The deep sea teleost fish fauna of the Brazilian North Coast

Alex Garcia Cavalleiro de Macedo Klautau, Israel Hidenburgo Aniceto Cintra, Matheus Marcos Rotundo, Alfredo Carvalho-Filho, Rodrigo Antunes Caires and Alexandre Pires Marceniuk

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.
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 Maritima 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 Parnaiba, 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; Espirito-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 tenius Springer, 1966, Malacocephalus okamurai Iwamoto, Arai, 1987, and Neobythites braziliensis 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 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 innumerous 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 carbonate 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 PRODERMERSAL 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 PRODERMERSAL 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 PRODERMERSAL (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 *Poeiopsetta inermis* is thought to be exclusive to the Caribbean and northern South America, *Aulotrachichthys argyrophanus* and *Centrodraco oreogonus* are assumed to be restricted to the northern and northeastern coast of Brazil, and *Neobythites braziliensis* is classified as endemic to Brazil.

### TABLE 1

| Order                  | Family               | Species                                                                 | A  | B   | C      | D          | E  | F     |
|------------------------|----------------------|-------------------------------------------------------------------------|----|-----|--------|------------|----|-------|
| Notacanthiformes       | Halosauridae         | *Halosaurax guentheri* Goode, Bean, 1896                               | -  | -   | -      | ? bathypelagic | 550 – 1600 | Atlantic |
| Aulopiformes           | Muraenidae           | *Gymnothorus conspersus* Poey, 1867                                    | Fig 2A | RZ | -      | - bathydemersal | 100 – 310  | Western Atlantic |
|                        |                      | *Gymnothorus polygonius* Poey, 1875                                     | Fig 2B | RZ | -      | - reef-associated | 10 – 256   | Atlantic |
| Derychthyidae          | Colloconger meadi    | Kanazawa, 1957                                                          | Fig 2C | RZ | -      | - bathydemersal | 650 – 925   | Western Atlantic |
|                        |                      | *Nettastoma melanura* Rafinesque, 1810                                 | -  | -   | -      | ? bathydemersal | 320 – 860   | Atlantic |
| Congridae              | *Ariosoma selenops* Reid, 1934                                   | Fig 2D | RZ | X    | -      | bathydemersal | 348 – 549   | Gulf of Mexico, Caribbean, northern South America |
|                        |                      | *Bathycongrus bullisi* (Smith, Kanazawa, 1977)                         | -  | -   | X      | - bathydemersal | 366 – 475  | Gulf of Mexico, Caribbean, northern South America |
|                        |                      | *Bathyuroconger vicinus* (Vaillant, 1888)                               | -  | -   | -      | ? bathydemersal | 900 – 1000  | Circumglobal except Eastern Pacific |
|                        |                      | *Paraconger caudilimbatus* (Poey, 1867)                                 | -  | -   | X      | - reef-associated | 35 – 411    | Gulf of Mexico, Caribbean, northern South America |
|                        |                      | *Xenomystax congroides* Smith, Kanazawa, 1989                          | -  | -   | X      | - bathydemersal | 140 – 825   | Atlantic |
| Serrivomeridae         | *Stemonidium hypomelas* Gilbert, 1905                             | -  | -   | X      | - bathypelagic | 175 – 1229  | Atlantic and Indo-Pacific |
| Alepocephaliformes     | Platyroctidae         | *Maulisia mauli* Parr, 1960                                            | -  | -   | -      | ? bathypelagic | 400 – 1200  | Atlantic and Indian Oceans |
| Alepocephalidae        | *Talassmania homoptera* (Vaillant, 1888)                            | -  | -   | -      | ? bathypelagic | 560 – 1700  | Tropical Atlantic |
| Stomiiformes           | Stomiidae            | *Heterophobus ophiistoma* Regan, Trewavas, 1929                        | -  | -   | X      | - bathypelagic | 200 – 850   | Circumglobal |
|                        |                      | *Stomias affinis* Günther, 1887                                        | -  | -   | -      | ? bathypelagic | 0 – 3800    | Circumglobal |
| Ateleopodiformes       | Ateleopodidae         | *Iljama antillarum* Howell Rivero, 1935                                | Fig 3A | PD | -      | - bathydemersal | 100 – 500   | Western Atlantic |
| Aulopiformes           | Synodontidae         | *Saurida caribbaea* Breder, 1927                                       | Fig 3B | RZ | -      | - demersal | 20 – 460    | Western Atlantic |
| Ipnotidae              |                      | *Bathypterois viridensis* (Roule, 1916)                                 | -  | -   | -      | ? bathydemersal | 476 – 1477  | Atlantic |
| Chlorophthalmidae      |                      | *Bathyphlops marionae* Mead, 1958                                      | -  | -   | -      | ? bathydemersal | 100 – 1920  | Atlantic and Indian Oceans |
|                        |                      | *Chlorophthalmus brasiliensis* Mead, 1958                              | -  | -   | X      | - bathydemersal | 366 – ?     | Gulf of Mexico, Caribbean, northern South America |
|                        |                      | *Paraspid truculenta* (Goode, Bean 1896)                               | Fig 3C | RZ | -      | X demersal | 133 – 181   | Western Atlantic |
| Alepisauridae          | *Alepisaurus brevisirostris* Gibbs, 1960                           | Fig 3D | PD | -      | - bathypelagic | 640 – 1591  | Circumglobal |
| Myctophiformes         | Neoscopelidae        | *Neoscopelus macrolepidotus* Johnson, 1863                             | -  | -   | -      | ? pelagic-oceanic | 300 –1180  | Circumglobal, except Indian Ocean |
### TABLE 1 (Continued)

| Order          | Family          | Species                                                                 | A  | B  | C  | D  | E  | F                       |
|----------------|-----------------|-------------------------------------------------------------------------|----|----|----|----|----|-------------------------|
|               |                 | **Centrobranchus nigroocellatus** (Günther, 1873)                      | -  | -  | X  |    |    | bathypelagic            | 0 – 800                   | Circumglobal              |
|               |                 | **Diaphus demerlii** (Bleeker, 1856)                                    | -  | -  | X  |    |    | pelagic-oceanic         | 50 – 500                  | Atlantic                  |
|               |                 | **Lampyromus tenuiformis** (Brassoc, 1906)                              | -  | -  | X  |    |    | bathypelagic            | 40 – 750                  | Circumglobal              |
|               |                 | **Lepidophasus guentheri** (Goode, Bean, 1896)                          | -  | -  | X  |    |    | pelagic-oceanic         | 50 – 800                  | Atlantic                  |
|               |                 | **Notoscopelus resplendens** (Richardson, 1845)                        | -  | -  | X  |    |    | bathypelagic            | 50 – 1550                 | Circumglobal              |
| Polymixiiformes| Polymixiidae    | **Polymixia lowei** Günther, 1859                                       | Fig. 3E | RZ | -  | X  |    | bathydemersal           | 150 – 600                 | Western Atlantic          |
| Zeiformes      | Oresomatiidae   | **Pseudocyttus maculatus** (Günther, 1906)                              | -  | -  |    |    |    | bathydemersal           | 900 – 1100                | Southern circumglobal     |
| Zeidae         |                 | **Zenopsis conchifer** (Lowe, 1852)                                    | Fig. 3F | PD | -  |    |    | benthopelagic           | 150 – 300                 | Circumglobal              |
| Gadiformes     | Macrouridae     | **Ctoerichthys occa** (Goode, Bean, 1885)                               | -  | -  |    |    |    | bathydemersal           | 400 – 2200                | Atlantic                  |
|               |                 | **Gadomus arcuatus** (Goode, Bean, 1886)                                | -  | -  |    |    |    | bathydemersal           | 610 – 1370                | Atlantic                  |
|               |                 | **Malacosteus laevis** (Lowe, 1843)                                    | Fig. 3G | RZ | -  |    |    | bathydemersal           | 200 – 1000                | Circumglobal              |
|               |                 | **Nexumbia atlantica** (Parr, 1946)                                    | -  | -  |    |    |    | bathydemersal           | 360 – 1100                | Western Atlantic          |
| Moridae        |                 | **Nexumbia sulle** Marshall, 1973                                       | -  | -  |    |    |    | bathydemersal           | 860 – 920                 | Western Atlantic          |
|               |                 | **Gadella imberbis** (Vaillant, 1888)                                   | -  | -  |    |    |    | benthopelagic           | 200 – 800                 | Atlantic                  |
|               |                 | **Laemonema barbatulum** Goode, Bean, 1883                              | -  | -  |    |    |    | bathydemersal           | 50 – 1600                 | Western Atlantic          |
|               |                 | **Physicus fulvus** Bean, 1884                                         | -  | -  |    |    |    | bathydemersal           | 70 – 800                  | Gulf of Mexico, Caribbean, northern South America |
|               |                 | **Physicus kaupi** Poey, 1865                                          | Fig. 4A | RZ | -  |    |    | bathydemersal           | 260 – 365                 | Western Atlantic          |
| Trachichthyiformes| Diretmidae      | **Diretemus argenteus** Johnson, 1864                                   | -  | -  | X  |    |    | bathypelagic            | 0 – 2000                  | Circumglobal              |
|               | Trachichthyidae | **Aulotracichthys argyrophanus** (Woods, 1961)                          | -  | -  | X  |    |    | bathypelagic            | 228                      | Brazilian North coast and off NE Brazil |
|               |                 | **Gephyroberyx darwini** (Johnson, 1866)                                | Fig. 4B | PD | -  |    |    | benthopelagic           | 200 – 500                 | Circumglobal              |
| Beryciformes   | Gibberichthyidae| **Gibberichthys pumilus** Parr, 1933                                   | -  | -  |    |    |    | bathydemersal           | 320 – 1100                | Western Atlantic          |
| Ophidiiformes  | Ophidiidae      | **Dicrotelen introniger** (Goode, Bean, 1883)                           | -  | -  |    |    |    | bathydemersal           | 1000 – 1600               | Atlantic                  |
|               |                 | **Monomitopus agassizii** (Goode, Bean, 1896)                           | -  | -  |    |    |    | bathydemersal           | 48 – 1125                 | Western Atlantic          |
|               |                 | **Neobythites braziliensis** Nielsen, 1999                              | -  | -  |    |    |    | bathydemersal           | 320 – 410                 | Brazil                    |
| Bythitidae     |                 | **Displacenhopoma brachysoma** Günther, 1876                            | -  | -  | X  |    |    | bathydemersal           | 460 – 1670                | Western Atlantic          |
| Pleuronectiformes| Paralichthyidae | **Paralichthys carthus** (Günther, 1880)                                | -  | -  |    |    |    | bathydemersal           | 140 – 400                 | Western Atlantic          |
|               | Pleuronectidae  | **Pocelipsetta inermis** (Breder, 1927)                                 | -  | -  | X  |    |    | bathydemersal           | 182 – 793                 | Caribbean and northern South America |
| Bothidae       |                 | **Chuscanopssetta lugubris** Alcock, 1894                               | Fig. 4C | RZ | -  |    |    | bathydemersal           | 60 – 3210                 | Circumglobal              |
|               |                 | **Monolene antillarum** Norman, 1933                                   | -  | -  | X  |    |    | demersal                | 0 – 370                   | Western Atlantic          |
|               |                 | **Monolene atrimana** Goode, Bean, 1886                                 | -  | -  | X  |    |    | demersal                | ? – 527                   | Western Atlantic          |
|               |                 | **Engyphrys senta** Ginsburg, 1933                                     | -  | -  | X  |    |    | demersal                | 35 – 180                  | Western Atlantic          |
| Callionymiformes| Callionymidae   | **Synchiropus agassizii** (Goode, Bean, 1888)                           | Fig. 4D | RZ | -  |    |    | bathydemersal           | 250 – 700                 | Western Atlantic          |
|               | Draconetidae    | **Centrotraco oreogenus** (Briggs, Berry, 1959)                         | -  | -  | X  |    |    | bathydemersal           | 229 – 411                 | Brazilian North coast     |
| Scombriformes  | Gymnolidae      | **Gephyroberyx serpens** Cuvier, 1829                                   | Fig. 4E | PT | -  |    |    | pelagic-oceanic         | 0 – 600                   | Circumglobal              |
|               |                 | **Lepidocybium flavobrunneum** (Smith, 1843)                            | Fig. 4F | PT | -  |    |    | pelagic-oceanic         | 200 – 1100                | Circumglobal              |
| Order         | Family      | Species                                                                 | A     | B     | C     | D     | E     | F                      |
|--------------|-------------|------------------------------------------------------------------------|-------|-------|-------|-------|-------|------------------------|
|              |             | Neolotus tripes Johnson, 1865                                          | -     | -     | -     | ?     | pelagic-oceanic        | 914 – 1640 Circumglobal |
|              |             | Neospinula americana (Gray, 1953)                                      | Fig. 4G | PD  | -     | -     | bentholagic             | 184 – 457 Western Atlantic |
|              |             | Nesiarichus nasutus Johnson, 1862                                      | -     | -     | -     | ?     | pelagic-oceanic        | 200 – 1200 Western Atlantic |
|              |             | Promethichthys prometheus (Cuvier, 1832)                               | -     | -     | -     | ?     | pelagic-oceanic        | 80 – 800 Circumglobal except Eastern Pacific |
|              |             | Revettus pretiosus Cocco, 1833                                         | Fig. 4H | PT/PD | -     | X     | bentholagic             | 100 – 800 Circumglobal |
| Arioimmatidae|             | Ariomma bondi Fowler, 1930                                             | Fig. 4L | RZ  | -     | -     | demersal               | 100 – 200 Western Atlantic |
|              |             | Ariomma melana (Ginsburg, 1954)                                        | Fig. 4J | PD  | -     | X     | bathydemersal          | 180 – 550 Western Atlantic |
| Perciformes  | Epigonidae  | Epigonus macrops (Brauer, 1906)                                        | -     | -     | -     | ?     | bathydemersal          | 550 – 1300 Circumglobal except Eastern Pacific |
|              |             | Epigonus pandionis (Goode, Bean, 1881)                                 | Fig. 4K | CEP | -     | -     | bathydemersal          | 200 – 600 Atlantic |
| Serranidae   |             | Anthias asperilinguis Günther, 1859                                     | Fig. 4L | PD  | X     | -     | reef-associated        | 230 – 320 Caribbean and northern South America |
|              |             | Anthias falcatus Günther, 1859                                         | Fig. 4M | RZ/PD | -     | -     | reef-associated        | 90 – 256 Caribbean and northern South America |
|              |             | Hyporthodus niveatus (Valenciennes, 1828)                               | -     | PD   | -     | -     | demersal               | 30 – 525 Western Atlantic |
|              |             | Bramia brasiliense (Bonnoterre, 1788)                                  | Fig. 5A | PD  | -     | -     | pelagic-neritic        | 0 – 200 Circumglobal |
|              |             | Cookius japonicus (Cuvier, 1829)                                       | Fig. 5B | PD  | -     | -     | reef-associated        | 165 – 200 Circumglobal |
|              |             | Lutjanus oculatus (Valenciennes, 1828)                                 | Fig. 5C | PD  | -     | -     | bathydemersal          | 100 – 450 Western Atlantic |
| Scorpaeiformes| Scorpaeidae | Pontinus nematophthalmus Günther, 1860                                  | -     | -     | X     | -     | reef-associated        | 82 – 410 Western Atlantic |
|              |             | Ponitus ruthbani Goode, Bean, 1896                                     | Fig. 5D | RZ  | -     | -     | reef-associated        | 73 – 150 Western Atlantic |
|              |             | Setarches guentheri Johnson, 1862                                      | Fig. 5E | RZ/PD | -     | X     | bentholagic             | 150 – 780 Circumglobal |
| Triglidae    |             | Bellator brachycephalus (Regan, 1914)                                   | Fig. 5F | RZ  | -     | -     | demersal               | 35 – 366 Western Atlantic |
|              |             | Prionotus beanii Goode, 1896                                           | -     | -     | X     | -     | demersal               | 33 – 200 Caribbean and South America |
|              |             | Prionotus tyromys Jordan, 1885                                         | -     | -     | X     | -     | reef-associated        | 1 – 171 Western Atlantic |
|              |             | Prionotus stearnsi Jordan, 1885                                        | Fig. 5G | RZ  | -     | -     | demersal               | 70 – 180 Western Atlantic |
| Peristeriidae|             | Peristion altipinnis Regan, 1903                                        | -     | -     | -     | ?     | demersal               | 100 – 200 Southwestern Atlantic |
|              |             | Peristion ecuadorense Teague, 1961                                     | -     | -     | -     | ?     | bathydemersal          | 392 – 910 Western Atlantic |
|              |             | Peristion sp.                                                          | Fig. 5H | RZ  | -     | -     | bathydemersal          |                  |
| Caproiformes | Caproidae   | Antigonia capros Lowe, 1843                                            | Fig. 5I | PD  | -     | -     | demersal               | 100 – 300 Circumglobal |
|              |             | Antigonia obtusa Berry, Rathjen, 1959                                   | Fig. 5J | RZ/PD | X     | -     | bathydemersal          | 115 – 585 Western Atlantic |
| Lophiiformes | Lophiidae   | Lophius ophus Günther, Bean, 1896                                      | Fig. 5K | PD  | -     | -     | bathydemersal          | 40 – 700 Western Atlantic |
| Chaunacidae  |             | Chauna piscus Lowe, 1846                                                | -     | -     | -     | ?     | bathydemersal          | 220 – 1060 Atlantic and Mediterranean |
|              |             | Chauna guttatus Günther, Bean, 1896                                     | Fig. 5L | RZ  | -     | -     | bathydemersal          | 200 – 980 Atlantic |
| Ogocephalidae|             | Dibranchus atlanticus Peters, 1876                                     | Fig. 5M | RZ  | -     | X     | bathydemersal          | 300 – 820 Atlantic |
| Diceratiidae |             | Biforoceras velifer (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 braziliensis) 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).
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.

**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.
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 4 | Species of the order Gadiformes, family Moridae. A. Physiculus kaupi, photograph by Revizee Score-North, order Trachichthyiformes, family Trachichthyidae. B. Gephyrobryx darwinii, photograph by PRODEMERSAL, order Pleuronecorthiformes, 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. Neopinnula americana, photograph by PRODEMERSAL. H. Ruvettus pretiosus, photograph by PRODEMERSAL, family Ariommatidae. 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 brachychir, photograph by Revizee Score-North, G. Priotus stearnsi, photograph by Revizee Score-North, family Peristediidae, H. Peristedion sp., photograph by Revizee Score-North, order Capriiformes, 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 Ogcocephalidae, **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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AUTHOR CONTRIBUTION
Alex Garcia Cavalleiro de Macedo Klautau: Data curation, Funding acquisition, Supervision.
Israel Hidenburgo Aniceto Cintra: Conceptualization, Project administration, Writing-original draft, Writing-review & editing.
Matheus Marcos Rotundo: Formal analysis, Investigation, Writing-original draft, Writing-review & editing.
Alfredo Carvalho-Filho: Formal analysis, Investigation, Writing-original draft, Writing-review & editing.
Rodrigo Antunes Caires: Formal analysis, Investigation, Writing-original draft, Writing-review & editing.
Alexandre Pires Marceniuk: Conceptualization, Formal analysis, Investigation, Supervision, Writing-original draft, Writing-review & editing.

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