melo, 2010[1]	2	2	2.4	44 (31–57)	3.3 (2.2–4.3)	FNR-PE	240–800	4.7–14.8
Pseudoscopelus scutatus Krefft, 1971	2	2	2.4	71 (67–75)	2.3 (2.0–2.7)	FNR	430–900	4.3–8.5
SCORPAENIFORMES								
Setarchidae								
Ectreposebastes imus Garman, 1899	2	27	4.9	167 (29–234)	144.0 (0.8–290.3)	FNR	90–800	4.7–25.1
CAPROIFORMES								
Caproidae								
Antigonia capros Lowe, 1843	2	1	1.2	29	1.9	FNR	440	8.5
Antigonia combatia Berry & Rathjen, 1959	2	1	1.2	38	2.7	FNR	800	4.7
LOPHIIFORMES								
Ceratiidae								
Ceratias uranoscopus Murray, 1877	2	1	1.2	76	8.1	FNR	800	4.7
Himantolophidae								
Himantolophus spp.*	1-2	13	12.2	30(9–50)	1.6(0.5–5.3)	FNR-RN	35–900	4.6–27.4
Melanocetidae								
Melanocetus johnsonii Günther, 1864	1-2	5	4.9	16 (14–19)	1.6 (0.7–3.3)	FNR	58–900	4.3–26.6
Thaumatichthyidae								
Thaumatichthys sp.*[8]	2	1	1.2	32	0.3	FNR	900	4.3
Oneirodidae								
Chaenophryne draco Beebe, 1932	2	2	2.4	72 (55–90)	60.3 (12.0–108.7)	FNR-PE	680–900	4.3–5.2
Chaenophryne ramifera Regan & Trewavas, 1932[8]	2	4	4.9	41 (32–50)	3.6 (2.5–6.2)	FNR-PE	505–800	4.7–7.0
Dolopichthys sp.*[8]	2	1	1.2	35	0.7	FNR	900–900	4,3
Oneirodes anisacanthus (Regan, 1925)[8]	2	2	2.4	39 (30–48)	3.0 (1.1–4.9)	FNR	505–900	4.3–7.0
Oneirodes carlsbergi (Regan & Trewavas, 1932)[8]	2	2	2.4	59 (19–98)	32.6 (0.4–64.8)	FNR-PE	680–720	4.9–5.2
Caulophrynidae								
Caulophryne sp.*[8]	1	1	1.2	6	0.2	FNR	68	24.5
Gigantactinidae								
Gigantactis watermani Bertelsen, Pietsch & Lavenberg, 1981[8]	2	1	1.2	170	45.1	FNR	900	4.7
Rhynchactis sp.*[8]	2	2	2.4	78 (42–113)	6.7 (4.0–9.4)	FNR-RN	720–780	4.6–4.9

*Specimen(s) damaged. **Potential new species. [1]Mincarone et al. (2022), [2]Mincarone et al. (2021a), [3]Villarins et al. (2022), [4]Afonso et al. (2021), [5]Eduardo et al. (2019), [6]Mincarone et al. (2019), [7]Eduardo et al. (2018b), [8]Mincarone et al. (2021b).
Classification follows Nelson et al. (2016), with exceptions noted in Villarins et al. (2022) for the Stomiiformes. Superscript numbers indicate species recorded for the first time in the Brazilian Exclusive Economic Zone and their respective references.

indicating that more species would be recorded with additional sampling using the same gears (Figure 2). Indeed, richness estimators indicated that about 100 (50%) additional mesopelagic species of fishes are expected to occur in the area (Figure 2). Additionally, 759 specimens representing about 40 fish taxa were sampled. However, they could not be identified to species level given their small size and/or poor condition. As it was not possible to determine whether these specimens belong to species not listed in Table 1, they were placed in a separate list to ensure a more robust assessment of species diversity (Supplementary Material 3).

Ranges of standard length (SL) and wet weight for all species collected on the two surveys are provided in Table 1. Overall, a wide size range was sampled, from 4 mm (*Diretmoides pauciradiatus*) to 1,880 mm SL (*Eumecichthys fiski*, Lophotidae). However, 90% of the specimens measured between 30 and 200 mm SL (Supplementary Material 4)

The five orders with the highest number of species were the Stomiiformes (at least 62 species, four families), Myctophiformes (35 spp., two families), Aulopiformes (18 spp., seven families), Beryciformes (16 spp., three families), and Lophiiformes (12 spp., seven families), accounting for 70% of the total number of species recorded on the two surveys. Thirteen orders included less than five species each. Considering families, the most representative were the Stomiidae (38 spp.), Myctophidae (34 spp.), Melamphaidae (11 spp.), Sternoptychidae (10 spp.), and Gonostomatidae (7 spp.) (Figure 3). Half of the families (28) were represented by a single species.

In terms of abundance, the most representative families when considering the two surveys were the Myctophidae (Myctophiformes; 36%), Sternoptychidae (Stomiiformes; 26%), Gonostomatidae (Stomiiformes; 16%), Stomiidae (Stomiiformes; 8%), and Melamphaidae (Beryciformes; 2%) (Figure 3). These families together accounted for 88% of all specimens collected. The remaining families represented individually no more than 2% of the total number of specimens collected. At the alpha taxonomic level, the following taxa represented almost 50% of all specimens collected: *Sternoptyx diaphana* (14%), *Cyclothone* spp. (11%; see Discussion), *Diaphus brachycephalus* (6%), *Argyropelecus affinis* (6%), *Chauliodus sloani* (5%), *Lampanyctus nobilis* (4%), and *Diaphus perspicillatus* (4%). About 126 species were represented by five specimens or less, of which 62 were represented by a single specimen.

Considering biomass, the most representative families were the Myctophidae (24%), Stomiidae (21%), Setarchidae (Scorpaeniformes, 11%), Sternoptychidae (10%), and Melamphaidae (7%) (Figure 3). These families together accounted for 73% of the biomass of all fishes collected. The remaining families individually accounted for less than 4% of the total weight. At the specific level, the following species represented 42% of the biomass: *Ectreposebastes imus* (11%), *Chauliodus sloani* (9%), *Borostomias elucens* (6%), *Eumecichthys fiski* (6%, a single specimen), *Sternoptyx diaphana* (4%), *Melamphaes polylepis* (3%), and *Argyropelecus affinis* (3%).

Distribution, vertical migration, biodiversity indexes, and size

Based on the two campaigns, 60 species (29%) were recorded in a wide longitudinal distribution (Table 1). In contrast, 133 species (64%) were collected only in a few localities, with 116 being restricted to the Fernando de Noronha Ridge area, which aggregates most specimens collected (Table 1). Considering depth and period, the highest diversity, abundance, and biomass were found between depths of 700 and 1,000 m during the day (Figure 4). At night, the highest number of species was recorded at lower mesopelagic depths (500–1,000 m). However, much larger values of number of species, abundance, and biomass were detected in shallow waters (0–

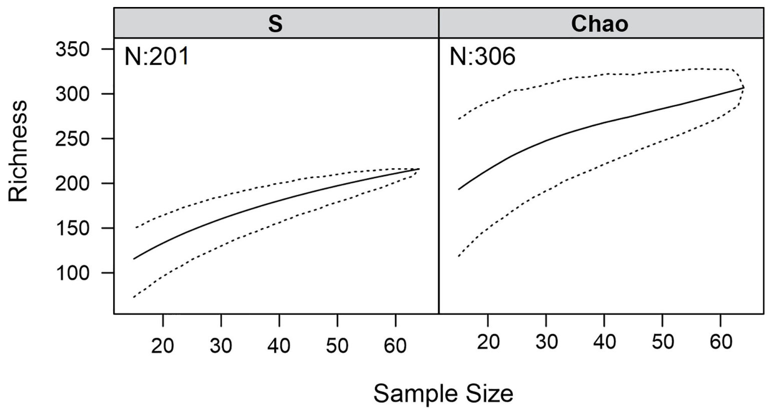

FIGURE 2
Species accumulation (S) and Chao1 estimator for ABRACOS 1 and 2 together. Dashed lines represent the confidence interval of 95%.

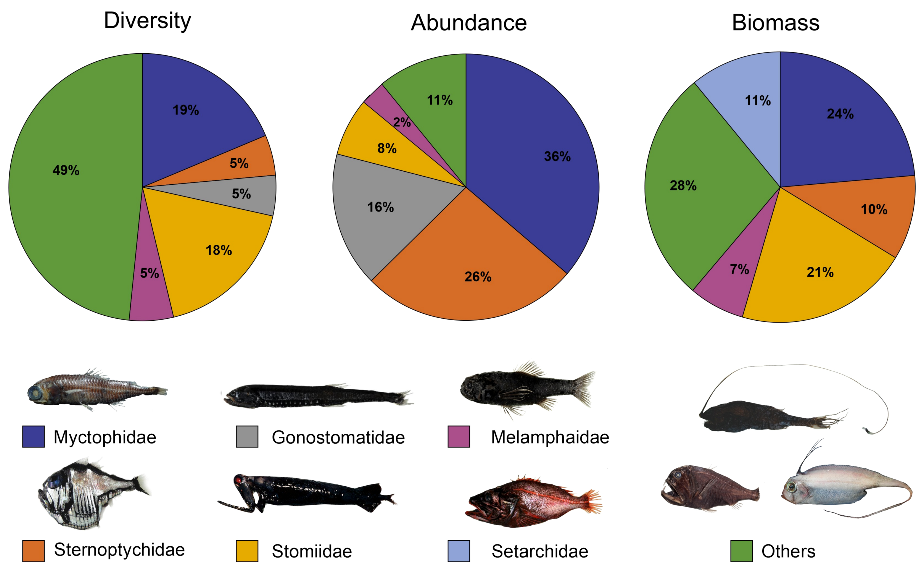

FIGURE 3
Main mesopelagic fish families collected on the surveys ABRACOS 1 and ABRACOS 2 when considering diversity, abundance, and biomass. Fish images represent only examples of species included in the group.

200 m), likely reflecting the ascent in the water column of several species at night. At least 50 species seem to have a wide range of depth distribution and tolerance to variations in water temperature (up to 800 m and 25°C; e.g., species of Sternoptychidae and Myctophidae). However, 66 species seem to be restricted to deeper (> 600 m) and colder waters (< 6° C) regardless of the time period (e.g., Lophiiformes and Beryciformes; Table 1).

Significant differences in biodiversity indexes (calculated only for ABS2, see methodology) were found when considering diel periods and depth. Higher values of richness and diversity were found in lower mesopelagic waters and during the daytime. However, dominance values were significantly higher in epipelagic waters and also during daytime (Figure 5). Detailed values for the calculated indexes are given in the Supplementary Material 5.

Discussion

Diversity and distribution

Based on our two campaigns, at least 201 species of mesopelagic fishes occur in the SWTA. Results also indicate that about 100 additional species could have been collected if sampling efforts were increased. The taxonomically diverse pool of mesopelagic species recorded in our surveys also reveals a vast array of diversity not only in terms of the number of species but also in terms of size, anatomy, and behaviour. In a recent global biogeographic classification of the mesopelagic zone (Sutton et al., 2017), the Tropical and western Equatorial Atlantic, which is the larger area encompassing the SWTA, was not considered a region particularly diverse in terms of mesopelagic fishes. However, the mesopelagic species richness revealed by our two campaigns is higher than those reported for other parts of the world, such as the Mediterranean (25 spp.; Olivar et al., 2012), central Equatorial Pacific (113 spp.; Barnett, 1984), southwestern Indian Ocean (121 spp.; Cherel et al., 2020), eastern Equatorial Atlantic (132 spp.; Olivar et al., 2017), and South China Sea (169 spp.; Wang et al., 2019). The species richness of mesopelagic fishes in the SWTA is actually more similar to that reported for the North Pacific (228 spp.; Barnett, 1984) and the Gulf of Mexico (approximately 300 spp.; Sutton et al., 2020), which are considered as comprising some of the most speciose deep-sea ichthyofaunas of the world (Sutton et al., 2017). Major factors driving deep-sea biodiversity, such as climate, seabed structure, water masses, and phylogenetic history, are likely responsible for the variation in species richness of different parts of the world. However, an asymmetry in collecting effort is certainly affecting the values recorded so far. In the Gulf of Mexico, a much higher sampling effort has been deployed to assess the deep-sea diversity compared with most regions of the world, with several expeditions conducted only in the last decade (Sutton et al., 2020). That situation is in striking contrast with the SWTA, where just a handful of expeditions to assess deep-sea diversity have been conducted in the last centuries.

The relatively high number of mesopelagic species of fishes recorded in our two campaigns is likely related to the diversity of

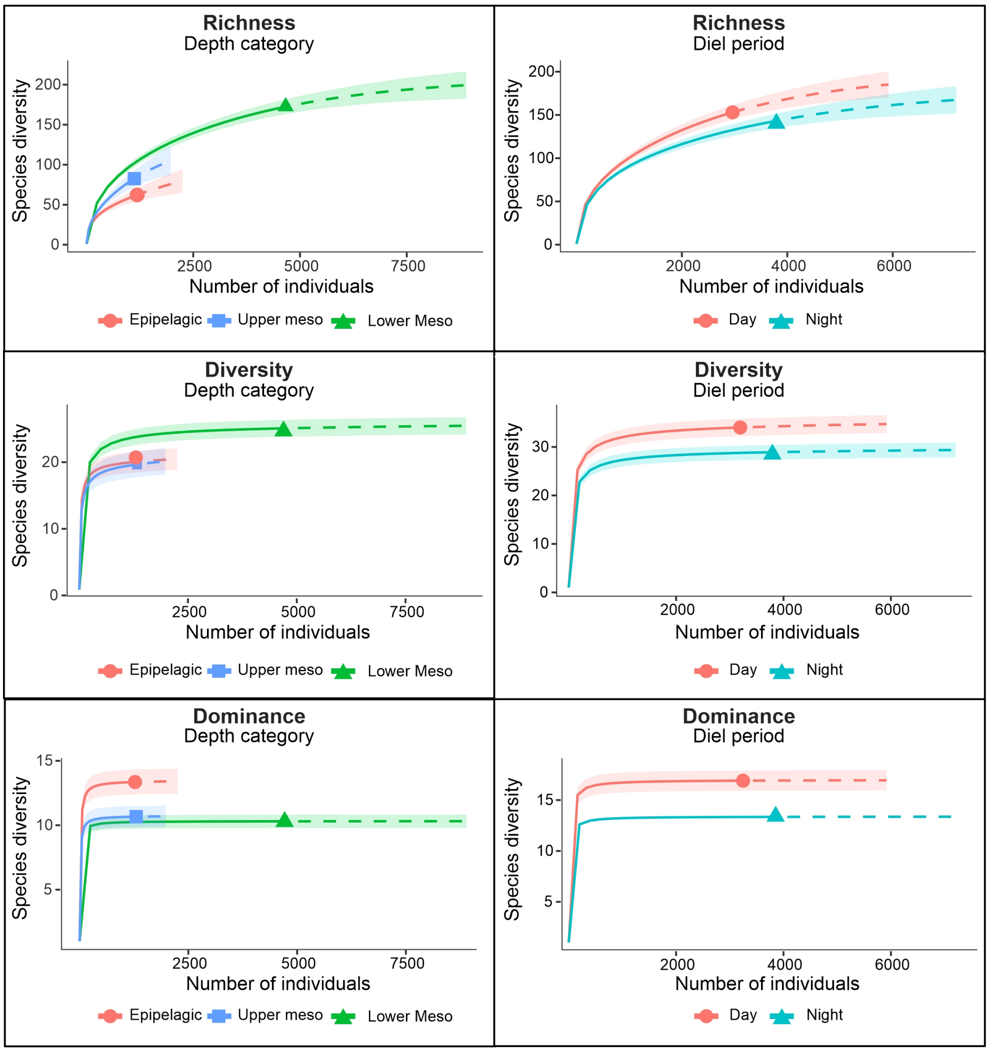

FIGURE 4
Sample-size-based rarefaction (solid line segment) and extrapolation (dotted line segments) sampling curves for species richness, diversity, and dominance of mesopelagic fish data at different depth categories and diel periods. Curves include the confidence intervals of 95% (shaded areas). For this analysis, only species recorded in the ABRACOS 2 survey were considered.

habitats and the high variability of oceanographic processes of the SWTA. Despite being located in an oligotrophic portion of the ocean, this region is also characterized by the presence of underwater canyons, oceanic islands, and several seamounts that interact with local currents and enhance marine productivity (Travassos et al., 1999; Tchamabi et al., 2017; Costa da Silva et al., 2021). As an example, small uplifting processes have been reported along the shelf-break and oceanic islands of the region (Travassos et al., 1999; MMA, 2006; Tchamabi et al., 2017; Silva et al., 2022), a situation that has been directly associated with the occurrence of hotspots of fish biodiversity (Hazin, 1993; Eduardo et al., 2018; Eduardo et al., 2020a). Distinct biogeographic provinces, with different thermodynamic features, current systems and water mass properties, are also present in the SWTA (Bourlès et al., 1999; Assunção et al., 2020; Costa da Silva et al., 2021; Dossa et al., 2021; Tosetto et al., 2021). This results in a high complexity of habitats and oceanographic conditions that likely contribute to higher levels of species diversity (Levin et al., 2001).

The highest levels of richness and diversity (considering only specimens collected during AB2, see methodology) were found at lower mesopelagic depths (500–1,000 m), with several species collected only at these depths (e.g., species of the Beryciformes and Lophiiformes). Interestingly, many of these species are considered bathypelagic and/or benthopelagic (Priede, 2017; Melo et al., 2020). The collection of those species in mesopelagic waters is likely related to the presence of seamounts and oceanic islands. In addition to being related to

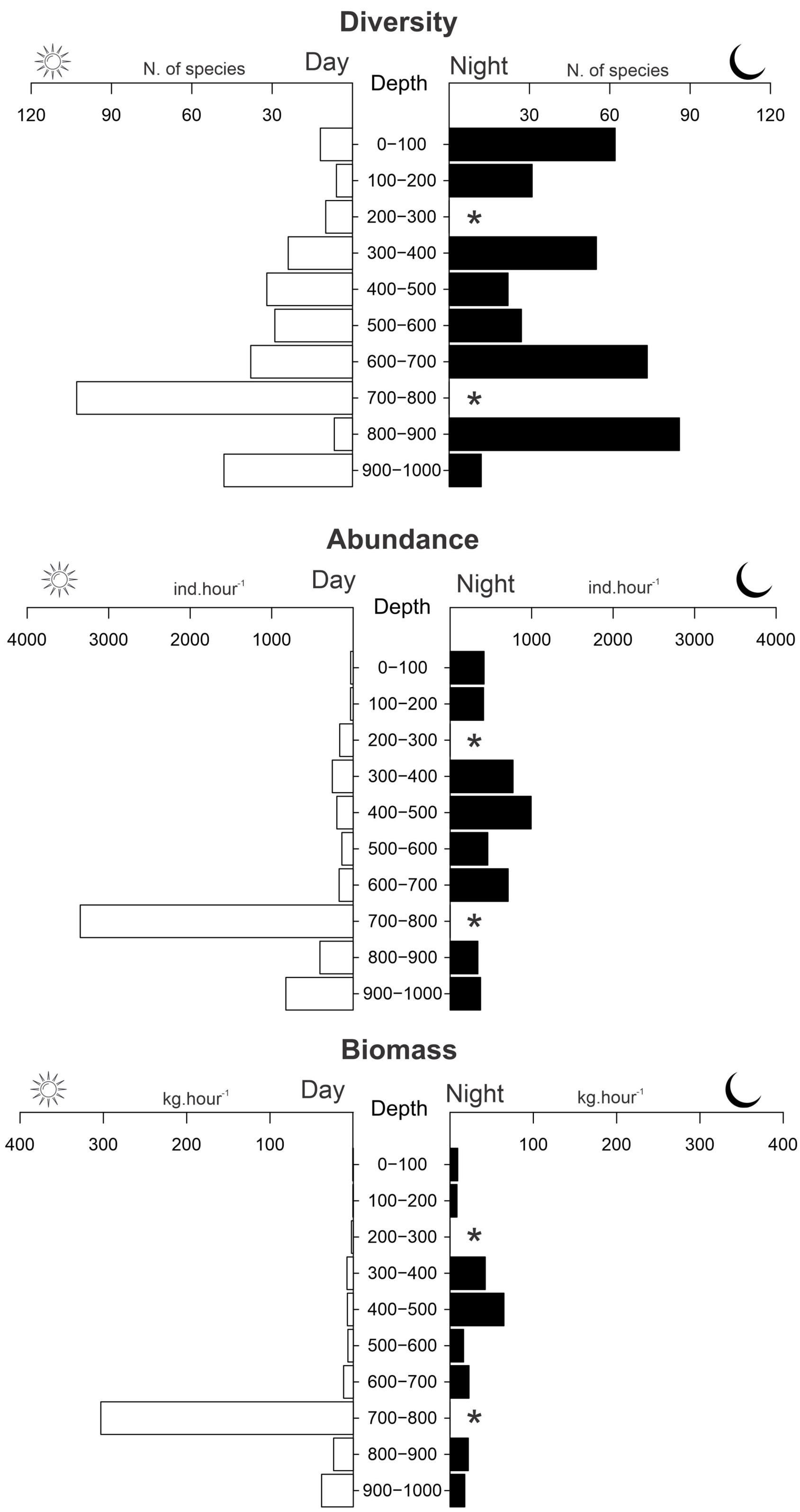

FIGURE 5
Number of species and average values of abudance (individuals.hour^{-1}) and biomass (kg.hour^{-1}x10^{2}) of mesopelagic species of fishes collected on the survey ABRACOS 2. *Depth strata not sampled.

an increase in habitat complexity, seamounts may increase the occurrence of pelagic and benthic predators that actively seek these areas to hunt for prey trapped by flow-topographic processes (Cascão et al., 2019). For instance, in the Azorean seamounts plateau, the micronekton community is dominated by non- or weakly migratory benthopelagic fishes (Cascão et al., 2019). In summary, our results also seem to indicate that seamounts play a significant role in the biodiversity structuring and ecology of mesopelagic fishes in the SWTA.

The two surveys conducted during this study resulted in different patterns of species richness. For example, 17 species were exclusively recorded in AB1 (mesopelagic trawl), whereas 136 species were recorded only in AB2 (micronekton trawl). The two campaigns were conducted in different seasons. However, since the study area is located in a tropical region, few oceanographic differences were noted in the mesopelagic zone (for further info refer to Assunção et al., 2020; Costa da Silva et al., 2021; Dossa et al., 2021). Therefore, the significant disparity in species richness between the two expeditions is clearly related to differences in sampling strategies. The use of multiple sampling gears is vital to maximizing the representation of fish diversity (Magurran, 2004), especially in the deep-sea. However, the sampling strategy used in AB2, which included the use of larger gear, with greater mesh sizes, deeper hauls, and broader sampling area, resulted in the collection of a higher number of specimens of different species in a broader size range (Supplementary Material 2 and 3).

In terms of taxonomic composition, five families of the Teleostei accounted for 52% of the species richness, 88% of the specimens, and 66% of the total biomass collected on the two surveys: the Stomiidae (38 spp., 8% of the specimens, 21% of the biomass), Myctophidae (34 spp., 36%, 24%), Melamphaidae (11 spp., 2%, 7%), Sternoptychidae (9 spp., 26%, 10%), and Gonostomatidae (7 spp., 16%, 4%). These families, therefore, seem to be the most represented in the mesopelagic fish fauna of the SWTA. The dominance of these families in mesopelagic waters has also been reported in other parts of the world (e.g., Gjøsaeter and Kawaguchi, 1980; Olivar et al., 2017; Wang et al., 2019; Cherel et al., 2020). A strong pattern of dominance was also observed within these families, with few species accounting for 50% of the total number of specimens: *Sternoptyx diaphana* (14%), *Cyclothone* spp. (11%), *Argyropelecus affinis* (6%), *Diaphus brachycephalus* (6%), *Chauliodus sloani* (5%), *Diaphus perspicillatus* (4%), and *Lampanyctus nobilis* (4%). The pattern of dominance at the species level detected in the SWTA was, however, distinct from other parts of the world. In the Eastern Tropical Atlantic, for instance, the lanternfishes *B. suborbitale*, *C. warmingii*, and *H. macrochir* were dominant (Olivar et al., 2017), whereas these same species were considered rare in our study. The viperfish *C. sloani* is usually globally recorded in low abundances (e.g., Olivar et al., 2017; Wang et al., 2019; Cherel et al., 2020), whereas the species is among the most relevant mesopelagic species in the SWTA considering the abundance and total weight (Eduardo et al., 2020c). These differences in the pattern of dominance at the species level in different parts of the world are likely associated with different sampling strategies employed and differences in oceanographic and biogeographic features (e.g., seabed structure, water masses, and hydrographic fronts), which are major factors driving the structure and composition of mesopelagic assemblages (Hulley and Krefft, 1985; Olivar et al., 2017; Cascão et al., 2019). *Cyclotone* is another seemingly abundant genus of mesopelagic fish in the SWTA (Olivar et al., 2017). Eight species of the genus were reported for the SWTA: *C. acclinidens*, *C. alba*, *C. braueri*, *C. microdon*, *C. obscura*, *C. pallida*, *C. parapallida*, and *C. pseudopallida* (Villarins et al., 2022) The sampling gears employed in the study, however, seemed to be only partially adequate to collect specimens of the genus. In several trawls we observed onboard that a substantial number of specimens of *Cyclothone* escaped back into the sea during the hoisting of the net. Additionally, given their poor condition of preservation, specimens of the genus could not be identified at species level. Therefore, the abundance of species of *Cyclothone* presented here is underestimated.

Notable records

Among the 201 species of mesopelagic fishes recorded during the ABRACOS expeditions, 50 (25%) represent new records for Brazilian waters, all of which have been dealt with in a series of recent papers (Table 1). In addition to these new records, eight species (five *Eustomias*, one *Melanostomias*, one *Melamphaes*, and one *Poromitra*) are potentially new and will be formally described later. Several species recorded here are also rare worldwide, and their occurrence in the SWTA adds new information on their global distribution. For instance, three specimens of *Platyberyx paucus* and one of *Platyberyx pietschi* were collected during the AB2. Before these records, only four specimens of *P. paucus* were known, from the central North Pacific and western Central Atlantic. *Platyberyx pietschi*, in turn, was known from just two specimens collected in the western Central Atlantic, one specimen collected in the central Pacific, and another from the western South Pacific (Stevenson and Kenaley, 2013; Mincarone et al., 2019). Other species considered rare worldwide that were collected in the ABRACOS expeditions are *Aulotrachichthys argyrophanus*, *Rhynchohyalus natalensis*, *Eumecichthys fiski*, *Macrouroides inflaticeps*, *Pseudoscopelus cordilluminatus*, *Melamphaes leprus*, and *Gigantactis watermani* (Pimentel et al., 2020; Afonso et al., 2021; Mincarone et al., 2021b; Mincarone et al., 2022).

Role of international cooperation for the decade of deep ocean science

The high number of new records made during the ABRACOS expeditions reflects not only the high diversity of the SWTA, but also the overall lack of scientific information on deep-sea diversity in the region, as noted previously (e.g., Reis et al., 2016; Mincarone et al., 2022). The United Nations Decade of Ocean Science roadmap recognizes the deep-sea as a frontier of science and discovery (Ryabinin et al., 2019). There is an unequal capacity to conduct science among nations, with developing economies facing substantial barriers to participating in deep-sea research. Consequently, the least-studied parts of the deep-sea are located off the least economically developed countries (Howell et al., 2020). These biases are highlighted by the fact that a French research institution financed the surveys described here, and that those expeditions are among the very few that have addressed the mesopelagic ichthyofauna of Brazil. To achieve sustainability, we need a well-known and predictable ocean. Only by thinking globally and strengthening international cooperation we will develop an ocean research that corrects asymmetry in funding and knowledge among countries, meeting the crucial need for a more encompassing deep-sea knowledge aimed at the conservation and sustainable use of its unique habitats.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Ethics statement

All collecting methods and specimen handling procedures were approved and carried out in accordance with relevant guidelines and regulations of the Brazilian Ministry of Environment (SISBIO; authorization number: 47270–5).

Author contributions

All co-authors declare no competing interests and agree with the submission of this manuscript. All authors significantly contributed to the development of the article.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2022.937154/full#supplementary-material

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