



The deep sea teleost fish fauna of the Brazilian North Coast

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Data on the deep sea fishes found off the northern Brazilian coast are restricted to the results of the surveys of the RV Oregon, a research vessel of the North American National Marine Fisheries Service, and the REVIZEE Program. The REVIZEE Score-Norte Program focused on commercial fish species and natural resources with potential for exploitation on the continental shelf and slope off the northern coast of Brazil. In this sense, the REVIZEE Score-Norte Program generated little information on species of no commercial value, did not catalog its inventory in zoological collections, and did not publish species lists. Given this considerable knowledge gap on the deep-sea fish found off the North coast of Brazil, we compiled all the available data on the deep-sea fish of this region and also retrieved photographic records from the REVIZEE Score-Norte Program, including the PRODEMERSAL and PROTUNA projects. Considering the published records, specimens deposited in zoological collections, and the interpretation of photographic records, we compiled a list of 63 species of deep-sea fish from the North coast of Brazil. An additional 30 species were found in the published records from the PRODEMERSAL and PROTUNA, but were considered to be doubtful or pending confirmation.

Keywords: Inventory, Marine biodiversity, PRODEMERSAL, PROTUNA, REVIZEE Score-Norte.

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Os dados sobre peixes de profundidade encontrados na costa Norte do Brasil são restritos aos resultados de coletas realizadas pelo RV Oregon, um navio do Serviço Nacional de Pesca Marítima da América do Norte, e do Programa REVIZEE. O Programa REVIZEE Score-Norte teve como foco as espécies de peixes com valor comercial e recursos naturais com potencial para exploração na plataforma continental da costa Norte do Brasil. Contudo, o REVIZEE Score-Norte gerou pouca informação sobre as espécies sem valor comercial, não catalogou o material da biodiversidade inventariada, assim como não gerou listas de espécies. Dada a lacuna no conhecimento sobre os peixes de profundidade da costa norte do Brasil, nós compilamos todos os dados disponíveis e recuperamos registros fotográficos do Programa REVIZEE Score-Norte, incluindo os projetos PRODEMERSAL e PROTUNA. Considerando os registros publicados, espécimes depositados em coleções zoológicas e os registros fotográficos, apresentamos uma lista de 63 espécies de peixes de profundidade na costa Norte do Brasil. Outras 30 espécies encontradas nos registros publicados do PRODEMERSAL e PROTUNA, foram consideradas duvidosas, carecendo de confirmação.

Palavras-chave: Biodiversidade marinha, Inventário de fauna, PRODEMERSAL, PROTUNA, REVIZEE Score-Norte.

INTRODUCTION

The northern Brazilian coast comprises the region between the mouths of the rio Oiapoque, which forms the frontier between Brazil and French Guiana, and the rio Parnaíba, which marks the frontier between the Brazilian states of Maranhão and Piauí. Considered to be one of the most productive regions in the Brazilian Exclusive Economic Zone (EEZ), the Brazilian North Coast is part of one of the world's most important fishing grounds, with a total area of approximately 223,000 km², which extends northward to the mouth of the Orinoco River, in Venezuela (Corrêa, Martinelli, 2009). Despite its considerable importance in ecological, biogeographical, and economic terms, the fish fauna of the North Coast is still poorly known (Marceniuk *et al.*, 2013, 2019). Although some inventories on the coastal fish fauna have been conducted (Eskinazi, Lima, 1968; Rocha, Rosa, 2001; Espírito-Santo, Isaac, 2005; Moura *et al.*, 2016; Marceniuk *et al.*, 2017, 2019), information on the deep-sea fishes is restricted basically to the results of two long-term surveys. One of these surveys was undertaken by the Oregon, a research vessel of the North American National Marine Fisheries Service, while the other was part of the Brazilian National Program for the Assessment of the Sustainable Potential of Natural Resources in the Exclusive Economic Zone (REVIZEE).

The RV Oregon conducted the most complete inventory of marine fishes off the northern coast of Brazil between 1957 and 1969. The results of this study indicated that this fish fauna is closely similar to that found off French Guiana, as well as providing the first evidence of the existence of a coral barrier off the mouth of the Amazon River (Collette, Rützler, 1977). The surveys carried out by the National Marine Fisheries Service generated an enormous amount of scientific material, which is deposited in North

American zoological collections, as well as the publication of a number of taxonomic studies, including species descriptions, many of deep-water fishes, such as *Centrodraco oregonus* (Briggs, Berry, 1959), *Scorpaena petricola* Eschmeyer, 1965, *Scorpaena melasma* Eschmeyer, 1965, *Schroederichthys tenuis* Springer, 1966, *Malacocephalus okamurai* Iwamoto, Arai, 1987, and *Neobythites brasiliensis* Nielsen, 1999.

The REVIZEE Score-Norte Program began to survey the northern Brazilian coast in 1996, sampling commercially-valuable natural resources and species with potential for exploitation on the continental shelf and slope (Lucena, Asano-Filho, 2006). However, this program generated little information on species with little or no commercial value, did not catalog specimens in zoological collections or publish species lists. Two distinct projects were developed within the scope of the REVIZEE Score-Norte Program: the PROTUNA, *Desenvolvimento Tecnológico para a captura de Grandes Pelágicos Oceânicos na Costa Norte do Brasil*, which was operational between 2000 and 2002 (Asano-Filho *et al.*, 2004); and the PRODEMERSAL, *Desenvolvimento Tecnológico para a Captura de Recursos Demersais com Arrasto na região Norte do Brasil*, which ran between 2002 and 2004 (Asano-Filho *et al.*, 2005). These two projects focused on the prospecting of potentially exploitable stocks of large pelagic fish and deep sea demersal species, respectively, and did generate species lists (Asano Filho *et al.*, 2004, 2005). However, both projects presented the same general deficiencies as the REVIZEE Score-Norte Program, and did not contribute to the scientific cataloging of the fish species from the northern coast of Brazil. A single exception is a very rare record of the occurrence of the goblin shark (*Mitsukurina owstoni* Jordan, 1898) in Brazil, through a specimen that is currently housed in the Univali Oceanographic Museum (MOVI), Santa Catarina, Brazil (see Asano-Filho *et al.*, 2005). No other specimens from the REVIZEE Score-Norte program is available for examination in museums.

Given the knowledge gap that exists on the deep-sea fish fauna of the northern coast of Brazil, we compiled all the available data on the region's deep-sea fish, including the identification of species observed in photographic records recovered from the REVIZEE Score-Norte program, including the PRODEMERSAL and PROTUNA projects.

MATERIAL AND METHODS

Study area. The northern coast of Brazil, which includes the sedimentary basins of the Amazon and Parnaíba Rivers, was formed during the Paleozoic and reactivated between the late Jurassic and early Cretaceous (Martins *et al.*, 1979). This highly diverse coastline has a total extension of some 2,500 km (Floriani *et al.*, 2004). The hydrological dynamics of this area, in particular at the mouth of the Amazon River, are intensely seasonal, being influenced primarily by the discharge of the Amazon, trade winds, and the North Brazil (or Guianas) current, which transport the waters of the external shelf and slope toward the northwest (Richardson *et al.*, 1994). The highly turbid Amazon plume may stretch up to 500 km to the northwest and more than 200 km into the Atlantic off the mouth of the river (Curtrin, 1986). The sediments adjacent to the mouth of the Amazon are formed primarily by silts, while the northeastern sector is rich in clays, a feature that is probably determined by tidal currents (Coutinho, Morais, 1970; Kowsmann, Costa, 1979). The region is also influenced by the Orinoco River, through the formation of

Amazon-Orinoco Plume, which creates unique oceanographic conditions (Hu *et al.*, 2004; Grodsky *et al.*, 2014). The surface temperatures of the water may reach 31°C near the coast, and 27°C on the continental shelf. A thermocline is found at depths of around 120 m in the adjacent oceanic waters, with temperatures of approximately 17°C at depths of up to 200 m. The salinity of the coastal and estuarine waters is strongly influenced by the fluvial discharge, increasing toward the open sea, and reaching 36.9% in the adjacent oceanic waters (Oliveira *et al.*, 2007; Grodsky *et al.*, 2014).

The northern continental shelf covers a wide area and is relatively flat, whereas the internal portion of the shelf, between the Parnaíba and Pará rivers, undulates considerably, forming ridges of coarse quartz sand that reach heights of up to 10 m. The inner continental shelf off Amapá is covered with deposits of fluvial mud, interspersed with relict areas of transgressive quartz sands, which were deposited during the periods of marine regression, on the coasts of the states of Pará and Maranhão. The internal shelf also has deposits of fluvial sand off the mouths of the Amazon and Pará rivers (Kowsmann, Costa, 1979). The Amazon Cone, which is adjacent to the mouth of the Amazonas, is formed by the accumulation of sediments from the Amazon River, which extend offshore beyond the outer limit of the Exclusive Economic Zone. The Amazon Cone does not have a typical continental elevation or slope, with varying depth gradients, but rather, a continuous slope, which extends all the way to the abyssal plain, being interrupted by paleochannels and other constructive or erosive geological features of non-tectonic origin. The external portion of the shelf is very rugged, with innumerable troughs and canyons, and an abrupt change in slope at a depth of around 80 m. Between the depths of 60 m to 120 m, three carbonatic facies are found, constructed of mollusks, benthic foraminifers, and Holocene algae typical of shallow coastal zones, as well as biodetritic sands (Kowsmann, Costa, 1979; Lana *et al.*, 1996; Oliveira *et al.*, 2007). The slope of the shelf tends to decrease as its width increases towards the extremes of the Amazon Gulf.

On the middle continental shelf, the penetration of sunlight is related directly to the influence of the Amazon plume and the tropical waters of the North Brazil Current. The Great Amazon Reef System (GARS) is a complex, consolidated bottom environment constituted by living organisms (Moura *et al.*, 2016; Francini-Filho *et al.*, 2018). Current knowledge indicates that the GARS has an area of 9,500 km², composed of typical mesophotic reefs, at depths of 70–220 m, formed principally of coralline algae and scleractinian corals, which may cover a total area of approximately 56,000 km² (Moura *et al.*, 2016). The enormous diversity of habitats, which include algae, rhodoliths, sponges, and soft coral and black coral, is influenced by the discharge of sediments and suspended matter from the Amazon River, and the strong local maritime currents (Francini-Filho *et al.*, 2018).

Data Collection. The surveys of the REVIZEE Score-Norte Program were conducted by the *Centro Nacional de Pesquisa e Conservação da Biodiversidade Marinha do Norte* (CEPNOR), a division of the *Instituto Brasileiro de Meio Ambiente e dos Recursos Naturais Renováveis* (IBAMA). Exploratory expeditions were based on standard fishing techniques such as bottom trawls, traps, and longlines (Lucena, Asano-Filho, 2006). Most of the information presented here is derived from the photographic records of the samples obtained by bottom trawls (REVIZEE, Fig. 1A), deep-water trawls

(PRODERMERSAL, Fig. 1B), and pelagic longlines (PROTUNA, Fig. 1C). As part of the REVIZEE Score-Norte Program, the RV Paulo Moreira trawled for fish and shrimp at 101 trawls between 25 and 639 m depths (Fig. 1A), including 36 at depths below 100 m (Lucena, Asano-Filho, 2006). The PRODEMERSAL project consisted of four exploratory cruises, with a total of 176 days at sea and 592 trawls between depths of 236 to 1,246 m (Fig. 1B) conducted by the fishing vessels *Mar Maria* and *Noé* (Asano-Filho *et al.*, 2005). The PROTUNA project involved 12 exploratory cruises, involving boats of the northern tuna fleet (Asano Filho *et al.*, 2004), which spent a total of 193 days at sea, with 99 pelagic longline operations (Fig. 1C).

The species identified here include those found in the photographic records recovered by researchers who participated in the REVIZEE Score-Norte Program (IHAC). Specimens recognized in these photographs were identified by three taxonomists (MMR, RAC, ACF), based on their expertise and data from literature (Nafpaktitis *et al.*, 1977; Uyeno *et al.*, 1983; Whitehead *et al.*, 1984a,b, 1986; Smith, Heemstra, 1986; Böhlke *et al.*, 1989; Cohen *et al.*, 1990; Nielsen *et al.*, 1999; Carpenter, 2002a,b), in addition to records from American ichthyological collections (<http://www.fishnet2.net>). Species nomenclature follows Fricke *et al.* (2020), while the supraspecific classification is based on Nelson *et al.* (2016).

RESULTS

The lists compiled by the PROTUNA and PRODEMERSAL projects include a total of 36 species of deep-sea fish (Asano Filho *et al.*, 2004, 2005, see Tab. 1, C column and also Tab. S1). A total of 28 species were identified based on material deposited in North American zoological collections (ANSP, CAS, MCZ, KU, UF, USNM and TU), most of which was collected by the RV Oregon (Tab. 1, B column). Based on the photographic records made during the REVIZEE Score-Norte Program (22 species) and associated projects, PROTUNA (3 species) and PRODEMERSAL (17 species), we identified a total of 37 species (Tab. 1, A column), in a recent collection effort in the Great Amazon Reef System by CEPNOR (Alexandre Marceniuk *et al.*, 2020 pers. comm.). Only four of these species (*Ariosoma selenops* Fig. 2D, *Anthias asperilinguis*, *Pontinus rathbuni*, and *Antigonia combatia*) are represented in zoological collections by specimens from the study area (Tab. 1, A and B column). Five others (*Parasudis truculenta*, *Polymixia lowei*, *Ruvettus pretiosus*, *Ariomma melana*, *Setarches guentheri*, and *Dibranchus atlanticus*) were included in the species list of the PROTUNA project (Tab. 1, A and C column).

Considering only the documented records (specimens deposited in zoological collections or with photographic record), a total of 63 species of deep-sea fish from the North coast of Brazil were recorded. A further 30 records from the literature were considered to be doubtful here, and are pending confirmation. The 63 confirmed species represent 11 orders, 25 families and 55 genera of deep-sea fish (Tab. 1). The most speciose families are Gempylidae (seven species), and Congridae, Myctophidae, and Macrouridae, with five species each. Thirty-seven of the species are bathydemersal, eight are bathypelagic, five benthopelagic, eight from deep reefs and five are epimesopelagic (Tab. 1, D column), ranging over depths up to 3,200 m (Tab. 1, E column). Twenty eight species are widely distributed in the western Atlantic, seven

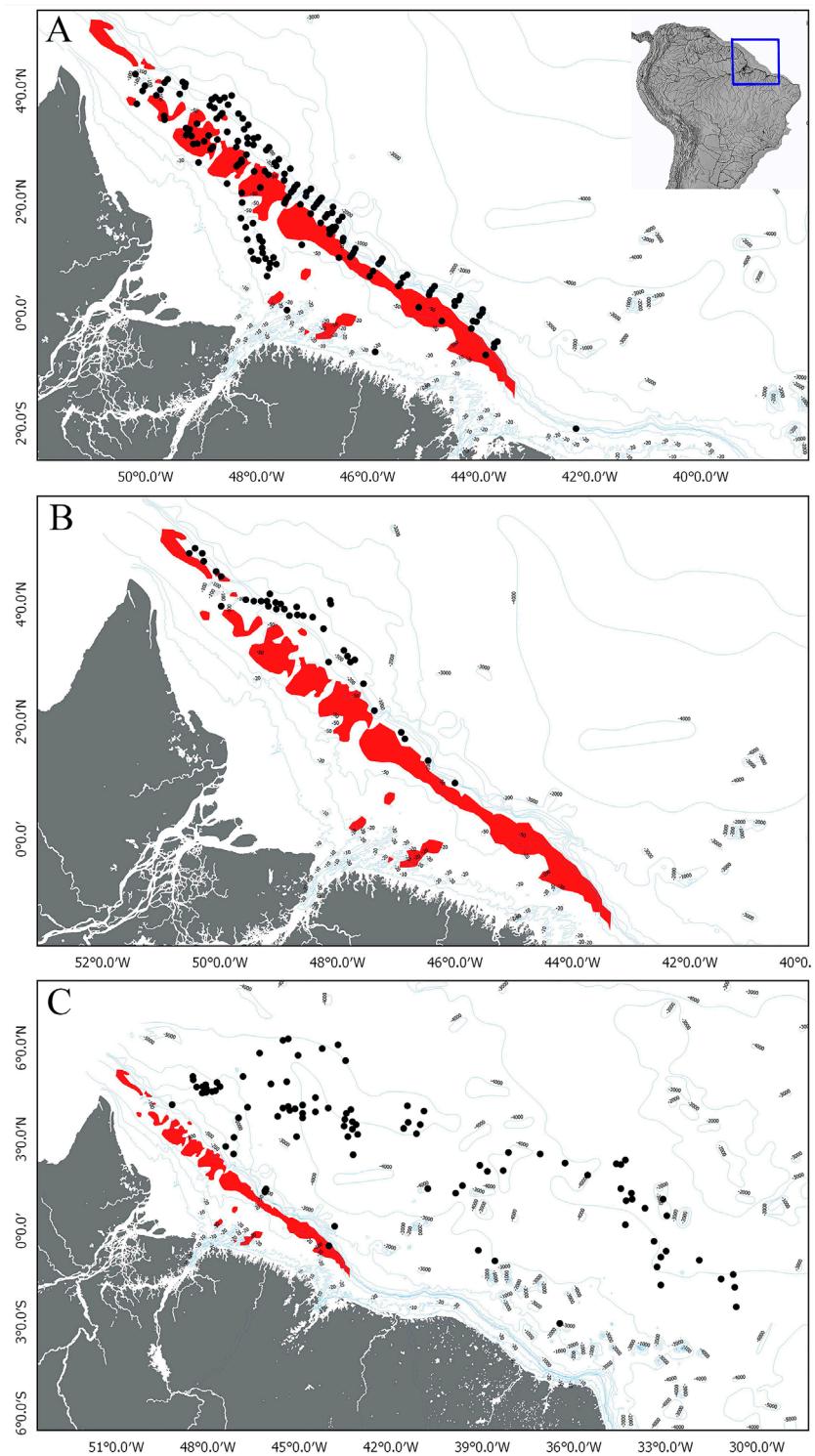


FIGURE 1 | Brazilian North coast, shaded in grey, with The Great Amazon Reef System, as defined by Moura *et al.* (2016), shaded in red and collection locations shaded in black (modified from resources and species with potential for exploitation on the continental shelf and slope (Lucena, Asano-Filho, 2006). **A.** collection locations of Program REVIZEE Score-North, **B.** collection locations of Program PRODEMERSAL, and **C.** collection locations of Program PROTUNA.

are also found in the eastern Atlantic, and 18 species are considered to be circumglobal (Tab. 1, F column). However, five species are thought to be restricted to the western Atlantic between the Gulf of Mexico and northern Brazil (Tab. 1, F column), *Anthias asperilinguis*, *Anthias nicholsi* and *Poecilopsetta inermis* is thought to be exclusive to the Caribbean and northern South America, *Aulotrachichthys argyrophanus* and *Centrodraco oregonus* are assumed to be restricted to the northern and northeastern coast of Brazil, and *Neobythites brasiliensis* is classified as endemic to Brazil.

TABLE 1 | The deep-sea teleost fish from the Brazilian North coast (bold, species with photographic record or specimens in the zoological collection). **A.** Specimens collected by the: REVIZEE Score-North (RZ), PRODEMERSAL (PD), PROTUNA (PT), and Centro Nacional de Pesquisa e Gestão de Recursos Pesqueiros do Litoral Norte (CEPNOR). **B.** Species with material deposited in North American zoological collections (see Supplementary Material). **C.** Specimens collected by the Program PROTUNA (Asano-Filho *et al.*, 2005), with photographic records or with specimens in zoological collections (X) and specimens without photographic records or specimens in zoological collections (?). **D.** Life habits. **E.** Depth range (meters). **F.** Distribution.

Order	Family	Species		A	B	C	D	E	F
Notacanthiformes	Halosauridae	<i>Halosaurus guentheri</i> Goode, Bean, 1896	-	-	-	?	bathypelagic	550 – 1600	Atlantic
Anguilliformes	Muraenidae	<i>Gymnothorax conspersus</i> Poey, 1867	Fig. 2A	RZ	-	-	bathydemersal	100 – 310	Western Atlantic
		<i>Gymnothorax polygonius</i> Poey, 1875	Fig. 2B	RZ	-	-	reef-associated	10 – 256	Atlantic
	Derychthyidae	<i>Coloconger meadi</i> Kanazawa, 1957	Fig. 2C	RZ	-	-	bathydemersal	650 – 925	Western Atlantic
	Nettastomatidae	<i>Nettastoma melanura</i> Rafinesque, 1810	-	-	-	?	bathydemersal	320 – 860	Atlantic
	Congridae	<i>Ariosoma selenops</i> Reid, 1934	Fig. 2D	RZ	X	-	bathydemersal	348 – 549	Gulf of Mexico, Caribbean, northern South America
		<i>Bathycongrus bullisi</i> (Smith, Kanazawa, 1977)	-	-	X	-	bathydemersal	366 – 475	Gulf of Mexico, Caribbean, northern South America
		<i>Bathyuroconger vicinus</i> (Vaillant, 1888)	-	-	-	?	bathydemersal	900 – 1000	Circumglobal except Eastern Pacific
		<i>Paraconger caudilimbatus</i> (Poey, 1867)	-	-	X	-	reef-associated	35 – 411	Gulf of Mexico, Caribbean, northern South America
		<i>Xenomystax congroides</i> Smith, Kanazawa, 1989	-	-	X	-	bathydemersal	140 – 825	Atlantic
	Serrivomeridae	<i>Stemonidium hypomelas</i> Gilbert, 1905	-	-	X	-	bathypelagic	175 – 1229	Atlantic and Indo-Pacific
Alepocephaliformes	Platytroctidae	<i>Maulisia mauli</i> Parr, 1960	-	-	-	?	bathypelagic	400 – 1200	Atlantic and Indian Oceans
	Alepocephalidae	<i>Talismania homoptera</i> (Vaillant, 1888)	-	-	-	?	bathypelagic	560 – 1700	Tropical Atlantic
Stomiiformes	Stomiidae	<i>Heterophotus ophistoma</i> Regan, Trewavas, 1929	-	-	X	-	bathypelagic	200 – 850	Circumglobal
		<i>Stomias affinis</i> Günther, 1887	-	-	-	?	bathypelagic	0 – 3800	Circumglobal
Ateleopodiformes	Ateleopodidae	<i>Ijimaia antillarum</i> Howell Rivero, 1935	Fig. 3A	PD	-	-	bathydemersal	100 – 500	Western Atlantic
Aulopiformes	Synodontidae	<i>Saurida caribbaea</i> Breder, 1927	Fig. 3B	RZ	-	-	demersal	20 – 460	Western Atlantic
	Ipnopidae	<i>Bathypterois viridensis</i> (Roule, 1916)	-	-	-	?	bathydemersal	476 – 1477	Atlantic
		<i>Bathytyphlops marionae</i> Mead, 1958	-	-	-	?	bathydemersal	100 – 1920	Atlantic and Indian Oceans
	Chlorophthalmidae	<i>Chlorophthalmus brasiliensis</i> Mead, 1958	-	-	X	-	bathydemersal	366 – ?	Gulf of Mexico, Caribbean, northern South America
		<i>Parasudis triculenta</i> (Goode, Bean 1896)	Fig. 3C	RZ	-	X	demersal	133 – 181	Western Atlantic
	Alepisauridae	<i>Alepisaurus brevirostris</i> Gibbs, 1960	Fig. 3D	PD	-	-	bathypelagic	640 – 1591	Circumglobal
Myctophiformes	Neoscopelidae	<i>Neoscopelus macrolepidotus</i> Johnson, 1863	-	-	-	?	pelagic-oceanic	300 – 1180	Circumglobal, except Indian Ocean



TABLE 1 | (Continued)

Order	Family	Species		A	B	C	D	E	F
	Mycophidae	<i>Centrobranchus nigroocellatus</i> (Günther, 1873)	-	-	X	-	bathypelagic	0 – 800	Circumglobal
		<i>Diaphus dumerili</i> (Bleeker, 1856)	-	-	X	-	pelagic-oceanic	50 – 500	Atlantic
		<i>Lampanyctus tenuiformis</i> (Brauer, 1906)	-	-	X	-	bathypelagic	40 – 750	Circumglobal
		<i>Lepidophanes guentheri</i> (Goode, Bean, 1896)	-	-	X	-	pelagic-oceanic	50 – 800	Atlantic
		<i>Notoscopelus resplendens</i> (Richardson, 1845)	-	-	X	-	bathypelagic	50 – 1550	Circumglobal
Polymixiiformes	Polymixiidae	<i>Polymixia lowei</i> Günther, 1859	Fig. 3E	RZ	-	X	bathydemersal	150 – 600	Western Atlantic
Zeiformes	Oreosomatidae	<i>Pseudocyttus maculatus</i> Gilchrist, 1906	-	-	-	?	bathydemersal	900 – 1100	Southern circumglobal
	Zeidae	<i>Zenopsis conchifer</i> (Lowe, 1852)	Fig. 3F	PD	-	-	benthopelagic	150 – 300	Circumglobal
		<i>Coelorinchus occa</i> (Goode, Bean, 1885)	-	-	-	?	bathydemersal	400 – 2200	Atlantic
		<i>Gadomus arcuatus</i> (Goode, Bean, 1886)	-	-	-	?	bathydemersal	610 – 1370	Atlantic
		<i>Malacocephalus laevis</i> (Lowe, 1843)	Fig. 3G	RZ	-	-	bathydemersal	200 – 1000	Circumglobal
		<i>Nezumia atlantica</i> (Parr, 1946)	-	-	-	?	bathydemersal	360 – 1100	Western Atlantic
	Moridae	<i>Nezumia suilla</i> Marshall, Iwamoto, 1973	-	-	-	?	bathydemersal	860 – 920	Western Atlantic
		<i>Gadella imberbis</i> (Vaillant, 1888)	-	-	-	?	benthopelagic	200 – 800	Atlantic
		<i>Laemonema barbatulum</i> Goode, Bean, 1883	-	-	-	?	bathydemersal	50 – 1600	Western Atlantic
		<i>Physiculus fulvus</i> Bean, 1884	-	-	X	-	bathydemersal	70 – 800	Gulf of Mexico, Caribbean, northern South America
		<i>Physiculus kaupi</i> Poey, 1865	Fig. 4A	RZ	-	-	bathydemersal	260 – 365	Western Atlantic
Trachichthyiformes	Diretmidae	<i>Diretmus argenteus</i> Johnson, 1864	-	-	X	-	bathypelagic	0 – 2000	Circumglobal
	Trachichthyidae	<i>Aulotrachichthys argyrophanus</i> (Woods, 1961)	-	-	X	-	bathypelagic	228	Brazilian North coast and off NE Brazil
		<i>Gephyroberyx darwini</i> (Johnson, 1866)	Fig. 4B	PD	-	-	benthopelagic	200 – 500	Circumglobal
		<i>Hoplostethus occidentalis</i> Woods, 1973	-	-	-	?	bathydemersal	485 – 850	Circumglobal except Eastern Pacific
Beryciformes	Gibberichthysidae	<i>Gibberichthys pumilus</i> Parr, 1933	-	-	-	?	bathypelagic	320 – 1100	Western Atlantic
Ophidiiformes	Ophidiidae	<i>Dicrolene introniger</i> (Goode, Bean, 1883)	-	-	-	?	bathydemersal	1000 – 1600	Atlantic
	Bythitidae	<i>Monomitopus agassizii</i> (Goode, Bean, 1896)	-	-	-	?	bathydemersal	48 – 1125	Western Atlantic
		<i>Neobythites brasiliensis</i> Nielsen, 1999	-	-	X	-	bathydemersal	320 – 410	Brazil
		<i>Diplacanthopoma brachysoma</i> Günther, 1887	-	-	-	?	bathydemersal	460 – 1670	Western Atlantic
Pleuronectiformes	Paralichthyidae	<i>Citharichthys cornutus</i> (Günther, 1880)	-	-	X	-	bathydemersal	140 – 400	Western Atlantic
<i>Poecilopsetta inermis</i> (Breder, 1927)	-	-	X	-	bathydemersal	182 – 793	Caribbean and northern South America		
	Bothidae	<i>Chascanopsetta lugubris</i> Alcock, 1894	Fig. 4C	RZ	-	-	bathydemersal	60 – 3210	Circumglobal
		<i>Monolepis antillarum</i> Norman, 1933	-	-	X	-	demersal	0 – 370	Western Atlantic
		<i>Monolepis atrimana</i> Goode, Bean, 1886	-	-	X	-	bathydemersal	? – 527	Western Atlantic
		<i>Engyophrys senta</i> Ginsburg, 1933	-	-	X	-	demersal	35 – 180	Western Atlantic
Callionymiformes	Callionymidae	<i>Synchiropus agassizii</i> (Goode, Bean, 1888)	Fig. 4D	RZ	-	-	bathydemersal	250 – 700	Western Atlantic
	Draconettidae	<i>Centrodraco oregonus</i> (Briggs, Berry, 1959)	-	-	X	-	bathydemersal	229 – 411	Brazilian North coast
		<i>Gempylidae</i>	<i>Gempylus serpens</i> Cuvier, 1829	Fig. 4E	PT	-	-	pelagic-oceanic	0 – 600
		<i>Lepidocybium flavobrunneum</i> (Smith, 1843)	Fig. 4F	PT	-	-	pelagic-oceanic	200 – 1100	Circumglobal



TABLE 1 | (Continued)

Order	Family	Species		A	B	C	D	E	F
		<i>Nealotus triples</i> Johnson, 1865	-	-	-	?	pelagic-oceanic	914 – 1640	Circumglobal
		<i>Neoepinula americana</i> (Grey, 1953)	Fig. 4G	PD	-	-	benthopelagic	184 – 457	Western Atlantic
		<i>Nesiarchus nasutus</i> Johnson, 1862	-	-	-	?	pelagic-oceanic	200 – 1200	Western Atlantic
		<i>Promethichthys prometheus</i> (Cuvier, 1832)	-	-	-	?	pelagic-oceanic	80 – 800	Circumglobal except Eastern Pacific
		<i>Ruvettus pretiosus</i> Cocco, 1833	Fig. 4H	PT/PD	-	X	benthopelagic	100 – 800	Circumglobal
	Ariommatidae	<i>Ariomma bondi</i> Fowler, 1930	Fig. 4I	RZ	-	-	demersal	100 – 200	Western Atlantic
		<i>Ariomma melana</i> (Ginsburg, 1954)	Fig. 4J	PD	-	X	bathymersal	180 – 550	Western Atlantic
Perciformes	Epigonidae	<i>Epigonus macrops</i> (Brauer, 1906)	-	-	-	?	bathymersal	550 – 1300	Circumglobal except Eastern Pacific
		<i>Epigonus pandonis</i> (Goode, Bean, 1881)	Fig. 4K	CEP	-	-	bathymersal	200 – 600	Atlantic
	Serranidae	<i>Anthias asperilinguis</i> Günther, 1859	Fig. 4L	PD	X	-	reef-associated	230 – 320	Caribbean and northern South America
		<i>Anthias nicholsi</i> Firth, 1933	Fig. 4M	RZ/PD	-	-	reef-associated	90 – 256	Caribbean and northern South America
		<i>Hyporthodus niveatus</i> (Valenciennes, 1828)	-	PD	-	-	demersal	30 – 525	Western Atlantic
	Bramidae	<i>Brama brama</i> (Bonnaterre, 1788)	Fig. 5A	PD	-	-	pelagic-neritic	0 – 200	Circumglobal
	Priacanthidae	<i>Cookeolus japonicus</i> (Cuvier, 1829)	Fig. 5B	PD	-	-	reef-associated	165 – 200	Circumglobal
	Lutjanidae	<i>Etelis oculatus</i> (Valenciennes, 1828)	Fig. 5C	PD	-	-	bathymersal	100 – 450	Western Atlantic
Scorpaeniformes	Scorpaenidae	<i>Pontinus nematophthalmus</i> (Günther, 1860)	-	-	X	-	reef-associated	82 – 410	Western Atlantic
		<i>Pontinus rathbuni</i> Goode, Bean, 1896	Fig. 5D	RZ	X	-	reef-associated	73 – 150	Western Atlantic
		<i>Setarches guentheri</i> Johnson, 1862	Fig. 5E	RZ/PD	-	X	benthopelagic	150 – 780	Circumglobal
	Triglidae	<i>Bellator brachy chir</i> (Regan, 1914)	Fig. 5F	RZ	-	-	demersal	35 – 366	Western Atlantic
		<i>Prionotus beanii</i> Goode, 1896	-	-	X	-	demersal	35 – 200	Caribbean and South America
		<i>Prionotus ophryas</i> Jordan, Swain, 1885	-	-	X	-	reef-associated	1 – 171	Western Atlantic
		<i>Prionotus stearnsi</i> Jordan, Swain, 1885	Fig. 5G	RZ	-	-	demersal	70 – 180	Western Atlantic
	Peristediidae	<i>Peristedion altipinnis</i> Regan, 1903	-	-	-	?	demersal	100 – 200	Southwestern Atlantic
		<i>Peristedion ecuadorensis</i> Teague, 1961	-	-	-	?	bathymersal	392 – 910	Western Atlantic
		<i>Peristedion sp.</i>	Fig. 5H	RZ	-	-	bathymersal		
		<i>Peristedion truncatum</i> (Günther, 1880)	-	-	-	?	bathymersal	150 – 900	Western Atlantic
Caproiformes	Caproidae	<i>Antigonia capros</i> Lowe, 1843	Fig. 5I	PD	-	-	demersal	100 – 300	Circumglobal
		<i>Antigonia combata</i> Berry, Rathjen, 1959	Fig. 5J	RZ/PD	X	-	bathymersal	115 – 585	Western Atlantic
Lophiiformes	Lophiidae	<i>Lophius gastrophysus</i> Miranda Ribeiro, 1915	Fig. 5K	PD	-	-	bathymersal	40 – 700	Western Atlantic
		<i>Sladenia shaefersi</i> Caruso, Bullis, 1976	Fig. 6A	PD	-	-	bathymersal	900 – 1200	Western Atlantic
	Chaunacidae	<i>Chaunax pictus</i> Lowe, 1846	-	-	-	?	bathymersal	220 – 1060	Atlantic and Mediterranean
		<i>Chaunax suttkusi</i> Caruso, 1989	Fig. 6B	RZ	-	-	bathymersal	200 – 980	Atlantic
	Ogcocephalidae	<i>Dibranchus atlanticus</i> Peters, 1876	Fig. 6C	RZ	-	X	bathymersal	300 – 820	Atlantic
	Diceratiidae	<i>Bufooceratias wedli</i> (Pietschmann, 1926)	-	-	-	?	bathypelagic	300 – 1500	Atlantic

DISCUSSION

The history of the biological exploration of Brazil's deep sea environments began with the visit of H.M.S. Challenger to the waters off the country's northeastern coast, in 1873, but it took almost another 100 years for the first Brazilian surveys to take place, with those conducted by the Almirante Saldanha, an oceanographic vessel of the Brazilian Navy, in 1967 (Eskinazi, Lima, 1968). There was a second foreign expedition in 1987, with the voyage of the French research vessel RV Marion Dufresne (Guille, Ramos, 1988; Tavares, 1999), followed 10 years later by the major expeditions of the French RV Thalassa and Brazilian vessels Diadorim and Atlântico Sul (Figueiredo *et al.*, 2002; Madureira *et al.*, 2004; Bernardes *et al.*, 2005). Subsequent surveys were funded by the Brazilian Oil company Petrobras (Petróleo Brasileiro S.A.) and focused on the northeastern Brazilian coast and the central Brazilian EEZ. These surveys were conducted by the Brazilian vessel N/RB Astro Garoupa and the American research vessels Luke Thomas, and Seward Johnson (Lavrado, Brasil, 2010; Lins Oliveira *et al.*, 2015). Most of the research expeditions in the Brazilian EEZ at the end of the 20th century was conducted within the scope of the REVIZEE Program, whose principal objective was to inventory the commercially exploitable natural resources of the zone, and consolidate efforts to expand its limits (CIRM, 1994). The recovery of photographic records from this program, together with the analysis of published data and the material in zoological collections, provided the baseline evidence for the present study, and the first comprehensive inventory of the deep-water fish fauna of the northern coast of Brazil.

The 63 deep-water teleost fish species reported here from northern Brazil represent only 8.2% of the total number of marine bony fish species found in the Brazilian North coast, estimated to be approximately 770 species (Alexandre Marceniuk *et al.*, 2020 pers. comm.). In other regions of Brazil and adjacent waters, deep sea species make up a much larger proportion of the total teleost diversity: (a) in São Paulo, represent 42.6% of the total of the 481 teleost species recorded by Menezes (2011), (b) in the Potiguar basin, Rio Grande do Norte, represent 30.8% of the known fauna of 373 species (Garcia Jr. *et al.*, 2015; Lins Oliveira *et al.*, 2015; Nóbrega *et al.*, 2015), (c) 30.4% of 1,155 deep water species in Brazil as a whole (Menezes *et al.*, 2003), (d) 44.4% of 405 species in Suriname and French Guyana (Uyeno *et al.*, 1983), and (e) 38% of 129 species in Patagonia (Nakamura, 1986). This would appear to imply that many other deep-sea species are yet to be reported from the Brazilian North Coast. In particular, it seems likely that many of the species found in the waters of neighboring areas, as Suriname and French Guyana (see Uyeno *et al.*, 1983), will be confirmed in Brazil, when new surveys are conducted off the northern coast.

Most deep sea species are thought to have a wide distribution, either circumglobal (e.g. *Alepisaurus brevirostris*, Fig. 3D, and *Zenopsis conchifer*, Fig. 3F), in the Atlantic (e.g. *Epigonus pandionis*, Fig. 4K) or the western Atlantic (*Ariomma bondi* and *A. melana*, Figs. 4I, J). However, some species have a more restricted distribution, either in northern and northeastern coast of Brazil (*Aulotrachichthys argyrophanus* and *Centrodraco oregonus*), endemic from Brazil (*Neobythites brasiliensis*) or including the Caribbean or the Gulf of Mexico (*Anthias asperilinguis*, Fig. 4L, *Anthias nicholsi*, Fig. 4M, *Bathycongrus bullisi*, *Paraconger caudilimbatus*, and *Physiculus fulvus*, Tab. 1, F column).

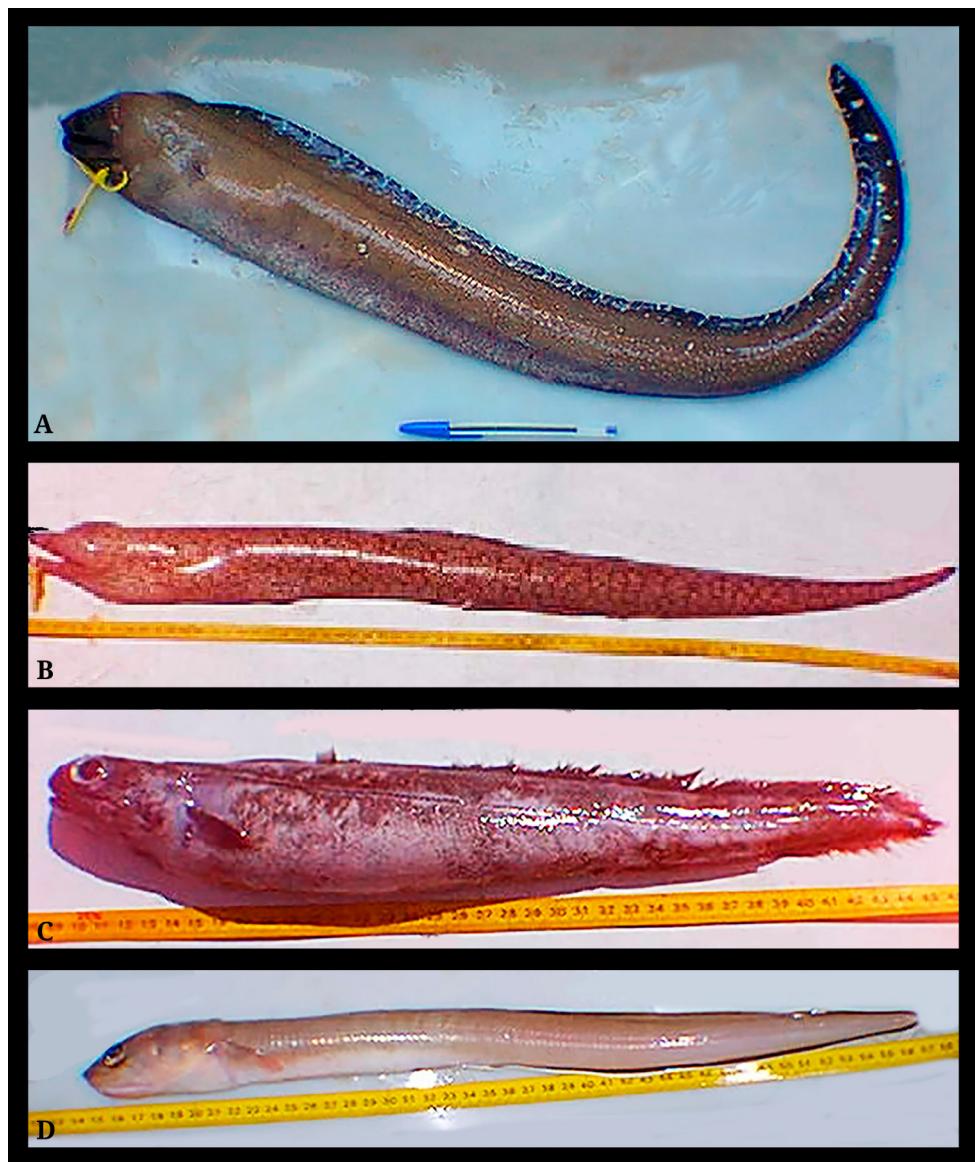


FIGURE 2 | Species of the order Anguilliformes, family Muraenidae, **A.** *Gymnothorax conspersus*, photograph by Revizee Score-North, **B.** *Gymnothorax polygonius*, photograph by Revizee Score-North, family Derychthyidae, **C.** *Coloconger meadi*, photograph by Revizee Score-North, and family Congridae, **D.** *Ariosoma selenops*, photograph by Revizee Score-North.

These differences in distribution patterns may reflect oceanographic and geographic processes, such as the establishment of the transcontinental flow of the Amazon River to the Atlantic Ocean in the mid to late Miocene, and the isolation of the Caribbean in the Tertiary-Quaternary, which implies that they influenced not only the coastal species, but also the deep sea fauna. This is especially true for some deep-water taxa, such as alepocephalids (Sazonov, 1976; Sazonov, Williams, 2001; Lavrado, Brasil, 2010) and stomiids (e.g. *Leptostomias* and *Melanostomias*; Bigelow *et al.*, 1964), although more data will be necessary to confirm these conclusions.

Taxonomic limitations still hamper our understanding of the occurrence and distribution patterns of many offshore fishes, including some of the lesser-known species identified in the present study. For example, we identified one deep sea flounder as *Chascanopsetta lugubris*, although the limits of the occurrence of this species have been questioned by some authors, in addition to the validity of *Chascanopsetta danae*, from the western Atlantic (Amaoka, Yamamoto, 1984; Foroshchuk, 1991). Inaccuracies in the taxonomic identification may also have occurred in some cases, such as *Chaunax suttkusi* (Fig. 6B) and *Epigonus pandionis* (Fig. 4K, Tab. 1), which were identified in

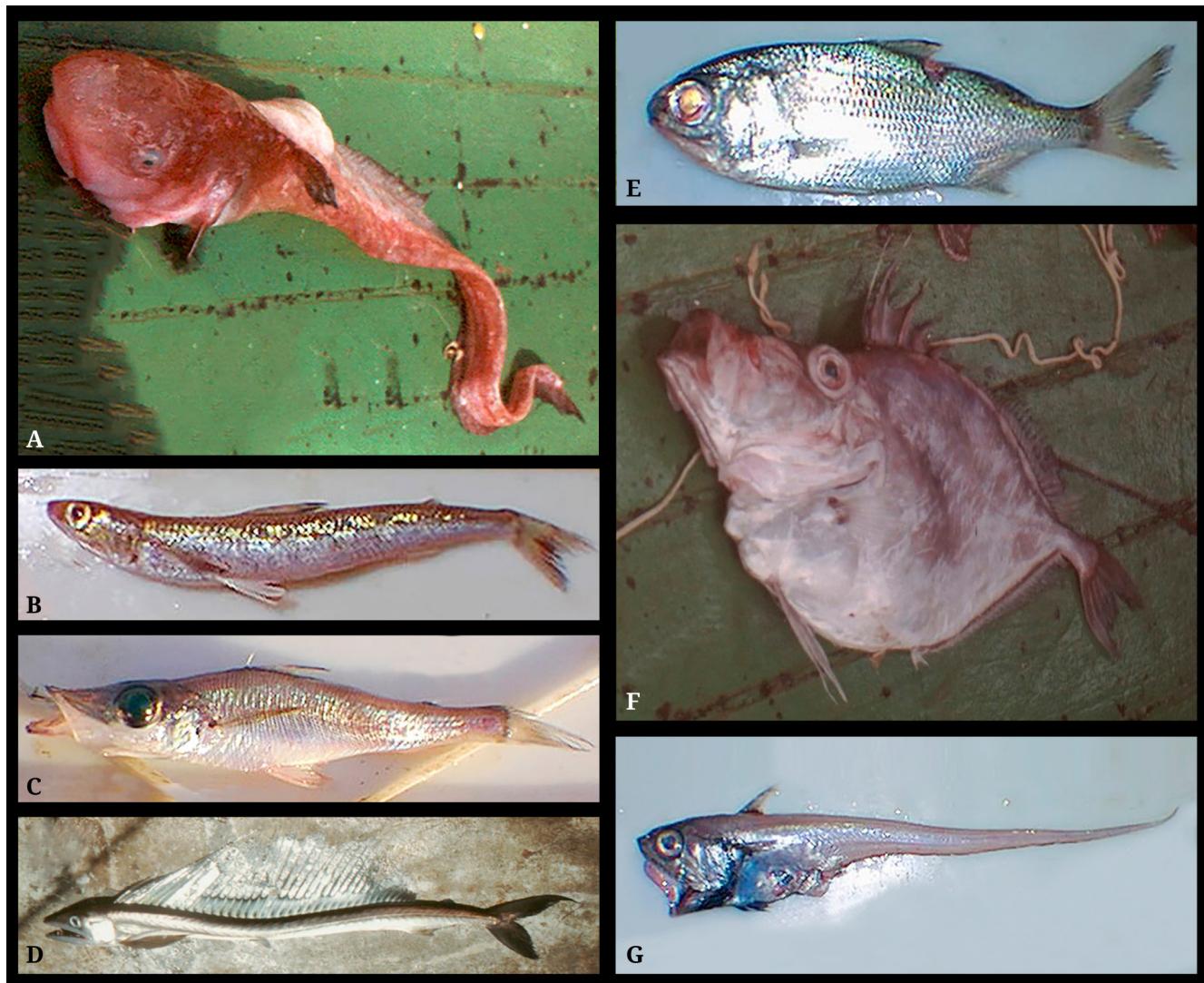


FIGURE 3 | Species of the order Ateleopodiformes, family Ateleopodidae, **A.** *Ijimaia antillarum*, photograph by PRODEMERSAL, Order Aulopiformes, family Synodontidae, **B.** *Saurida caribbaea*, photograph by Revizee Score-North, family Chlorophthalmidae, **C.** *Parasudis truculenta*, photograph by Revizee Score-North, family Alepisauridae, **D.** *Alepisaurus brevirostris*, photograph by PRODEMERSAL, order Polymixiiformes, family Polymixiidae, **E.** *Polymixia lowei*, photograph by Revizee Score-North, order Zeiformes, family Zeidae, **F.** *Zenopsis conchifer*, photograph by PRODEMERSAL, and order Gadiformes, family Macrouridae, **G.** *Malacocephalus laevis*, photograph by Revizee Score-North.

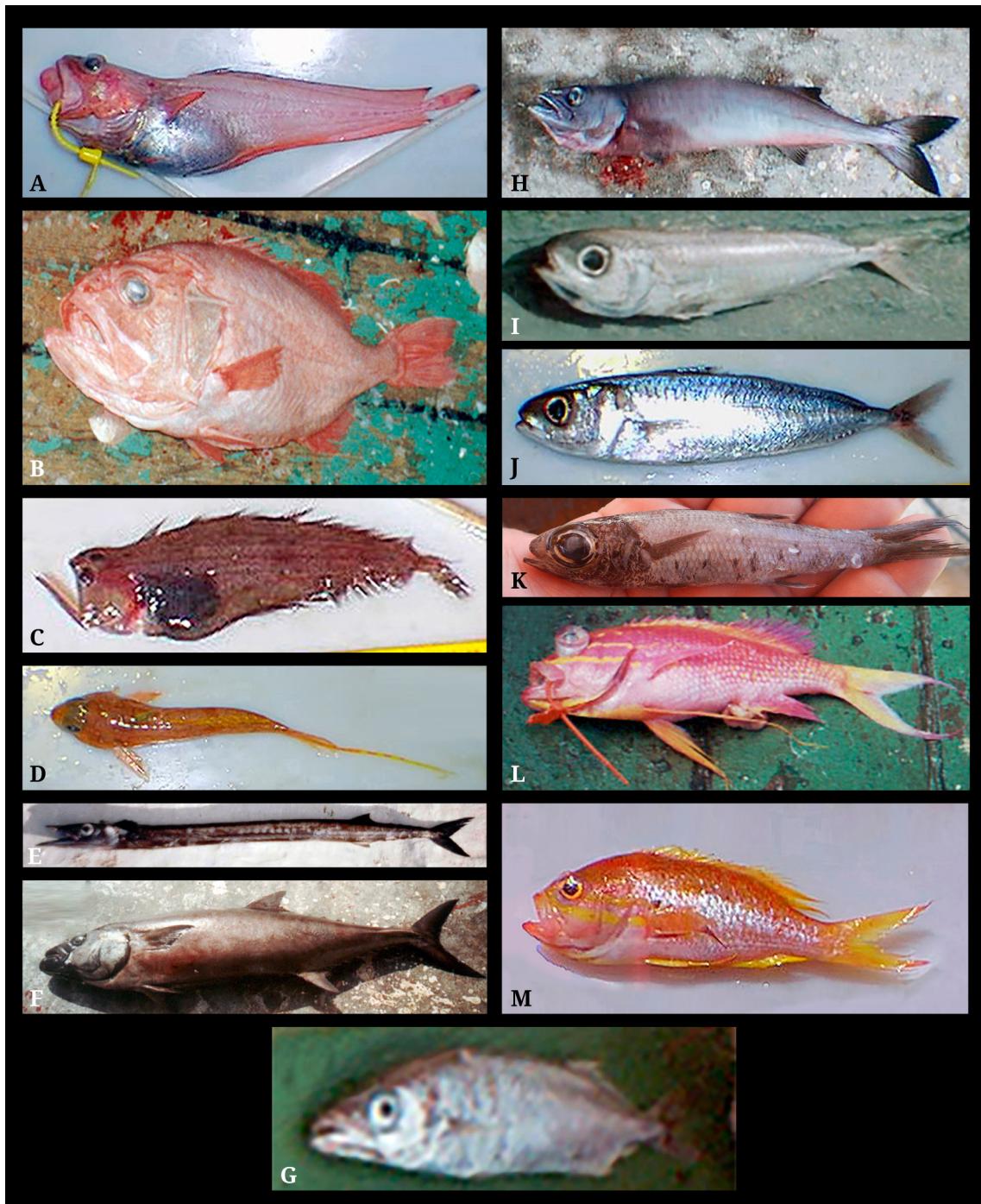


FIGURE 4 | Species of the order Gadiformes, family Moridae, **A.** *Physiculus kaupi*, photograph by Revizee Score-North, order Trachichthyiformes, family Trachichthyidae, **B.** *Gephyroberyx darwini*, photograph by PRODEMERSAL, order Pleuronectiformes, family Bothidae, **C.** *Chascanopsetta lugubris*, photograph by Revizee Score-North, order Callionymiformes, family Callionymidae, **D.** *Synchiropus agassizii*, photograph by Revizee Score-North, order Scombriformes, family Gempylidae **E.** *Gempylus serpens*, photograph by PROTUNA, **F.** *Lepidocybium flavobrunneum*, photograph by PROTUNA, **G.** *Neoepinnula americana*, photograph by PRODEMERSAL, **H.** *Ruvettus pretiosus*, photograph by PRODEMERSAL, family Ariommataidae, **I.** *Ariomma bondi*, photograph by Revizee Score-North, **J.** *Ariomma melana*, photograph by PRODEMERSAL, order Perciformes, family Epigonidae, **K.** *Epigonus pandionis*, photograph by CEPNOR, and family Serranidae, **L.** *Anthias asperilinguis*, photograph by PRODEMERSAL, **M.** *Anthias nicholsi*, photograph by PRODEMERSAL.



FIGURE 5 | Species of the order Perciformes, family Bramidae, **A.** *Brama brama*, photograph by PRODEMERSAL, family Priacanthidae, **B.** *Cookeolus japonicus*, photograph by PRODEMERSAL, family Lutjanidae, **C.** *Etelis oculatus*, photograph by PRODEMERSAL, order Scorpaeniformes, family Scorpaenidae, **D.** *Pontinus rathbuni*, photograph by Revizee Score-North, **E.** *Setarches guentheri*, photograph by PRODEMERSAL, family Triglidae, **F.** *Bellator brachypterus*, photograph by Revizee Score-North, **G.** *Prionotus stearnsi*, photograph by Revizee Score-North, family Peristediidae, **H.** *Peristedion* sp., photograph by Revizee Score-North, order Caproiformes, family Caproidae, **I.** *Antigonia capros*, photograph by PRODEMERSAL, **J.** *Antigonia combatia*, photograph by PRODEMERSAL, and order Lophiiformes, family Lophiidae, **K.** *Lophius gastrophysus*, photograph by PRODEMERSAL.

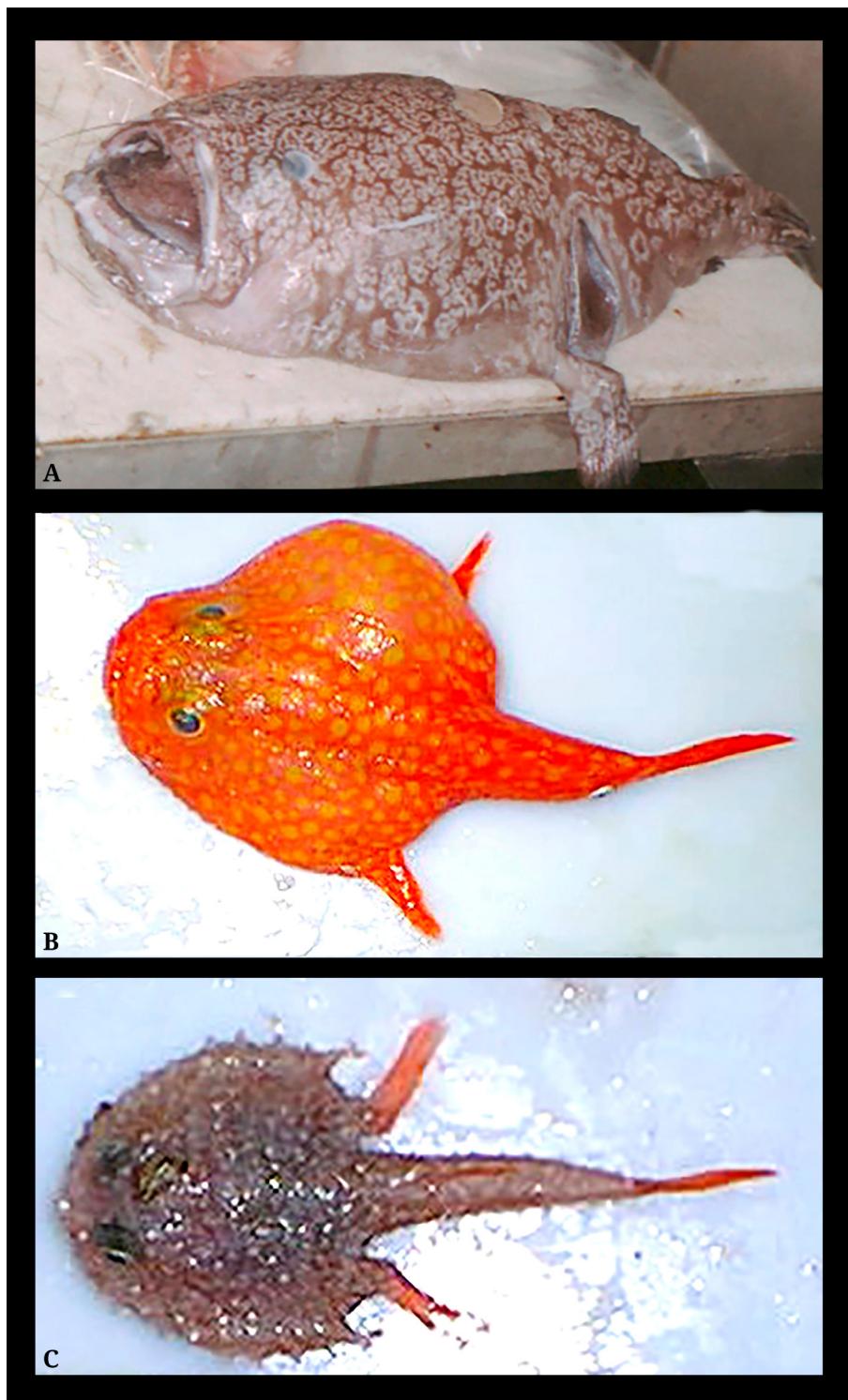


FIGURE 6 | Species of the order Lophiiformes, family Lophiidae, **A.** *Sladenia shaefersi*, photograph by PRODEMERSAL, family Chaunacidae, **B.** *Chaunax suttkusi*, photograph by Revizee Score-North, and family Ogocephalidae, **C.** *Dibranchus atlanticus*, photograph by Revizee Score-North.

Asano-Filho *et al.* (2005) as *Chaunax pictus* and *Epigonus macros* (Tab. 1). Other species, including *Urophycis cirrata*, *Urophycis mystacea* and some *Peristedion* species (Caires, 2014; Lemes, 2017) have been recorded previously in the Gulf of Mexico and southern Brazil, but not in northern Brazil.

The paucity of specimens of deep sea fish species from the northern Brazilian coast in ichthyological collections is a fundamental problem for the understanding of the teleost diversity of this region. Despite the enormous efforts of the REVIZEE program, almost no data on the region's deep sea fish fauna are available, given that most, of the material collected during these surveys cannot be located or examined. Clearly, investment is required for basic research (surveys) and the cataloging and storage of material to guarantee the development of more systematic study on the taxonomy, ecology and distribution of the fauna of the Brazilian Exclusive Economic Zone, in particular, that of the North Coast.

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