

Incidental capture and diversity of Elasmobranchii and Teleostei caught by red snapper and lobster fisheries in the Great Amazon Reef System

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ABSTRACT

The Great Amazon Reef System is one of the least known mesophotic environments on the Atlantic coast of northern South America, threatened by oil and gas exploration projects and explored by different industrial fisheries. Here, we provide the first inventory of the cartilaginous and bony fishes captured by industrial fisheries of the red snapper and lobster in the Great Amazonian Reef System, including a list of species with ecological and conservation information, in addition to biogeographic considerations. A total of 143 species were recorded, with 17 elasmobranchs and 126 teleosts. A specimen likely representing a hybrid between *Cephalopholis fulva* and *Cephalopholis furcifer* (Serranidae) was also recorded. Community ecology descriptors were employed to explore the diversity patterns of the species captured by different fishing gears. Our results highlight the relevance of monitoring fishery activities to enhance knowledge of the biodiversity in poorly sampled areas and understanding the local impacts of human activities.

KEYWORDS: mesophotic corals, fisheries monitoring, fishing gears, Amazon River plume

Captura acidental e diversidade de Elasmobranchii e Teleostei na pesca do pargo e lagosta no Grande Sistema de Recifes da Amazônia

RESUMO

O Grande Sistema de Recifes da Amazônia é um dos ambientes mesofóticos menos conhecidos da costa do Atlântico no norte da América do Sul, ameaçado por projetos de exploração de petróleo e gás e explorado por diferentes pescarias industriais. Apresentamos aqui o primeiro inventário dos peixes ósseos e cartilagosos capturados pela pesca industrial do pargo e da lagosta no Grande Sistema de Recifes da Amazônia, incluindo uma lista de espécies com informações ecológicas e de conservação, além de considerações biogeográficas. Um total de 143 espécies foram registradas, sendo 17 elasmobrânquios e 126 teleosteos. Um espécime representando um provável híbrido entre *Cephalopholis fulva* e *Cephalopholis furcifer* (Serranidae) também foi registrado. Descritores ecológicos de comunidades foram utilizados para explorar os padrões de diversidade das espécies capturadas por diferentes artes de pesca. Nossos resultados destacam a relevância do monitoramento das atividades pesqueiras para aumentar o conhecimento da biodiversidade em áreas pouco amostradas e a compreensão dos impactos locais de atividades humanas.

PALAVRAS-CHAVE: corais mesofóticos, monitoramento pesqueiro, artes de pesca, pluma do Rio Amazonas

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INTRODUCTION

The northern coast of Brazil has high biological productivity and a complex food web, which is intensively exploited by local fisheries (Isaac-Nahum 2006; Isaac and Ferrari 2017) that together comprise the world's most important fisheries in tropical areas (Isaac and Ferrari 2017; Goulding *et al.* 2019; Araujo *et al.* 2021). The Amazon River discharge greatly influences this area, modulating salinity, light availability, pH, and dissolved nutrients (Mahiques *et al.* 2019). In this area, the Great Amazon Reef System (GARS) is a complex environment with a consolidated substrate formed by living organisms (Cordeiro *et al.* 2015; Moura *et al.* 2016; Francini-Filho *et al.* 2018), bounded by the discharge of sediments and suspended material from the Amazon River and strong marine currents (Francini-Filho *et al.* 2018).

Four large-scale fishery activities occur on the northern coast of Brazil. Two of them occur on soft substrata (muddy, sandy, or gravel), namely the pair trawling for the Lulao catfish, *Brachyplatystoma vaillantii* (Valenciennes 1840), and the bottom trawling for the pink shrimps *Penaeus subtilis* (Pérez Farfante 1967) and *Penaeus brasiliensis* Latreille 1817. These activities are relatively well studied, and their bycatch is well described in the scientific literature (Barthem 1985; Paiva *et al.* 2009; Jimenez *et al.* 2013; Aragão *et al.* 2015; Maia *et al.* 2016; Silva *et al.* 2016; Klautau *et al.* 2016b; Marceniuk *et al.* 2019; Marceniuk *et al.* 2023). The two other large-scale fishery activities in the region occur predominantly on consolidated substrates of the GARS: the fishery of the red snappers *Lutjanus campechanus* (Poey, 1860) and *Lutjanus purpureus* (Poey, 1866), and of the lobsters *Panulirus meripurpuratus* Giraldez & Smyth 2016 and *Scyllarides delfosi* Holthuis 1960. The bycatch of the GARS fisheries is scarcely described (Cintra *et al.* 2019; Santos *et al.* 2019), and there is no systematic measurement of the fishing effort affecting target species or by-catch biodiversity (Klautau *et al.* 2016).

The commercial exploration of red snappers and lobsters on the northeastern Brazilian coast started in the 1960s (Fonteles-Filho 1972). When the yield decreased, the fisheries expanded to the northern coast (Paiva 1997). These fisheries are carried out by small and average mid-sized vessels ranging from 8 to 20 m, with traps, handlining, and longlining aimed at reef fish between the middle and external platforms of the marginal sedimentary basins of Pará-Maranhão at depths ranging from 70 m to 220 m (Moura *et al.* 2016; Mahiques *et al.* 2019). Information on these fisheries is presented by Porto *et al.* (2005), Lima *et al.* (2014), Costa *et al.* (2017), Santos *et al.* (2019), and Freitas *et al.* (2021), but these studies do not specifically refer to the GARS and only superficially address bycatch composition (Santos *et al.* 2019).

Industrial fisheries always result in bycatch, that is, species captured unintentionally (Eayrs 2007; Davies *et al.* 2009). In any marine resource exploitation, knowledge of

the unintended catch of undersized individuals and species is crucial for the development and sustainability of a fishery (Bastardie *et al.* 2021). Appropriate monitoring and fisheries management can mitigate bycatch (Gilman *et al.* 2020). Systematic bycatch monitoring can enhance understanding of species-specific risks, and which fisheries and gear types pose the most significant threats (Jensen *et al.* 1988; Cook 2019), allowing to project potential impacts of expanding the fishery into unfished areas or re-entering historical fishing grounds for which no information exists.

Despite the relevance in biogeographic, ecological, and commercial terms, the fauna of the Great Amazon Reef System is still poorly studied in terms of its biota and natural resources (Moura *et al.* 2016). So, considering the importance of understanding fisheries bycatch in the context of ecosystem management, our objective in this study was to describe the bycatch of the red snapper and lobster fisheries in the GRAS in terms of species composition, diversity patterns and ecological attributes by type of fishing gear employed in these activities.

MATERIAL AND METHODS

Study area

The GARS is a complex environment with a consolidated substrate, first recognized by Collette and Rützler (1977). The existence of the GARS was later reinforced by dredge probes and underwater photography obtained by the Deep Worker submarine at depths between 70 m and 250 m (Cordeiro *et al.* 2015; Moura *et al.* 2016; Francini-Filho *et al.* 2018) (Figure 1). The available evidence indicates that GARS is a typical mesophotic coral ecosystem occurring at depths of between 70 m and 220 m, primarily constituted of calcareous algae, sponges, and scleractinian corals, which may potentially cover a total area up to 56,000 km² (Moura *et al.* 2016; Francini-Filho *et al.* 2018). The high species diversity of the GARS includes algae, rhodoliths, sponges, soft coral, and black corals (Cordeiro *et al.* 2015) influenced by the discharge of sediments and suspended material from the Amazon River, as well as strong marine currents. On the middle of the continental shelf, sunlight penetration is determined by an interplay between the Amazon River plume and the more transparent waters of the North Brazil Current (Francini-Filho *et al.* 2018).

Fishing surveys

We summarized the outcome of four fishing gears employed in GARS fishing: traps (used to capture red snappers and lobsters, Figure 2a), bottom nets (used for lobsters, Figure 2b), fishing hooks (used for red snappers, Figure 2c), and handlines (used for red snappers, Figure 2d) (Cintra *et al.* 2019; Santos *et al.* 2019). The first three gears have been monitored by observers of the Centro Nacional de Pesquisa e Conservação da Biodiversidade Marinha da Costa Norte do Brasil (CEPNOR) at Belém, Pará state (SISBIO license #

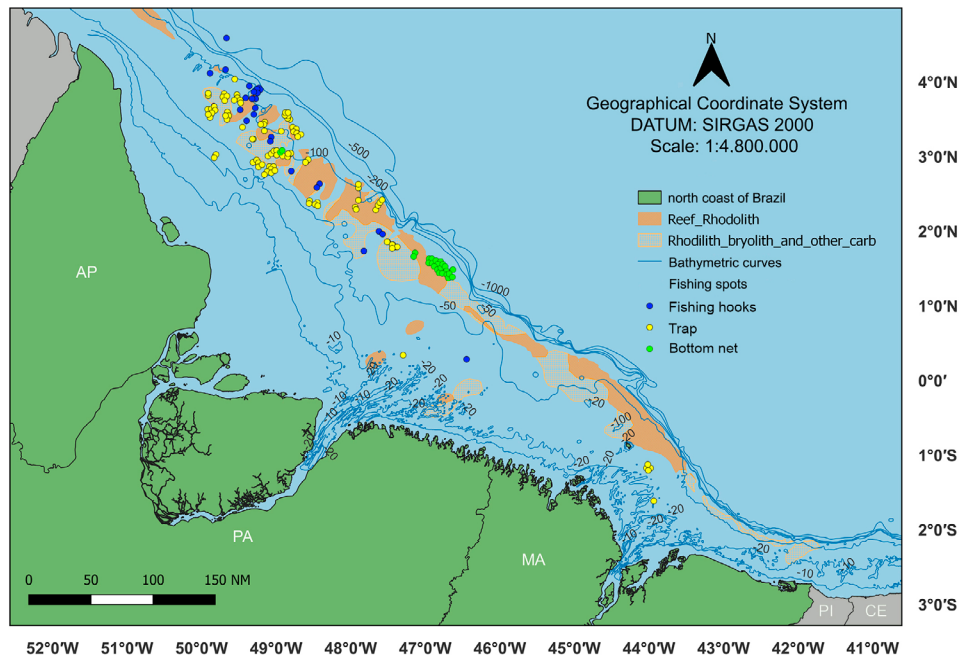


Figure 1. Location of the Great Amazon Reef System along the northern coast of Brazil (states of Amapá, AP, Pará, PA and Maranhão, MA). Circles indicate sampling points according to the fishing gear employed, conducted by observers of Centro Nacional de Pesquisa e Conservação da Biodiversidade Marinha do Norte (CEPNOR-ICMBio) embarked on lobster and red snapper fishing vessels.

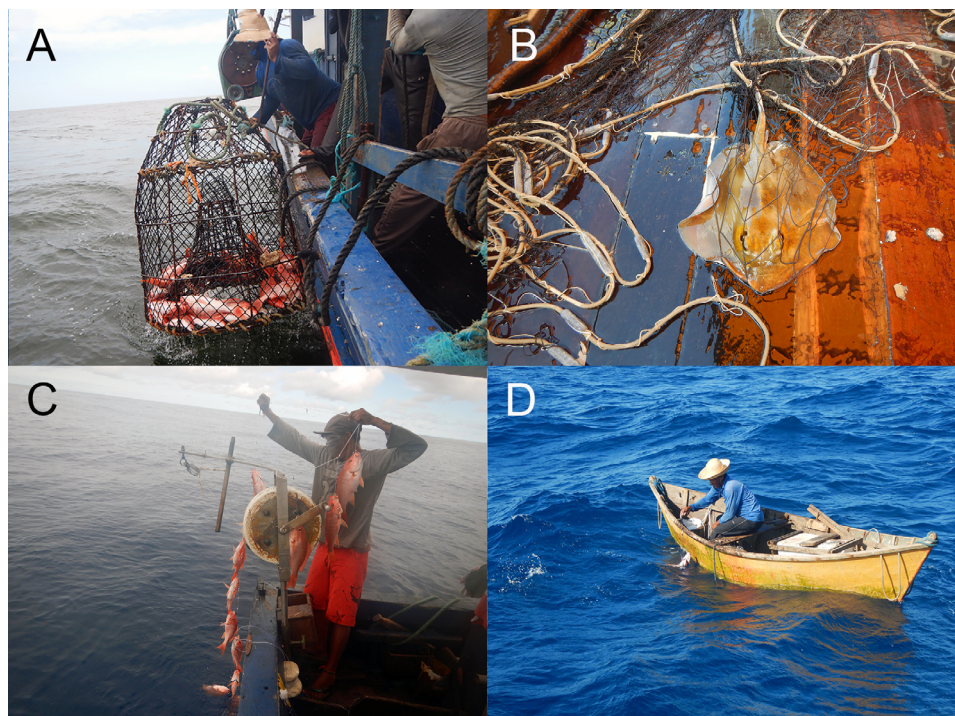


Figure 2. Monitoring fisheries at the Great Amazon Reef System. **A** – trap for lobsters and red snappers; **B** – bycatch in a bottom net; **C** – fishing hooks; **D** – fishermen spend the day fishing with handline and are retrieved by the fishing vessel at the end of the day.

44915-7). Monitoring occurred from June 2019 to May 2022, between 4°9'57.883"N and 1°36'48.104"S (Figure 1). In total, sampling encompassed 1,524 fishing hours over 120 days (370

hours and 36 days of lobster fishery, and 1,154 hours and 84 days of red snapper fishery). Handlines were used during the time intervals between other gear deployment and recovery.

Taxonomic procedure

The observers photographed specimens onboard and deposited voucher specimens in the ichthyological collection of Museu Paraense Emílio Goeldi (MPEG), the zoological collection of Universidade Santa Cecília (AZUSC), and the collection of the Laboratory of Fish Biology and Genetics of Universidade Estadual Paulista Júlio de Mesquita (LBP/UNESP). Fishermen also provided additional photographic records. Species identification followed the descriptions and identification keys of Cervigón *et al.* (1992), Carpenter (2002) and Marceniuk *et al.* (2021), as well as comparison with material from the abovementioned collections or consultation with experts (Dr. Ross Robertson, Smithsonian Tropical Research Institute). Species were grouped by order and family following Nelson *et al.* (2016).

Habit and conservation status

For each species, we presented information on depth range in which the species was captured, feeding habits (herbivore, invertivore, piscivorous, omnivorous, planktonic) (Marceniuk *et al.* 2021a,b), frequency of occurrence by fishing gear (fishing hook, trap, bottom net), occurrence area on the continental shelf (middle platform, coastal areas, and estuaries; see Marceniuk *et al.* 2024), habitat (deep water, estuarine, fresh water, coastal marine, oceanic; see Marceniuk *et al.* 2021b, 2024), substrate association (reef, soft bottom, water column; see Marceniuk *et al.* 2021b), habit (benthic, demersal, pelagic; see Marceniuk *et al.* 2021b), commercial value (used as food or bait, without commercial value; based on Marceniuk *et al.* 2021a,b and the results of this study), and conservation status according to the Brazilian Red List of Threatened Species (ICMBio 2023) and the IUCN Red List of Threatened Species (IUCN 2022) when the species was not assessed in Brazil (categories: critically endangered, endangered, vulnerable, near threatened, least concern, data deficient, or not evaluated).

Diversity patterns

We quantified the sample coverage of bycatch and species diversity, with the different fishing gears according to Chao and Jost (2007) as the ratio of the observed number of species over the expected number of species through a sample-coverage rarefaction (Supplementary Material, Figure S1). In addition, we applied Jost's partitioning of the gamma diversity into independent alpha and beta components (Hill 1973; Jost 2007). In this context, gamma diversity represents the total number of bycatch species captured in all samples from any fishing gear, alpha diversity represents the number of species captured in a single sample from any fishing gear, and beta diversity summarizes the change in community composition, either by changes in richness (nestedness) or species identity (turnover) (Baselga 2010). We used a binary matrix for the partitioning of the gamma diversity. Finally, we tested differences in alpha diversity among the three fishing

gears using analysis of variance (ANOVA). Data analysis was performed using the packages *entropart* (Marcon and Hérault 2015) and *betapart* (Baselga *et al.* 2020) in the R environment (R Core Team 2018). Only specimens collected by on-board samplers were included in the analyses, while specimens collected by fishermen were excluded (marked with a dash in Supplementary Material, Table S1).

Distribution of species by habitat

We tested if species were more associated to reef or soft bottom habitats using chi-squared tests. We used all the individual records from the fishing hooks and traps. We did not include the bottom nets in this analysis because this sampling method was applied only in the reef habitat and could potentially bias the analysis. For each species, we tested if all its occurrences were significantly different from the observed percentage of individuals in reef or soft bottom habitats. Overall, 60% of all individuals sampled occurred in the reef habitat and 40% in the soft bottom habitat. If the occurrence of a given species is random between the two habitats, its occurrence in our samples should not significantly differ from these proportions. We considered species with at least five sampled individuals.

RESULTS

We recorded 126 species of Teleostei (Figure 3) (including the two target species) and a hybrid specimen (not included in the statistics), belonging to 21 orders and 44 families, in addition to 17 species of Elasmobranchii (Figure 4) belonging to seven orders and 10 families (Supplementary Material, Table S1). Fishes were captured at depths ranging from 30 m to 170 m. A total of 19 species were captured at depths higher than previously reported in the literature. Perciformes showed highest diversity among the bony fishes, including 47 species, Serranidae and Lutjanidae presenting the highest richness, with 15 and 12 species, respectively (Figure 5a,b; Supplementary Material, Table S1). Among the Serranidae, we recorded one specimen that is likely a hybrid between *Cephalopholis fulva* (Linnaeus, 1758) and *Cephalopholis furcifer* (Valenciennes, 1828) (Figure 3g), which is sometimes recognized as *Menephorus punctiferus* Poey, 1875 as reported by Smith (1966). Carcharhiniformes and Carcharhinidae were the most diverse order and family among cartilaginous fishes, with seven and four species, respectively (Figure 5c,d; Supplementary Material, Table S1).

Feeding habits

Most of the species recorded are carnivorous, with 68 (47%) identified as piscivorous/invertivorous, 38 (27%) exclusively invertivorous, and 21 (15%) exclusively piscivorous. Non-carnivores were represented by eight (6%) omnivorous, six (4%) planktivorous, and two (1%) herbivorous (Figure 6a; Supplementary Material, Table S1).



Figure 3. Examples of Teleostei fish species caught as bycatch of red snapper and lobster fisheries in the Great Amazon Reef System on the northern coast of Brazil. Order Anguilliformes, family Muraenidae: **A** – *Enchelycore nigricans*. Order Holocentridae, family Holocentridae: **B** – *Holocentrus rufus*. Order Scombriformes, family Scombridae: **C** – *Scomberomorus maculatus*; family Nomeidae: **D** – *Psenes cyanophrys*. Order Perciformes, family Epigonidae: **E** – *Epigonus occidentalis*; family Serranidae: **F** – *Cephalopholis cruentata*; **G** – *Menephorus punctiferus*, a hybrid of *Cephalopholis fulva* and *Cephalopholis furcifer*; **H** – *Paralabrax dewegeri*; family Haemulidae: **I** – *Haemulon striatum*; family Lutjanidae: **J** – *Pristipomoides macrophthalmus*. Order Scorpaeniformes, family Scorpaenidae: **K** – *Scorpaena* aff. *dispar*. Order Acanthuriformes, family Sciaenidae: **L** – *Eques lanceolatus*; **M** – *Pareques iwamotoi*. Order Lophiiformes, family Antennariidae: **N** – *Fowlerichthys ocellatus*.

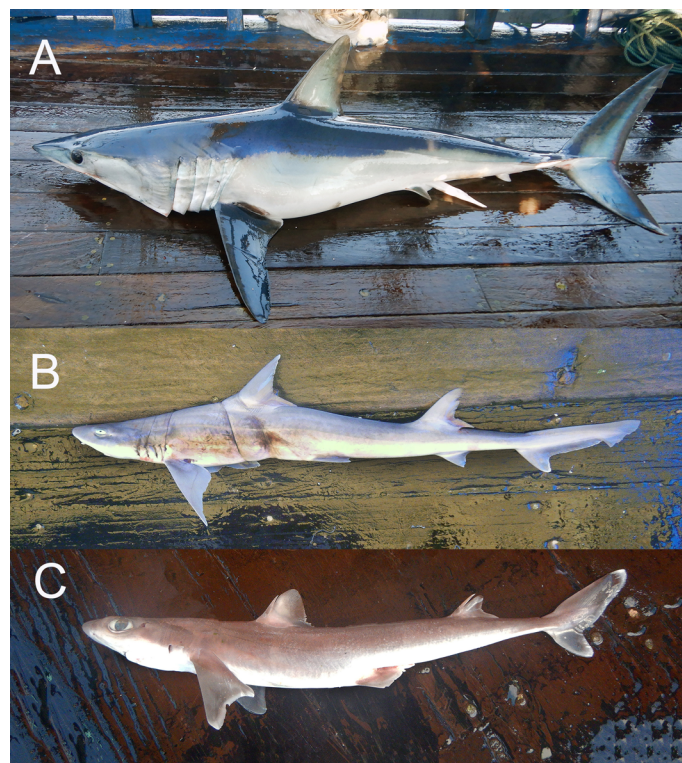


Figure 4. Examples of Elasmobranchii fish species caught as bycatch of red snapper and lobster fisheries in the Great Amazon Reef System on the northern coast of Brazil. Order Lamniformes, family Lamnidae: **A** – *Isurus oxyrinchus*. Order Carcharhiniformes, family Triakidae: **B** – *Mustelus* sp. Order Squaliformes, family Squalidae: **C** – *Squalus albicaudus*.

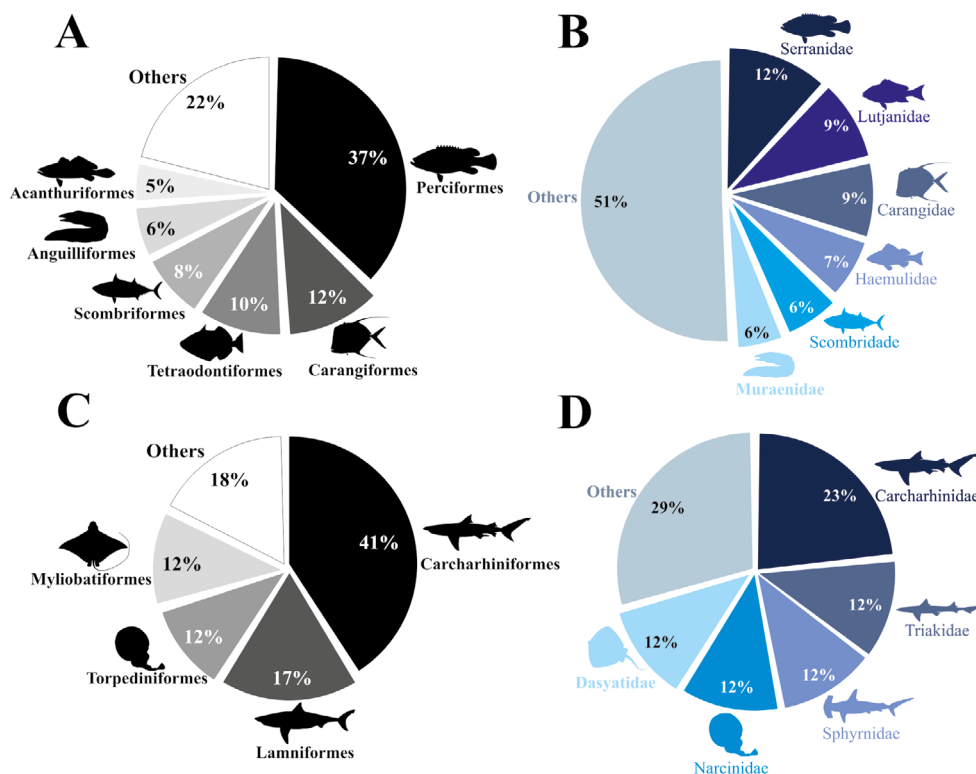


Figure 5. Representativeness (%) by order and family of fish species caught in the Great Amazon Reef System, northern coast of Brazil. Teleostei orders (A) and families (B); Elasmobranchii – orders (C) and families (D).

Use of habitat and the continental platform

Eighty-four (59%) species are typical of coastal marine areas, whereas 38 (27%) live in both estuaries and coastal marine areas. Only 11 (8%) species live in both coastal and oceanic environments, three (2%) in both coastal and deep waters, two (1%), *Psenes cyanophrys* Valenciennes, 1833 (Figure 3d) and *Epigonus occidentalis* Goode & Bean, 1896 (Figure 3e) are restricted to deep sea environments, three (2%) live in coastal marine, deep water and estuarine environments, and two (1%) in all environments (including freshwater) (Figure 6c; Supplementary Material, Table S1).

Fifty-three (59%) species occur exclusively in the middle continental shelf (sand and gravel substrate), one (1%) exclusively in the coastal areas and estuaries (mud bottom substrate) and 36 (40%) occur in both environments (Figure 6b; Supplementary Material, Table S1). Thirty-six (25%) species are restricted to consolidated substrate, 10 (7%) to the water column, 65 (46%) are associated with both consolidated and unconsolidated substrate, 30 (21%) with both consolidated substrate and the water column, and only two (1%) occur on all substrata (Figure 6d; Supplementary Material, Table S1).

Habit

Seventy-two species (50%) were demersal, 36 (25%) pelagic, 25 (18%) benthonic, nine (6%) demersopelagic, and only one (1%) benthodemersal (Figure 6e; Supplementary Material, Table S1).

Commercial value

In addition to the two red snapper species, *L. campechanus* and *L. purpureus*, 40 other species (29%) have commercial value, 30 (21%) are used as bait or as subsistence food by fishermen, and 71 (50%) do not have any commercial value and are always discarded (Figure 6f; Supplementary Material, Table S1).

Conservation status

Eighty-six of the bycatch species (60%) are classified as of least concern, 16 (11%) as near threatened, 10 (7%) as vulnerable, two (1%), *Sphyrna lewini* (Griffith & Smith, 1834) and *Epinephelus itajara* (Lichtenstein, 1822), as critically endangered, two (1%), *Sphyrna mokarran* (Rüppell, 1837) and *Hyphorhodus nigritus* (Holbrook, 1855), as endangered, 23 (17%) as data deficient, and four (3%) as not evaluated (Figure 6g; Supplementary Material, Table S1).

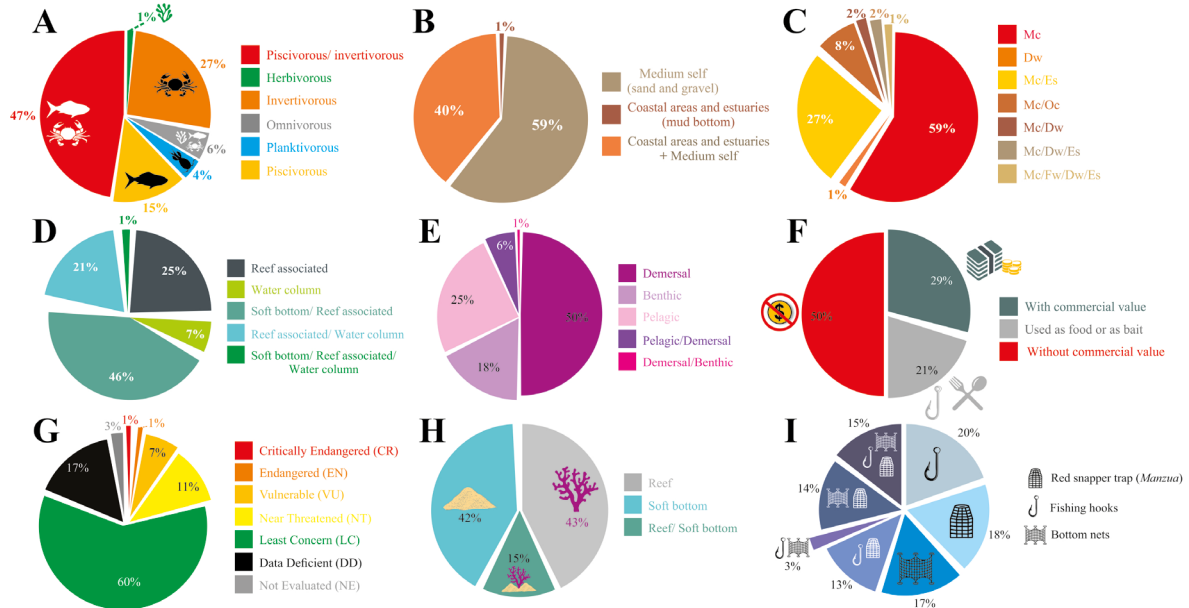


Figure 6. Representativeness (%) by type of diet, habitat, commercial value, conservation status and type of fishing gear of fish species caught in the Great Amazon Reef System, northern coast of Brazil. **A** – diet; **B** – distribution on the continental shelf; **C** – habitat (Dw - deep water; Es - estuarine; Fw - fresh water; Mc - coastal marine; Oc – oceanic); **D** – substrate; **E** - habit; **F** - commercial value; **G** - conservation status; **H** – habitat of capture; **I** – employed fishing gear.

Captures by substrate and fishing gear

Sixty-one species (43%) were recorded exclusively on consolidated substrate, 21 (15%) exclusively on unconsolidated substrate, and 60 (42%) on both substrates (Figure 6h; Supplementary Material, Table S1). Eighty-six species were captured by traps, 69 by bottom nets, and 72 by fishing hooks. Of the total number of species captured, 78 were captured with only one fishing gear: 26 (18%) only by traps, 28 (20%) only by fishing hooks, and 24 (17%) only by bottom nets. Twenty (14%) species were captured by both traps and bottom nets, 19 (13%) by fishing hooks and traps, four (3%) by bottom nets and fishing hooks; and 21 (15%) by all three fishing gears (Figure 6i; Supplementary Material, Table S1).

Sample coverage was higher than 60% for all the fishing events and for each fishing gear separately. Bottom nets showed the highest sample coverage (SC = 96%), followed by traps (SC = 95%), and fishing hooks (SC = 74%). Traps exhibited the largest gamma diversity (${}^0D = 74$ species), followed by bottom nets (${}^0D = 66$ species), and fishing hooks (${}^0D = 58$ species). Bottom nets exhibited the highest average values of alpha diversity (${}^0D_{\text{alpha}} = 9.5$ species) when compared with traps (${}^0D_{\text{alpha}} = 4.0$) and fishing hooks (${}^0D_{\text{alpha}} = 2.8$) (ANOVA; $p < 0.0001$, $F = 48.9$, $df = 2$; Figure 7a). Beta diversity was the highest for fishing hooks (${}^0D_{\text{beta}} = 20.4$ completely distinct communities), followed by traps (${}^0D_{\text{beta}} = 18.4$ completely distinct communities) and bottom nets (${}^0D_{\text{beta}} = 6.97$ completely distinct communities), indicating the largest change in species composition between different samples taken by fishing hooks. Overall, turnover

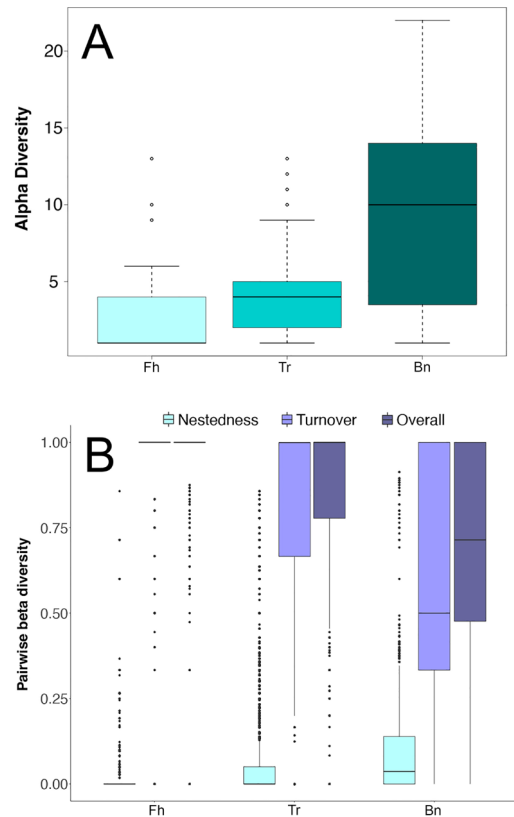


Figure 7. Diversity indicators of fish captured with three different fishing gears as bycatch of red snapper and lobster fisheries in the Great Amazon Reef System on the northern coast of Brazil. **A** – alpha diversity (expressed as the effective number of species); **B** – overall pairwise beta diversity (separated in this nestedness and turnover components registered in A). Fh = fishing hooks; Tr = traps; Bn = bottom nets.

was the main component explaining beta diversity for all fishing gears (Figure 7b), indicating that different samples of the same fishing gear exhibited similar number of captured species but different species.

Distribution of species by habitat

Among the 143 species analyzed regarding their habitat preferences, 35 exhibited a non-random occurrence pattern between the two available habitats, and nine species occurred randomly in any habitat [e.g., *Caranx crysos* (Mitchill, 1815) and *Epinephelus morio* (Valenciennes, 1828)]. Nineteen species were mostly associated with the reef habitat, with 71 to 100% of individuals captured in this habitat, and included species such as *Lutjanus vivanus* (Cuvier, 1828), *Holacanthus ciliaris* (Linnaeus 1758) and *Chaetodon ocellatus* Bloch, 1787. Fifteen species were mostly associated with the soft bottom habitat, with 50 to 93% of individuals captured in this habitat, including species such as *Lutjanus jocu* (Bloch & Schneider, 1801), *Pterois volitans* (Linnaeus, 1758) and *Micropogonias furnieri* (Desmarest, 1823) (Supplementary Material, Table S2).

DISCUSSION

Previous checklists of the GARS region recorded between 26 (Collette and Rützler 1977) and 73 species (Moura *et al.* 2016) of cartilaginous and bony fishes. Here, we present a list of 143 for the GARS, with only 41 of them registered previously. This highlights the effectiveness of monitoring fishery activities to enhance knowledge of biodiversity in poorly sampled areas and to understand local impacts of human activities.

Fishing gear and biodiversity

Regional gamma diversity was similar among fishing gears, with the highest value for traps and the lowest for fishing hooks. However, in terms of alpha diversity, fishing hooks resulted in a lower number of bycatch species compared to bottom nets and traps.

Conversely, the highest values of beta regional diversity were recorded for fishing hooks and traps, approximately three times more than for bottom nets. These numbers indicate that although the number of bycatch species is low in each fishing hook sample, there is a higher species substitution from one sample to another compared to the other fishing gears. For example, in bottom nets, species tend to be caught repeatedly in different samplings, resulting in a low species substitution. This is consistent with Humphries *et al.* (2019), who also showed a higher selectivity of fishing hooks than of harpoon fishing in the coral reefs of Lombok Island (Indonesia). Nevertheless, it should be highlighted that different fishing procedures using the same gears might also alter selectivity, as observed in the fishery of red snappers and groupers in Indonesia using

different techniques (Amorim *et al.* 2020). The selectivity might reflect the functional traits of captured species (both targeted and bycatch), as observed in the fisheries activities developed in the conservation unit Costa dos Corais, on the northeastern Brazilian coast (Carvalho *et al.* 2021).

Altogether, single samplings using bottom nets can return a higher bycatch richness, while fishing hooks will produce a lower bycatch richness. Despite fishing hooks having produced a lower catch, all types of fishing gear assessed in this study can potentially impact the local fish diversity, whether by catching different species at once (e.g., higher alpha diversity, as with the bottom nets) or by having higher rates of substitution per catching (e.g., higher beta diversity, as with the fishing hooks and traps). In this sense, we highlight the importance of knowing the typical bycatch of each fishery activity in the GARS and nearby areas, partially because fish populations are affected by more than one activity. This knowledge, coupled with continuous monitoring, favors a real-time assessment of species conservation status and management actions (Humphries *et al.* 2019; Amorim *et al.* 2020; Carvalho and Humphries 2021; Yudawan *et al.* 2022).

Ichthyofauna and the environment

Regarding habitat use, most of the recorded species are typically found in marine coastal areas or estuaries, and at least 87 are common at depths below 30 m, suggesting that the GARS can function as a refuge from over fishing or climate change for species from coastal areas. A total of 35% of the recorded species are found only in the GARS, while 39% also occur in the middle shelf (30 to 70 m deep), and 27% in the middle shelf and coastal zones (0 to 30 m). This pattern corroborates the hypothesis that the Amazon River plume is a barrier to species typically found in saline and transparent waters associated with consolidated substrate (Moura *et al.* 2016; Mahiques *et al.* 2019). The existence of a characteristic reef fish fauna at the GARS highlights the importance of the Amazon-Orinoco plume as an environmental and biogeographical filter that inhibits the occurrence of some species not adapted to the environmental conditions in these areas, such as brackish and/or turbid waters (Soares *et al.* 2021). Such a pattern is exemplified by *Hypanus marianae* (Gomes, Rosa & Gadig, 2000), a shallow-water reef species frequently collected in the GARS but absent from northern Brazilian coastal areas with a soft bottom (Marceniuk *et al.* 2019, 2023).

As previously suggested, the GARS might be interpreted as an ecotonal habitat between the Brazilian and Caribbean biogeographical provinces (Francini *et al.* 2018). This hypothesis is supported by the occurrence in the GARS of species of both the Caribbean and North Atlantic ichthyofauna. These species are not present on other parts of the Brazilian coast [e.g., *Cephalopholis cruentata*

(Lacepède, 1802), *Pristipomoides macrophthalmus* (Müller & Troschel, 1848), *Pareques iwamotoi* Miller & Woods, 1988, *Fowlerichthys ocellatus* (Bloch & Schneider, 1801), *Mycteroperca phenax* Jordan & Swain, 1884], and/or are endemic to the Brazilian province, such as *Hypanus marianae* (Figure 2b) and *Lutjanus alexandrei* Moura & Lindeman, 2007, which are absent from the Caribbean and North Atlantic.

Besides the biogeographic importance its ichthyofauna, the monitoring of fishery in the GARS showed a higher number of species in the reef area than that on muddy substrate. This demonstrates the ecological importance of reefs in maintaining marine environmental quality (Gao *et al.*, 2022; Hodge and Price, 2022). The high structural complexity of reefs allows a higher number of microhabitats and sustains a higher species diversity (Carminatto *et al.* 2020; Carvalho *et al.* 2021; Sgarlatta *et al.* 2023), including species that occur in adjacent habitats (Bastos *et al.* 2022; Gao *et al.* 2022; Swadling *et al.* 2022). Besides the connectivity among habitats, the high diversity in habit and trophic levels of the bycatch points to a complex food web in the area, which is essential for the short- and long-term maintenance of ecological communities using the reefs in part or exclusively (Gao *et al.* 2022; Skinner *et al.* 2022; Quigg *et al.* 2023). Our results support the hypothesis that the GARS potentially connects the Caribbean and Brazilian marine ichthyofauna, providing a mesophotic corridor for species dispersal (Rocha 2003; Floeter *et al.* 2008), and is an important habitat for the ecological functioning of the fish fauna in the region.

Conservation status

The GARS is subject to intense fishing activity and is the most important mesophotic ecosystem for red snapper and the lobster industrial fisheries on the Atlantic coast of South America, being of great importance to the regional economy (Santos *et al.* 2020). The GARS is also threatened by petroleum and gas extraction projects (Mahiques *et al.* 2019). Despite these impacts, there is still a lack of consolidated knowledge about its ichthyofauna. The harvest of bycatch alters community structure and food webs (Anderson *et al.* 2013), causing significant ecological impacts (Clucas 1997; Stobutzki *et al.* 2001) and posing challenges for fisheries management (Davies *et al.* 2009). Therefore, the incomplete knowledge of species accidentally captured by the industrial fisheries, especially in understudied areas, hampers the development of effective measures for protecting the local fauna and managing the ecosystems (Thrush *et al.* 1998).

We recorded a high number of threatened and critically endangered species, as well as species that are data deficient or not assessed. The latter two categories reflect the fact that the ecological attributes of many bycatch species are still relatively unknown, preventing the assessment of their actual

status (Howard and Bickford 2014; Bland *et al.* 2015; Luiz Jr *et al.* 2016; Fitzgerald *et al.* 2021; Borgelt *et al.* 2022). In this sense, different approaches for assessing the conservation status of little known species showed that these species are usually threatened, yet not protected by current legislation and/or conservation programs due to the lack of data on their distribution and life history (Morais *et al.* 2013; Howard and Bickford 2014; Bland *et al.* 2015; Jetz and Freckleton 2015; Luiz Jr *et al.* 2016; Farooq *et al.* 2020; Borgelt *et al.* 2022).

Besides the high number of threatened species, the presence of the invasive lionfish, *Pterois volitans* demands quick conservation actions (Luiz Jr *et al.* 2021; Cintra *et al.* 2022, 2023), since this fish is known to cause local extinction of native species, alter food webs, impact fisheries, and pose threats to human health (Arndt *et al.* 2018; Haddad Jr *et al.* 2022; Soares *et al.* 2022). Therefore, obtaining high quality data with robust methods through the monitoring of fisheries and research on the ecological aspects of fish populations should be a priority to subsidize the effective management of fisheries (Kritzer 2020; Petersen *et al.* 2021; Davis and Hanich 2022; Glaviano *et al.* 2022; Stephenson *et al.* 2022).

CONCLUSIONS

Our results indicate that the monitoring of fishing activities in the GARS is urgently needed due to the high fish species diversity found in the area and the lack of knowledge on the regional biota. The identification of the fisheries bycatch in the GARS is a fundamental step towards establishing guidelines for fisheries zonation, planning of conservation strategies and the delimitation of protected areas. To address this, the Ministry of the Environment has promoted the revival of the National Program of Onboard Observers in the Fishing Fleet (PROBORDO). This initiative aims to provide insights into the impacts of fishing on species and ecosystems, as well as to uncover the realities of unregulated, “invisible” fishing within the country.

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DATA AVAILABILITY: The data that support the findings of this study are available from the corresponding author [A. L. Marцениuk], upon reasonable request.



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SUPPLEMENTARY MATERIAL

Marцениuk *et al.* Incidental capture and diversity of Elasmobranchii and Teleostei caught by red snapper and lobster fisheries in the Great Amazon Reef System

Table S1. Elasmobranchii and Teleostei caught as bycatch of red snapper and lobster fisheries in the Great Amazon Reef System, northern coast of Brazil, listed by class, order, family and species. * (one asterisk) = species recorded by Collette and Rutzler (1977); ** (two asterisks) = species recorded by Moura *et al.* (2016). Dp = capture depth (in parentheses the greatest previous record of depth; unpublished data by Ross Robertson) (asterisk indicates species common below 30 m; unpublished data by Alfredo Carvalho-Filho); Dt = diet (He – herbivore, In – invertivore, Pi – piscivorous, On – omnivorous and Pa – planktonic); F% (Frequency of occurrence in the fisheries studied: FH% – fishing hooks, FT% – red snapper trap “manzua” and FN% – bottom nets); DC = distribution on the continental shelf (Me – medium shelf, sand and gravel, Co – coastal areas and estuaries, mud bottom); HT = habitat (Dw – deep water, Es – estuarine, Fw – fresh water, Mc – coastal marine, Oc – oceanic); SB = substrate (Ra – reef associated, Sb – soft bottom, Wc – water column); LH = habit (Be – benthic, De – demersal, Pl – pelagic); \$ = commercial value (* – with commercial value, ** – used as food or bait, *** – without commercial value); CS = conservation status in the Brazilian List of Endangered Fauna (CR – critically endangered, EN – endangered, VU – vulnerable, NT – near threatened, LC – least concern, DD – data deficient; NE = not evaluated; asterisk indicates IUCN conservation status); CH = capture habitat (R – reef, S – soft bottom); FG = fishing gear (H – fishing hooks, T – red snapper trap, N – bottom nets).

Taxon	Dp	Dt	FH%	FT%	FN%	DC	HT	SB	LH	\$	CS	HC	FG
Chondrichthyes													
Orectolobiformes													
Ginglymostomatidae													
<i>Ginglymostoma cirratum</i> (Bonnaterre, 1788) **	69-105*	Pi/In	0,8	0,4	2	Me	Mc/Es	Sb/Ra	Be	*	VU	R/S	T/N/H
Laminiformes													
Lamnidae													
<i>Isurus oxyrinchus</i> Rafinesque, 1810	63-102	Pi	1,5	0	0	-	Mc/Es	Wc	De	*	NT	R	T
Triakidae													
<i>Mustelus norrisi</i> Springer, 1939	80-140*	Pi/In	0	0,8	0	Me	Mc/Es	Wc	De	***	NT	R	T/N
<i>Mustelus</i> sp.	90-121*	Pi/In	0	0	2,2	Me	Mc/Es	Wc	De	***	LC	R	N
Carcharhiniformes													
Carcharhinidae													
<i>Carcharhinus acronotus</i> (Poey, 1860)	83-90 (64)*	Pi	1,5	0	0	Me	Mc	Ra	Pl	*	NT	S	H
<i>Carcharhinus falciformis</i> (Bibron, 1839)	70-170	Pi/In	5,3	0	0	Me	Mc/Dw	Ra	Pl/De	*	NT	R/S	H
<i>Carcharhinus limbatus</i> Valenciennes, 1839	87	Pi/In	0,8	0	0	Me	Mc/Fw/Dw/Es	Sb/Ra	Pl/De	*	NT	S	H
<i>Rhizoprionodon porosus</i> (Poey, 1861)	76-123	Pi/In	3,8	0	0	Me	Mc/Fw/Dw/Es	Sb/Ra	Pl/De	*	DD	R	H
Galeocerdonidae													
<i>Galeocerdo cuvier</i> Péron & Lesueur in Lesueur, 1822	120*	Pi/In	0,8	0	0	Me	Mc/Dw/Es	Sb/Ra	Pl/De	***	NT	R/S	T
Sphyrnidae													
<i>Sphyrna lewini</i> (Griffith & Smith, 1834)	87*	Pi/In	0,8	0	0	Me/Co	Mc/Dw/Es	Sb/Ra	Pl	***	CR	S	H
<i>Sphyrna mokarran</i> (Rüppell, 1837)	79-83*	Pi/In	0,8	0	0	Me/Co	Mc/Dw/Es	Sb/Ra	Pl	*	EN	S	H
Squaliformes													
Squalidae													
<i>Squalus albicaudus</i> Viana, Carvalho & Gomes, 2016	100*	Pi/In	0	0	0,2	-	Mc/Dw	Sb/Ra	Pl	*	DD*	R	N
Torpediniformes													
Narcinidae													
<i>Narcine brasiliensis</i> (Olfers, 1831)	102 (80)	In	0	0	0,2	Me	Mc	Sb/Ra	Be	*	DD	R	N
<i>Narcine</i> sp.	128*	In	0	0,2	0	Me	Mc	Sb/Ra	Be	*	NE	R	N
Rhinopristiformes													
Rhinobatidae													
<i>Pseudobatos percellens</i> (Walbaum, 1792)	70*	In	0	0	0,2	Me	Mc	Sb/Ra	Be	*	DD	R	N
Myliobatiformes													
Dasyatidae													
<i>Hypanus berthelutzae</i> Petean, Naylor & Lima, 2020**	80-96*	Pi/In	0,8	0,2	0,2	Me/Co	Mc/Es	Sb/Ra	Be	***	DD	R	T/N/H
<i>Hypanus marianae</i> (Gomes, Rosa & Gadig, 2000)	69-90 (50)	Pi/In	0	0,2	4,4	-	Mc	Ra	Be	***	DD	R	N

Table S1. Continued

Taxon	Dp	Dt	FH%	FT%	FN%	DC	HT	SB	LH	\$	CS	HC	FG
Osteichthyes													
Albuliformes													
Albulidae													
<i>Albula vulpes</i> (Linnaeus, 1758)	-	In	0	0,2	0	Me/Co	Mc/Es	Sb/Ra	De	***	DD	-	-
Anguilliformes													
Muraenidae													
<i>Channomuraena vittata</i> (Richardson, 1845)	102*	Pi/In	0	0	0,2	-	Mc	Ra	Be	***	LC	R	N
<i>Enchelycore nigricans</i> (Bonnaterre, 1788)	70-115*	Pi/In	0	0,2	0	-	Mc	Ra	Be	***	LC	R/S	T/H
<i>Gymnothorax conspersus</i> Poey, 1867	82*	Pi/In	0	0,2	0	Me	Mc/Es	Sb/Ra	Be	***	DD	R	T
<i>Gymnothorax funebris</i> Ranzani, 1839	89-99*	Pi/In	0	0,8	0	Co	Mc/Es	Ra	Be	***	DD	R/S	T
<i>Gymnothorax moringa</i> (Cuvier, 1829)	75-121*	Pi/In	0,8	0	1,5	-	Mc	Ra	Be	***	DD	R	T/N/H
<i>Gymnothorax ocellatus</i> Agassiz, 1831*/**	79-112*	Pi/In	0,8	0,2	0	Me	Mc/Es	Sb/Ra	Be	***	DD	R/S	T/H
<i>Gymnothorax vicinus</i> (Castelnau, 1855)*/**	76-121*	Pi/In	0	0,2	2,5	-	Mc	Ra	Be	***	DD	R	T/N
Congridae													
<i>Ariosoma balearicum</i> (Delaroche, 1809)	50	Pi/In	-	-	-	-	Mc	Sb/Ra	De/Be	***	LC	S	H
Clupeiformes													
Clupeidae													
<i>Opisthonema oglinum</i> (Lesueur, 1818)	87 (50)	Pa	0,8	0	0	Me/Co	Mc/Es	Ra	PI	***	LC	R	H
Aulopiformes													
Synodontidae													
<i>Trachinocephalus myops</i> (Forster 1801)	30-90*	Pi/In	0	0,2	0	Me/Co	Mc/Es	Sb/Ra	Be	***	LC	R/S	T/H
Holocentriformes													
Holocentridae													
<i>Holocentrus ascensionis</i> (Osbeck, 1765)*/**	61-121*	In	3,8	4,5	8,1	Me	Mc	Ra	De	***	LC	R/S	T/N/H
<i>Holocentrus rufus</i> (Walbaum, 1792)	75-112*	In	0	2,1	0,5	-	Mc	Ra	De	***	LC*	R/S	T/N/H
<i>Myripristis jacobus</i> Cuvier, 1829*/**	79-121*	Pa	0,8	0,2	2,2	Me	Mc	Ra	De	***	LC	R/S	T/N/H
Batrachoidiformes													
Batrachoididae													
<i>Amphichthys cryptocentrus</i> (Valenciennes, 1837)	75-109 (70)*	In	0	0,8	1,2	Me/Co	Mc/Es	Sb/Ra	Be	***	LC	R/S	T/N
Beloniformes													
Exocoetidae													
<i>Parexocoetus hillianus</i> (Gosse, 1851)	-	Pa	0	0,6	0	Me/Co	Mc	Wc	PI	***	LC*	R/S	T/H
Hemiramphidae													
<i>Euleptorhamphus velox</i> Poey, 1868	44-50	Pa	-	-	-	-	Mc/Oc	Wc	PI	***	LC	R/S	H
Carangiformes													
Coryphaenidae													
<i>Coryphaena equiselis</i> Linnaeus, 1758	94	Pi	0,8	0	0	Me	Mc/Oc	Ra/Wc	PI	**	LC	S	H
<i>Coryphaena hippurus</i> Linnaeus, 1758	79-115	Pi	0,8	0	0	Me	Mc/Oc	Ra/Wc	PI	**	LC	R/S	T/H
Rachycentridae													
<i>Rachycentron canadum</i> (Linnaeus, 1766)	63-88*	Pi	3,1	0,4	0,2	Me/Co	Mc	Ra/Wc	PI	*	LC	R/S	T/N/H
Echeneidae													
<i>Echeneis naucrates</i> Linnaeus, 1758	65-84*	Pi	0	0,4	0	Me/Co	Mc	Ra/Wc	PI	***	LC	S	T
Carangidae													
<i>Alectis ciliaris</i> (Bloch, 1787)	102 (100)*	Pi/In	0	0	0,2	Me/Co	Mc/Es	Ra/Wc	PI	***	LC	R	N
<i>Carangoides bartholomaei</i> (Cuvier, 1833)	62-104 (93)	Pi	0,8	1,1	1	Me	Mc/Es	Ra/Wc	PI	**	LC	R/S	T/N/H

Table S1. Continued

Taxon	Dp	Dt	FH%	FT%	FN%	DC	HT	SB	LH	\$	CS	HC	FG
<i>Carangoides crysos</i> (Mitchill, 1815)	61-104*	Pi/In	4,6	0,2	0,2	Me	Mc/Es	Ra/Wc	PI	**	LC	R/S	T/N/H
<i>Caranx hippos</i> (Linnaeus, 1766)	61-84*	Pi/In	3,1	0	0	Me/Co	Mc/Es	Ra/Wc	PI	**	LC	R/S	H
<i>Caranx latus</i> Agassiz, 1831**	76-102*	Pi/In	0,8	0	1,2	Me/Co	Mc/Es	Ra/Wc	PI	**	LC	R	N/H
<i>Caranx lugubris</i> Poey, 1860	62-121*	Pi	0,8	0,2	3,2	-	Mc	Ra/Wc	PI	*	LC	R	T/N/H
<i>Decapterus tabl</i> Berry, 1968	92-104	Pa	0	0	1,5	Me	Mc	Ra/Wc	PI	***	LC	R	N/H
<i>Elagatis bipinnulata</i> (Quoy & Gaimard, 1825)	95	Pi/In	0,8	0	0	-	Mc	Ra/Wc	PI	**	LC	S	T/H
<i>Seriola dumerili</i> (Risso, 1810)	30-128*	Pi/In	1,5	7,1	0,5	-	Mc	Ra/Wc	PI	*	LC	R/S	T/N/H
<i>Seriola rivoliana</i> Valenciennes, 1833**	30-121*	Pi/In	3,1	3,8	5,2	-	Mc	Ra/Wc	PI	*	LC	R/S	T/N/H
<i>Uraspis helvola</i> (Forster, 1801)	69-75	Pi/In	0	0	0,5	-	Mc	Ra/Wc	PI	***	LC	R	N
Istiophoriformes													
Sphyraenidae													
<i>Sphyraena guachancho</i> Cuvier, 1829	80-80	Pi	2,3	0	0	Me/Co	Mc/Es	Ra/Wc	PI	**	LC	R	H
Pleuronectiformes													
Paralichthyidae													
<i>Cyclopsetta fimbriata</i> (Goode & Bean, 1885)	84-110*	In	0	0	0,7	-	Mc/Es	Sb/Ra	Be	***	LC	R	N
<i>Syacium papillosum</i> (Linnaeus, 1758)	-	In	0	0,2	0	Me/Co	Mc	Sb/Ra	Be	***	LC	R	N
Pleuronectiformes													
Bothidae													
<i>Bothus maculiferus</i> (Poey, 1860)	76-102 (45)*	In	0	0	1,5	-	Mc	Sb/Ra	Be	***	LC	R	N
Syngnathiformes													
Syngnathidae													
<i>Hippocampus reidi</i> Ginsburg, 1933	113	Pa	-	-	-	-	Mc/Es	Sb/Ra	Be	***	VU	R	T
Dactylopteridae													
<i>Dactylopterus volitans</i> (Linnaeus, 1758)**	64-121*	Pi/In	0	0,2	6,9	Me/Co	Mc/Es	Sb/Ra	Be	**	LC	R	T/N
Scombriformes													
Scombridae													
<i>Acanthocybium solandri</i> (Cuvier, 1832)	76	Pi	0,8	0	0	Me/Co	Mc/Oc	Ra/Wc	PI	*	LC	R	H
<i>Euthynnus alletteratus</i> (Rafinesque, 1810)	79-102*	Pi	6,9	0	0	-	Mc/Oc	Ra/Wc	PI	*	LC	R/S	T/N/H
<i>Katsuwonus pelamis</i> (Linnaeus, 1758)	93	Pi	0	0	0,2	-	Mc/Oc	Wc	PI	*	LC	R	N
<i>Scomberomorus cavalla</i> (Cuvier, 1829)	80*	Pi	0,8	0	0	Me/Co	Mc/Oc	Ra/Wc	PI	*	LC	R	H
<i>Scomberomorus maculatus</i> (Mitchill, 1815)	79*	Pi	0,8	0	0	Me/Co	Mc/Oc	Ra/Wc	PI	*	LC*	S	H
<i>Thunnus albacares</i> (Bonnaterre, 1788)	76	Pi	0,8	0	0	-	Mc/Oc	Wc	PI	*	LC	R	H
<i>Thunnus atlanticus</i> (Lesson, 1831)	-	Pi	-	-	-	-	Mc/Oc	Wc	PI	*	LC	S	H
<i>Thunnus obesus</i> (Lowe, 1839)	76	Pi	0,8	0	0	-	Mc/Oc	Wc	PI	*	NT	R	H
Scombriformes													
Nomeidae													
<i>Psenes cyanophrys</i> Valenciennes, 1833	-	In	0	0,2	0	-	Dw	Wc	PI	***	LC	R	T
Scombriformes													
Trichiuridae													
<i>Trichiurus lepturus</i> Linnaeus, 1758	82*	Pi/In	0	0,2	0	Me/Co	Mc/Es	Sb/Ra/Wc	De	***	LC	R	T
Labriformes													
Labridae													
<i>Halichoeres cyanocephalus</i> (Bloch, 1791)**	90-94*	In	0	0,4	0	-	Mc	Ra	De	***	LC	R	T/N
Scaridae													
<i>Sparisoma amplum</i> (Ranzani, 1841)	63-113	In	0	0,2	0	Me	Mc	Ra	De	***	NT	S	T/H
<i>Sparisoma axillare</i> (Steindachner, 1878)	97 (60)*	In	0	0,2	0	Me	Mc	Ra	De	***	VU	R	T
<i>Sparisoma frondosum</i> (Agassiz, 1831)*/**	71-110*	In	0	1,9	1	Me	Mc	Ra	De	***	VU	R/S	T/N

Table S1. Continued

Taxon	Dp	Dt	FH%	FT%	FN%	DC	HT	SB	LH	\$	CS	HC	FG
Perciformes													
Epigonidae													
<i>Epigonus occidentalis</i> Goode & Bean, 1896	105	Pi/In	0	0	0,2	-	Dw	Ra/Wc	PI	***	LC	R	N
Mullidae													
<i>Pseudupeneus maculatus</i> (Bloch, 1793)*/**	86*	In	0	0,2	0	Me	Mc	Sb/Ra	De	***	LC	R	T/N
Serranidae													
<i>Cephalopholis cruentata</i> (Lacepède, 1802)	90*	Pi/In	0	0,2	0	-	Mc	Ra	De	*	LC*	R	N
<i>Cephalopholis fulva</i> (Linnaeus, 1758)*/**	61-125*	Pi/In	3,8	3,4	0,7	Me	Mc	Ra	De	*	LC	R/S	T/N/H
<i>Cephalopholis furcifer</i> (Valenciennes, 1828)*/**	61-125*	In	7,6	0	0	Me	Mc	Ra	De	***	LC	R/S	H
<i>Dermatolepis inermis</i> (Valenciennes, 1833)**	84-121*	Pi/In	0,8	0,9	0,2	-	Mc	Sb/Ra	De	**	DD	R/S	T/N/H
<i>Epinephelus itajara</i> (Lichtenstein, 1822)**	80	Pi/In	0,8	0	0	Me/Co	Mc/Es	Sb/Ra	De	*	CR	R	H
<i>Epinephelus morio</i> (Valenciennes, 1828)*/**	61-109	Pi/In	0,8	3,2	0	Me	Mc	Sb/Ra	De	*	VU	R/S	T/H
<i>Hyporthodus flavolimbatu</i> s Poey, 1865	121*	Pi/In	0	0	0,2	-	Mc	Sb/Ra	De	*	DD	R	N
<i>Hyporthodus nigritus</i> (Holbrook, 1855)**	125*	Pi/In	0,8	0	0	Me	Mc	Sb/Ra	De	*	EN	R	H
<i>Hyporthodus niveatus</i> (Valenciennes, 1828)**	86-121*	Pi/In	0	0,2	0,2	Me	Mc	Sb/Ra	De	*	VU	R	T/N
<i>Menephorus punctiferus</i> Poey, 1875	80	Pi/In	0	0,2	0	-	Mc/Es	Sb/Ra	De	**	NE	S	T
<i>Mycteroperca bonaci</i> (Poey, 1860)	30-103*	Pi/In	0	0,6	0,2	-	Mc	Sb/Ra	De	*	VU	R/S	T/N
<i>Mycteroperca interstitialis</i> (Poey, 1860)	79	Pi/In	0	0,2	0	-	Mc	Sb/Ra	De	*	VU	S	T
<i>Mycteroperca phenax</i> Jordan & Swain, 1884	81	Pi/In	0	0,2	0	-	Mc	Sb/Ra	De	*	DD*	R/S	T
<i>Paralabrax dewegeri</i> (Metzelaar, 1919)	83-98 (50)*	Pi/In	0	0,4	0	Me	Mc	Ra	De	**	LC	R/S	T
<i>Rypticus saponaceus</i> (Bloch & Schneider, 1801)	49-80	Pi/In	-	-	-	-	Mc	Ra	De	***	LC	S	T/H
Priacanthidae													
<i>Heteropriacanthus cruentatus</i> (Lacepède, 1801)	82-121*	Pi/In	0	0,6	0,2	-	Mc	Ra/Wc	De	**	LC	R/S	T/N
<i>Priacanthus arenatus</i> Cuvier, 1829)*/**	74-121*	Pi/In	0,8	1,1	0,5	Me	Mc	Ra/Wc	De	**	LC	R/S	T/N/H
<i>Pristigenys alta</i> (Gill, 1862)	100-121*	Pi/In	0	0	0,5	-	Mc	Ra/Wc	De	***	LC	R	N
Chaetodontidae													
<i>Chaetodon ocellatus</i> Bloch, 1787)*/**	62-110*	In	0	3,9	0,7	Me	Mc	Ra	De	**	DD	R/S	T/N
<i>Chaetodon sedentarius</i> Poey, 1860)*/**	82-97	In	0	0,4	0	Me	Mc	Ra	De	***	DD	R/S	T
Pomacanthidae													
<i>Holacanthus ciliaris</i> (Linnaeus, 1758)*/**	62-128 (125)*	On	0	0,9	4,9	Me	Mc	Ra	De	***	DD	R	T/N
<i>Holacanthus tricolor</i> (Bloch, 1795)**	75-76*	On	0	0	0,5	-	Mc	Ra	De	***	DD	R	N
<i>Pomacanthus paru</i> (Bloch, 1787)*/**	74-100	On	0	1,1	5,2	Me/Co	Mc	Ra	De	**	DD	R/S	T/N
Malacanthidae													
<i>Malacanthus plumieri</i> (Bloch, 1786)	87-115*	Pi/In	2,3	0	0,2	Me	Mc	Ra	De	***	LC	R/S	N/H
Haemulidae													
<i>Orthopristis scapularis</i> Fowler, 1915**	67-92 (70)	In	0	6,8	0	Me/Co	Mc/Es	Sb/Ra	De	***	LC	R/S	T
<i>Anisotremus surinamensis</i> (Bloch, 1791)	69-87*	Pi/In	0,8	0	0	Me/Co	Mc	Sb/Ra	De	***	DD	R/S	T/N/H
<i>Anisotremus virginicus</i> (Linnaeus, 1758)	76-112 (90)*	Pi/In	0	2,1	0	Me/Co	Mc	Sb/Ra	De	***	LC	R/S	T
<i>Haemulon atlanticum</i> Carvalho et al., 2020)*/**	61-116*	In	3,1	4,7	0	Me	Mc	Sb/Ra	De	***	NE	R/S	T/H
<i>Haemulon aurolineatum</i> Cuvier, 1830)*/**	61*	On	0,8	0	0	Me	Mc	Ra	De	***	LC	S	H
<i>Haemulon melanurum</i> (Linnaeus, 1758)	74-79*	In	0	0	1,7	-	Mc	Sb/Ra	De	***	LC	R	N/H
<i>Haemulon parra</i> (Desmarest, 1823)	61-82 (80)	Pi/In	0,8	0,4	0	Me/Co	Mc	Sb/Ra	De	***	LC	R/S	T/H
<i>Haemulon plumieri</i> (Lacepède, 1801)*/**	30	Pi/In	0	0,2	0	-	Mc	Sb/Ra	De	***	DD	S	T
<i>Haemulon striatum</i> (Linnaeus, 1758)	-	Pi/In	0,8	0	0	-	Mc	Ra	De	**	LC*	R	H

Table S1. Continued

Taxon	Dp	Dt	FH%	FT%	FN%	DC	HT	SB	LH	\$	CS	HC	FG
Lutjanidae													
<i>Lutjanus alexandrei</i> Moura & Lindeman, 2007	112	Pi/In	0	0,2	0	-	Mc/Es	Sb/Ra	De	*	LC	S	T
<i>Lutjanus buccanella</i> (Cuvier, 1828)	30*	Pi/In	0	0,2	0	Me	Mc	Sb/Ra	De	*	LC	S	T
<i>Lutjanus campechanus</i> (Poey, 1860)	80*	Pi/In	1	1	1	Me	Mc	Sb/Ra	De	*	VU*	R	T
<i>Lutjanus jocu</i> (Bloch & Schneider, 1801)	30-121*	Pi/In	1,5	2,3	1,7	Me/Co	Mc/Es	Sb/Ra	De	*	NT	R/S	T/N/H
<i>Lutjanus purpureus</i> (Cuvier, 1828)*/**	74-121*	Pi/In	1	1	1	Me	Mc	Sb/Ra	De	*	VU	R/S	T/N
<i>Lutjanus synagris</i> (Linnaeus, 1758)*/**	30-103*	Pi/In	1,5	7,9	0	Me/Co	Mc/Es	Sb/Ra	De	*	NT	R/S	T/H
<i>Lutjanus vivanus</i> (Cuvier, 1828)	61-121*	Pi/In	1,5	0,6	0,2	Me	Mc/Es	Sb/Ra	De	*	NT	R/S	T/N/H
<i>Ocyurus chrysurus</i> (Bloch, 1791)*/**	30-80	Pi/In	2,3	0,6	0	Me	Mc	Sb/Ra	De	*	NT	R/S	T/H
<i>Pristipomoides aquilonaris</i> (Goode & Bean, 1896)	91*	Pi	0,8	0	0	Me	Mc	Sb/Ra	Pl/De	**	LC	S	H
<i>Pristipomoides freemani</i> Anderson, 1966	61-91*	Pi	2,3	0,2	0	Me	Mc	Sb/Ra	Pl/De	**	LC	R/S	T/N/H
<i>Pristipomoides macrophthalmus</i> (Müller & Troschel, 1848)	125*	Pi	0,8	0	0	-	Mc	Sb/Ra	Pl/De	**	LC*	R	H
<i>Rhomboplites aurorubens</i> (Cuvier, 1828)*/**	30-125*	Pi/In	5,3	6,2	0,7	Me	Mc	Sb/Ra	De	*	NT	R/S	T/N/H
Scorpaeniformes													
Scorpaenidae													
<i>Pterois volitans</i> (Linnaeus, 1758)	70-100*	Pi/In	0	0,2	0,2	-	Mc/Es	Sb/Ra	De	***	LC	R/S	T/H
<i>Scorpaena</i> aff. <i>dispar</i> Longley & Hildebrand, 1940	80*	Pi/In	0,8	0	0	-	Mc	Sb/Ra	Be	***	LC*	R	H
<i>Scorpaena isthmensis</i> Meek & Hildebrand, 1928**	91	Pi/In	0,8	0	0	Me	Mc/Es	Sb/Ra	Be	***	LC*	S	H
Moroniformes													
Ephippidae													
<i>Chaetodipterus faber</i> (Broussonet, 1782)	85-92 (82)	In	0	0,8	0	Me/Co	Mc/Es	Sb/Ra/Wc	Pl/De	**	LC	R/S	T/H
Acanthuriformes													
Acanthuridae													
<i>Acanthurus chirurgus</i> (Bloch, 1787)*/**	62-104	He	0	1,9	3,5	Me	Mc	Ra	De	***	LC	R/S	T/N
<i>Acanthurus coeruleus</i> Bloch & Schneider, 1801	76 (71)	He	0	0	0,2	-	Mc	Ra	De	***	LC	R	N
Sciaenidae													
<i>Cynoscion similis</i> Randall & Cervigón, 1968	68-125 (100)	In	1,5	0,8	0	Me/Co	Mc/Es	Sb/Ra	De	**	NE	R/S	T/H
<i>Eques lanceolatus</i> (Linnaeus, 1758)*/**	-	In	0,8	0	0	-	Mc	Ra	De	***	LC	R	H
<i>Micropogonias furnieri</i> (Desmarest, 1823)	69-98*	In	0	2,3	0	Me/Co	Mc/Es	Sb/Ra	De	***	LC	R/S	T
<i>Pareques iwamotoi</i> Miller & Woods, 1988	122*	In	0	0	0,2	-	Mc	Ra	De	***	LC*	R	N
Spariformes													
Sparidae													
<i>Calamus calamus</i> (Valenciennes, 1830)	84 (75)	In	0	0,2	0	Me	Mc/Es	Sb/Ra	Be	***	LC	S	T
<i>Calamus penna</i> (Valenciennes, 1830)	81*	In	0	0,2	0	Me	Mc	Sb/Ra	De	**	DD	R	T
Lophiiformes													
Antennariidae													
<i>Fowlerichthys ocellatus</i> (Bloch & Schneider, 1801)	80-90*	Pi	0	0,2	0	-	Mc	Ra	Be	***	LC*	R	T
Ogcocephalidae													
<i>Ogcocephalus vespertilio</i> (Linnaeus, 1758)	70-84*	In	0	0	0,5	Me/Co	Mc/Es	Sb/Ra	Be	***	LC	R	N
Tetraodontiformes													
Ostraciidae													
<i>Acanthostracion polygonius</i> Poey, 1876*/**	63-121 (110)	In	0	0,6	6,9	Me/Co	Mc	Sb/Ra	De	***	LC	R/S	T/N
<i>Acanthostracion quadricornis</i> (Linnaeus, 1758)*/**	75	On	0	0	0,2	Me/Co	Mc	Sb/Ra	De	***	LC	R	N

Table S1. Continued

Taxon	Dp	Dt	FH%	FT%	FN%	DC	HT	SB	LH	\$	CS	HC	FG
Balistidae													
<i>Balistes capriscus</i> Gmelin, 1789	61-94	In	0,8	6,2	0	Me	Mc	Sb/Ra	PI	**	LC	R/S	T/H
<i>Balistes vetula</i> Linnaeus, 1758*/**	62-121*	In	0	3,2	5,2	Me	Mc	Sb/Ra	PI	***	LC	R/S	T/H
<i>Canthidermis maculata</i> (Bloch, 1786)	76*	In	0	0,2	0,2	-	Mc	Ra/Wc	PI	**	NT	R	T
<i>Xanthichthys ringens</i> (Linnaeus, 1758)	74-102	In	0	0	1,2	-	Mc	Ra/Wc	De	**	NT	R/S	T/N
Monacanthidae													
<i>Aluterus heudelotii</i> Hollard, 1855	100	On	0	0	0,2	Me	Mc	Ra/Wc	De	**	LC	R	N
<i>Aluterus monoceros</i> (Linnaeus, 1758)*/**	74-110*	In	0	0,9	5,2	Me	Mc	Ra/Wc	De	**	NT	R/S	T/N
<i>Aluterus scriptus</i> (Osbeck, 1765)	62-104	On	0	2,1	0,5	-	Mc	Ra/Wc	De	**	LC	R/S	T/N
<i>Cantherhines macrocerus</i> (Hollard, 1853)	63-128*	On	0	2,1	2,5	-	Mc	Ra	De	**	LC	R/S	T/N
Tetraodontidae													
<i>Lagocephalus laevigatus</i> (Linnaeus, 1766)	81-112	Pi/In	0,8	0,9	0	Me/Co	Mc/Es	Ra	PI/De	***	LC	R/S	T/H
Diodontidae													
<i>Chilomycterus antillarum</i> Jordan & Rutter, 1897**	69-121	In	0	0	3,7	Me/Co	Mc/Es	Sb/Ra	De	***	LC	R	N
<i>Diodon holocanthus</i> Linnaeus, 1758	-	In	0	0,2	0	-	Mc/Dw	Ra/Wc	De	***	LC	R	T

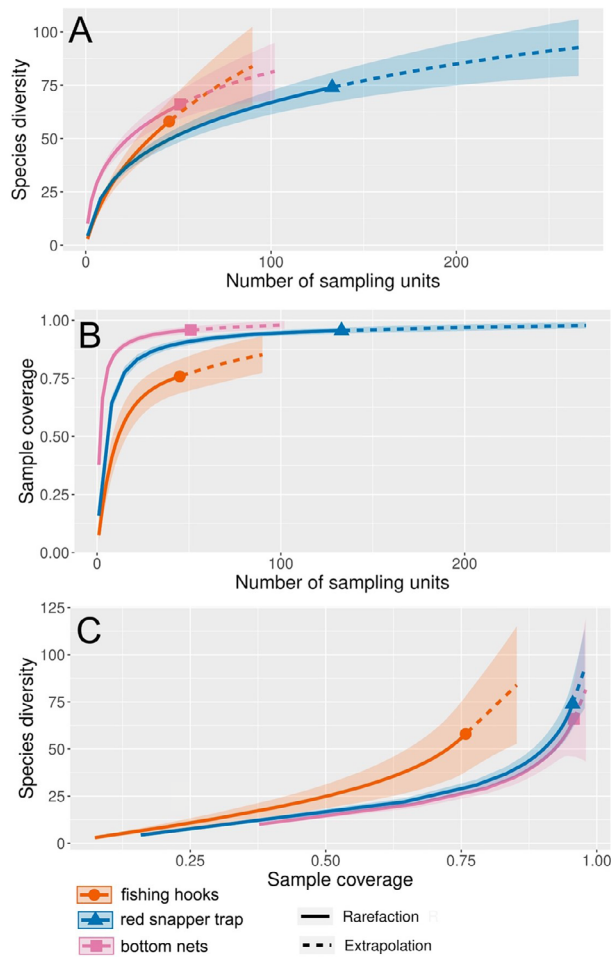


Figure S1. Rarefaction plots of the fish bycatch by the red snapper and lobster fishing fleet in the region of the Great Amazon Reef System. Plots were calculated in iNEXT (<https://chao.shinyapps.io/iNEXTOnline/>). **A** – evolution of species diversity with the number of samples; **B** – evolution of sample coverage with the number of samples; **C** – evolution of species diversity with sample coverage.

Table S2. Association with habitat of 58 species of Elasmobranchii and Teleostei caught as bycatch of red snapper and lobster fisheries in the Great Amazon Reef System, northern coast of Brazil. We indicate the p-value of chi-square tests comparing the number of records in reef habitat (NR) and the number of records on soft bottom (NS). p-values in bold highlight significant values ($p < 0.05$).

Species	NR	NS	p	Species	NR	NS	p
Elasmobranchii				<i>Aluterus monoceros</i>	27	1	< 0.001
<i>Carcharhinus falciformis</i>	7	2	0.4310	<i>Anisotremus virginicus</i>	4	7	< 0.001
<i>Ginglymostoma cirratum</i>	14	1	< 0.001	<i>Balistes capriscus</i>	21	22	< 0.001
<i>Mustelus</i> sp.	10	0	< 0.001	<i>Balistes vetula</i>	40	2	< 0.001
<i>Rhizoprionodon porosus</i>	7	0	< 0.001	<i>Bothus maculiferus</i>	6	0	< 0.001
Teleostei				<i>Cantherhines macrocerus</i>	22	2	< 0.001
<i>Aluterus scriptus</i>	14	5	0.8810	<i>Caranx latus</i>	6	0	< 0.001
<i>Cephalopholis fulva</i>	27	9	0.8796	<i>Caranx lugubris</i>	19	0	< 0.001
<i>Cephalopholis furcifer</i>	8	3	0.7122	<i>Chaetodipterus faber</i>	1	5	< 0.001
<i>Myripristis jacobus</i>	13	4	0.6254	<i>Chilomycterus antillarum</i>	18	0	< 0.001
<i>Rhomboplites aurorubens</i>	36	11	0.6053	<i>Cynoscion similis</i>	2	4	< 0.001
<i>Seriola rivoliana</i>	41	12	0.4893	<i>Dactylopterus volitans</i>	34	0	< 0.001
<i>Euthynnus allteratus</i>	7	2	0.4310	<i>Decapterus tabl</i>	7	0	< 0.001
<i>Lutjanus vivanus</i>	7	2	0.4310	<i>Gymnothorax moringa</i>	9	0	< 0.001
<i>Sparisoma frondosum</i>	14	4	0.4310	<i>Gymnothorax vicinus</i>	24	0	< 0.001
<i>Heteropriacanthus cruentatus</i>	4	1	0.1949	<i>Haemulon atlanticus</i>	15	17	< 0.001
<i>Seriola dumerili</i>	37	9	0.1628	<i>Haemulon melanurum</i>	8	0	< 0.001
<i>Lutjanus jocu</i>	19	9	0.1379	<i>Holacanthus ciliaris</i>	27	0	< 0.001
<i>Epinephelus morio</i>	18	9	0.0790	<i>Holocentrus adscensionis</i>	64	6	< 0.001
<i>Chaetodon ocellatus</i>	24	5	0.0539	<i>Hypanus marianae</i>	22	0	< 0.001
<i>Holocentrus rufus</i>	13	7	0.0325	<i>Lagocephalus laevigatus</i>	4	4	< 0.001
<i>Caranx bartholomaei</i>	11	2	0.0186	<i>Lutjanus purpureus</i>	34	1	< 0.001
<i>Amphichthys cryptocentrus</i>	7	4	0.0143	<i>Lutjanus synagris</i>	19	32	< 0.001
<i>Caranx crysos</i>	7	4	0.0143	<i>Malacanthus plumieri</i>	2	3	< 0.001
<i>Dermatolepis inermis</i>	7	4	0.0143	<i>Micropogonias furnieri</i>	1	13	< 0.001
<i>Rachycentron canadum</i>	7	4	0.0143	<i>Ocyurus chrysurus</i>	3	7	< 0.001
<i>Xanthichthys ringens</i>	6	1	0.0092	<i>Orthopristis scapularis</i>	5	33	< 0.001
<i>Acanthostracion polygonius</i>	37	1	< 0.001	<i>Pomacanthus paru</i>	29	1	< 0.001
<i>Acanthurus chirurgus</i>	27	2	< 0.001	<i>Priacanthus arenatus</i>	6	8	< 0.001