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Fish biodiversity of Saint Peter and Saint Paul's Archipelago, Mid-Atlantic Ridge, Brazil: new records and a species database

Hudson T. Pinheiro[1*] | Bruno C. L. Macena[2,3*] | Ronaldo B. Francini-Filho[4] | Carlos E. L. Ferreira[5] | Fernanda V. Albuquerque[6] | Natalia P. A. Bezerra[3] | Alfredo Carvalho-Filho[7] | Romulo C. P. Ferreira[3] | Osmar J. Luiz[8] | Thayna J. Mello[9] | Sibele A. Mendonça[3] | Diogo M. Nunes[10] | Caio R. Pimentel[11] | Alessandra M. A. Pires[3] | Abilio Soares-Gomes[5] | Danielle L. Viana[3] | Fabio H. V. Hazin[3] | Luiz A. Rocha[1]

[1]Department of Ichthyology, California Academy of Sciences, San Francisco, California

[2]Departamento de Oceanografia e Pescas, Instituto do Mar, Universidade dos Açores, Horta, Portugal

[3]Departamento de Pesca e Aquicultura, Universidade Federal Rural de Pernambuco, Recife, Brazil

[4]Centro de Biologia Marinha, Universidade de São Paulo, São Sebastião, Brazil

[5]Departamento de Biologia Marinha, Universidade Federal Fluminense, Niterói, Brazil

[6]Departamento de Sistemática e Ecologia, Universidade Federal da Paraíbal, João Pessoa, Brazil

[7]Fish Bizz Ltda, São Paulo, Brazil

[8]Research Institute for the Environment and Livelihoods, Charles Darwin University, Darwin, Australia

[9]Programa de Pós-Graduação em Ecologia, Centro de Biociências, Universidade Federal do Rio Grande do Norte, Natal, Brazil

[10]Unidade Acadêmica de Serra Talhada, Universidade Federal Rural de Pernambuco, Serra Talhada, Brazil

[11]Departamento de Oceanografia e Ecologia, Universidade Federal do Espírito Santo, Vitória, Brazil

Correspondence
Hudson T. Pinheiro, California Academy of Sciences, 55 Music Concourse Drive, Golden Gate Park, San Francisco, CA 94118, USA.
Email: htpinheiro@gmail.com

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Abstract

Saint Peter and Saint Paul's Archipelago (SPSPA), one of the smallest and most isolated island groups in the world, is situated on the Mid-Atlantic Ridge, between Brazil and the African continent. SPSPA has low species richness and high endemism; nonetheless, the diversity of fishes from deep habitats (>30 m depth) had not been previously studied in detail. Several expeditions conducted between 2009 and 2018 explored the shallow and deep reefs of SPSPA using scuba, closed-circuit rebreathers, manned submersibles, baited remote underwater stereo-videos (stereo-BRUV) and fishing between 0 and 1050 m depth. These expeditions yielded 41 new records of fishes for SPSPA: 9 in open waters, 9 in shallow waters (0–30 m), 8 in mesophotic ecosystems (30–150 m) and 15 in deeper reefs (>150 m). Combined with literature records of adult pelagic, shallow and deep-reef species, as well as larvae, the database of the fish biodiversity for SPSPA currently comprises 225 species (169 recorded as adult fishes and 79 as larvae, with 23 species found in both stages). Most of them (112) are pelagic, 86 are reef-associated species and 27 are deep-water specialists. Species accumulation curves show that the number of fish species has not yet

* These authors contributed equally to this study.

reached an asymptote. Whereas the number of species recorded in SPSPA is similar to that in other oceanic islands in the Atlantic Ocean, the proportion of shorefishes is relatively lower, and the endemism level is the third highest in the Atlantic. Twenty-nine species are listed as threatened with extinction. Observations confirm the paucity of top predators on shallow rocky reefs of the island, despite the presence of several pelagic shark species around SPSPA. Because all of the endemic species are reef associated, it is argued that the new marine-protected areas created by the Brazilian government do not ensure the protection and recovery of SPSPA's biodiversity because they allow exploitation of the most vulnerable species around the archipelago itself. This study suggests a ban on reef fish exploitation inside an area delimited by the 1000 m isobath around the islands (where all known endemics are concentrated) as the main conservation strategy to be included in the SPSPA management plan being prepared by the Brazilian government.

KEYWORDS

Brazil; BRUVs; closed-circuit rebreather; deep sea; disphotic; endemism; fishing; mesophotic; pelagic; reef fish; remote island; submersible

1 | INTRODUCTION

Fish biodiversity assessments of Saint Peter and Saint Paul's Archipelago (SPSPA), also known as Saint Paul's Rocks, began in 1873 with the visit of the H.M.S. *Challenger* (Moseley, 1892). The *Challenger* expedition spent 2 days in SPSPA and collected seven species of fish (Günther, 1880). Nonetheless, the first comprehensive fish species checklist was published only more than a century later by Lubbock and Edwards (1981), who recorded 50 species during an 8-day visit to the islands in 1979, when they used scuba to sample rocky reefs up to 60 m depth. It was only in 1998, however, that the Brazilian Navy established a scientific station in SPSPA, and a significant increase in the number of ichthyological studies was observed (Oliveira *et al*., 2018; Viana *et al*., 2009). The number of fish species recorded increased from 75 in 2003 (Feitoza *et al*., 2003) to 116 when pelagic species obtained from fishing surveys nearby SPSPA were included (Vaske Jr *et al*., 2005). An extensive database and biogeographical analyses of the southwestern Atlantic (SA) reef fishes present a checklist of 117 fish species for SPSPA reefs, 68 being considered resident (Pinheiro *et al*., 2018). The study of Pinheiro *et al*. (2018), as well as other biogeographical studies that included SPSPA (Edwards & Lubbock, 1983; Floeter *et al*., 2008; Hachich *et al*., 2015; Rocha, 2003), highlighted its high reef fish endemism, with species that are unique to SPSPA and other species that are shared only with the neighbouring oceanic islands of Fernando de Noronha, Rocas Atoll, Ascension and St. Helena.

The archipelago's isolation also produced populations with unique colour morphs, and cases of albinism are documented in a few species (Feitoza *et al*., 2003; Luiz, 2003). Some widespread species in the Atlantic present divergent genetic lineages at SPSPA (Anderson *et al*., 2017; Neves *et al*., 2016; Rocha *et al*., 2005) or display unusual behaviour (Gasparini *et al*., 2008; Luiz, 2005). Ecological studies point to a comparatively high fish biomass in SPSPA (Morais *et al*., 2017; Quimbayo *et al*., 2019), dominated by planktivorous and omnivorous fishes (Luiz *et al*., 2015). The steep drop-offs around the islands that are easily accessed from the shore make SPSPA one of the best places in the Brazilian province to explore the biodiversity and ecology of mesophotic (30–150 m, *sensu* Rocha *et al*., 2018), rariphotic (150–300 m, *sensu* Baldwin *et al*., 2018) and disphotic (>300 m) ecosystems. Previous studies described mesophotic reefs with the dominance of black corals and sponges, which provide shelter and food for endemic and juvenile fishes (Francini-Filho *et al*., 2019; Rosa *et al*., 2016). While exploring rariphotic and disphotic reefs (170–700 m) of SPSPA using baited bottom traps, Nunes *et al*. (2016) found 10 fish species, most of them previously unrecorded and one new species (Pires *et al*., 2019), showing that the composition of fish assemblages is strongly structured by depth.

Research on SPSPA's fishes has also disclosed human impacts from fishing activities. Fishing at SPSPA started in the late 1950s by Japanese tuna longliners and increased significantly in the late 1980s with the addition of Brazilian boats using various gears (handline, longline and trolling) (Divovich & Pauly, 2015; Oliveira *et al*., 1997; Viana *et al*., 2015). The scientific programme run by the Secretaria da Comissão Interministerial para os Recursos do Mar (SECIRM) also allows fishing by commercial boats used to transport and support researchers in SPSPA. Intensive fishing in such a remote and small ecosystem greatly reduced the local population of Galapagos shark *Carcharhinus galapagensis* (Snodgrass & Heller, 1905), suggested as functionally extinct (Luiz & Edwards, 2011). Historical records mention a high abundance of reef and pelagic sharks around SPSPA from the 1870s to the 1970s (Edwards & Lubbock, 1982; Luiz & Edwards, 2011). More recently, with the prohibition of the boarding of the silky shark *Carcharhinus falciformis* (Müller & Henle, 1839),

established by the International Commission for the Conservation of Atlantic Tunas in 2011, and the ban on longline fishing in the proximity of SPSPA imposed by SECIRM, in 2012, an increase in the presence of pelagic sharks, including Galapagos sharks, around SPSPA has been noticed (Hazin *et al*., 2018; Pimentel *et al*., 2020).

To advance the knowledge of the fish biodiversity of SPSPA and to support conservation initiatives, several scientific expeditions using a combination of freediving, conventional scuba, closed-circuit rebreathers, manned submersibles, baited remote underwater stereo-videos (stereo-BRUV) and fishing were conducted between 2009 and 2018. Based on the results of these expeditions, this study reports new records of teleost and elasmobranch species to SPSPA and, together with literature data, provides an updated checklist of the fish biodiversity of the region (including a list of fish larvae records). This study also describes the current conservation status of the local fish biodiversity. This work aims to contribute to the management plan of the large marine-protected area (MPA) recently created by the Brazilian government (CAT III and V – IUCN; Giglio *et al*., 2018).

2 | MATERIALS AND METHODS

SPSPA is a small group of emergent rocks situated along the Mid-Atlantic Ridge (MAR) 1010 km from the Brazilian coast and 1890 km from Senegal, Africa, at 00° 55' N and 029° 21' W (Figure 1). The archipelago is 625 km from Fernando de Noronha, 725 km from Rocas Atoll, 1915 km from Ascension Island and 3175 km from St. Helena. The shallow marine habitats are composed of rocky shores, tide pools and a small bay (0–35 m depth) (Figure 2a). Steep drop-offs and walls with rocky slopes and canyons are found around the islands, down to *ca*. 100 m (Figure 2b), then dropping again into another wall between 130 and 140 m depth. The deeper part of SPSPA consists of a large submarine mountain, with an extensive rocky reef habitat in the mesophotic and disphotic zones. The bottom between 150 and 600 m depth is composed of large outcrops, fields of boulders and soft bottoms where coarse sediments predominate, although fine grains are also observed in some sites (Figure 2c). Outcrops and boulders are covered by filter-feeding benthos, such as sponges, cnidarians, echinoderms and polychaetes, and soft-bottoms are heavily colonized by brittle stars and other invertebrates (ASG, pers. comm.). The topography of SPSPA favours the occurrence of up- and downwelling currents, thus attracting many species from the pelagic ecosystem (Figure 2d).

The database of the fish biodiversity of SPSPA includes ecological and biological information on the species and is based on primary data and a compilation of records from the literature from the past 39 years, that is, since the seminal paper by Lubbock and Edwards (1981), totalling 27 publications (Supporting Information S1). The primary data consist of unpublished records from the deep-sea monitoring programme, which studied fish biodiversity using fishing

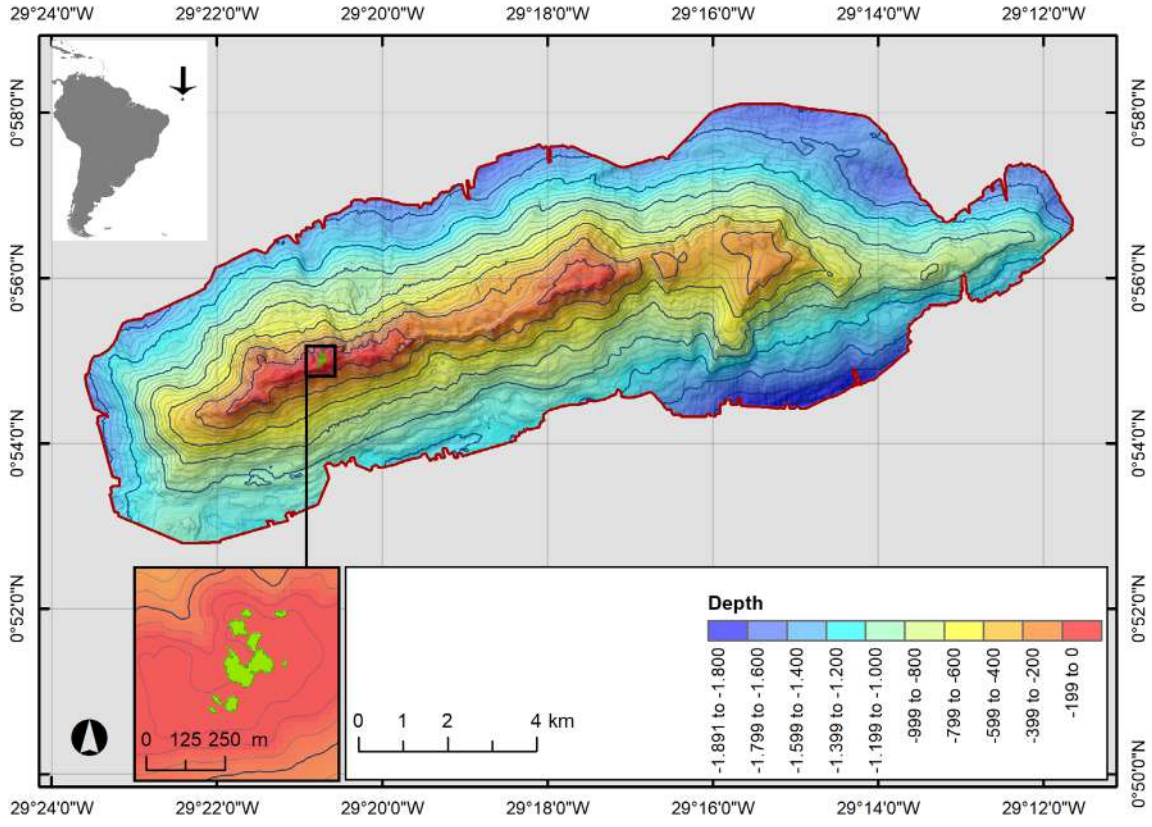

FIGURE 1 Map of Saint Peter and Saint Paul's Archipelago, Mid-Atlantic Ridge, Brazil, with bathymetric contour every 200 m depth. Legend: (▬) St. Peter and St. Paul Rocks, (▭) Bathymetry Recovery, (——) Bathymetric Contour (200 m)

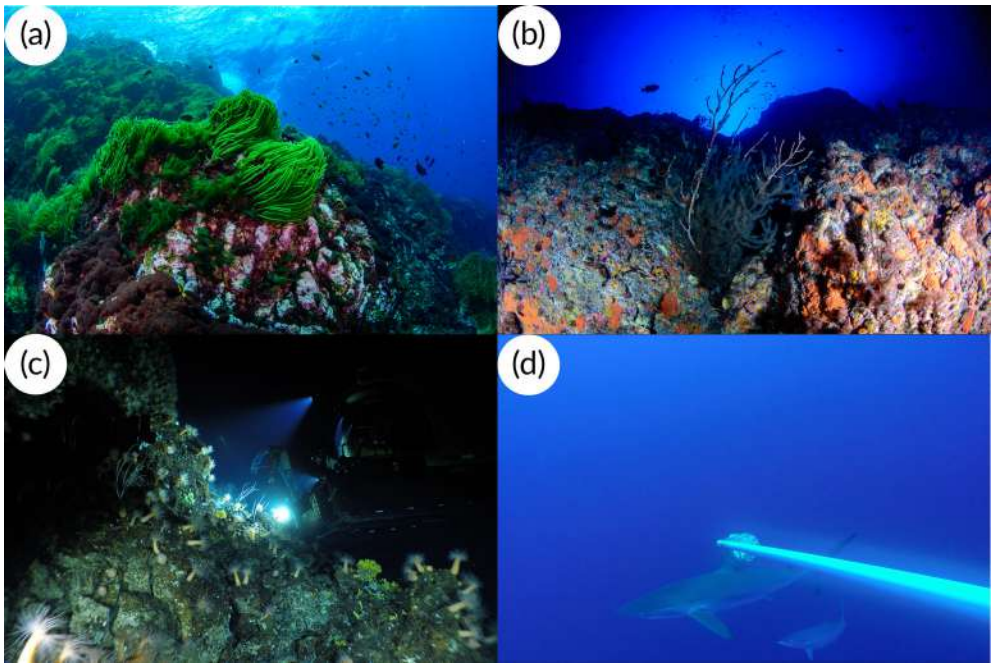

FIGURE 2 Diversity of ecosystems investigated in the study of the fish biodiversity of Saint Peter and Saint Paul's Archipelago, Mid-Atlantic Ridge. (a) Shallow zone, (b) mesophotic zone, (c) disphotic zone and (d) pelagic ecosystem

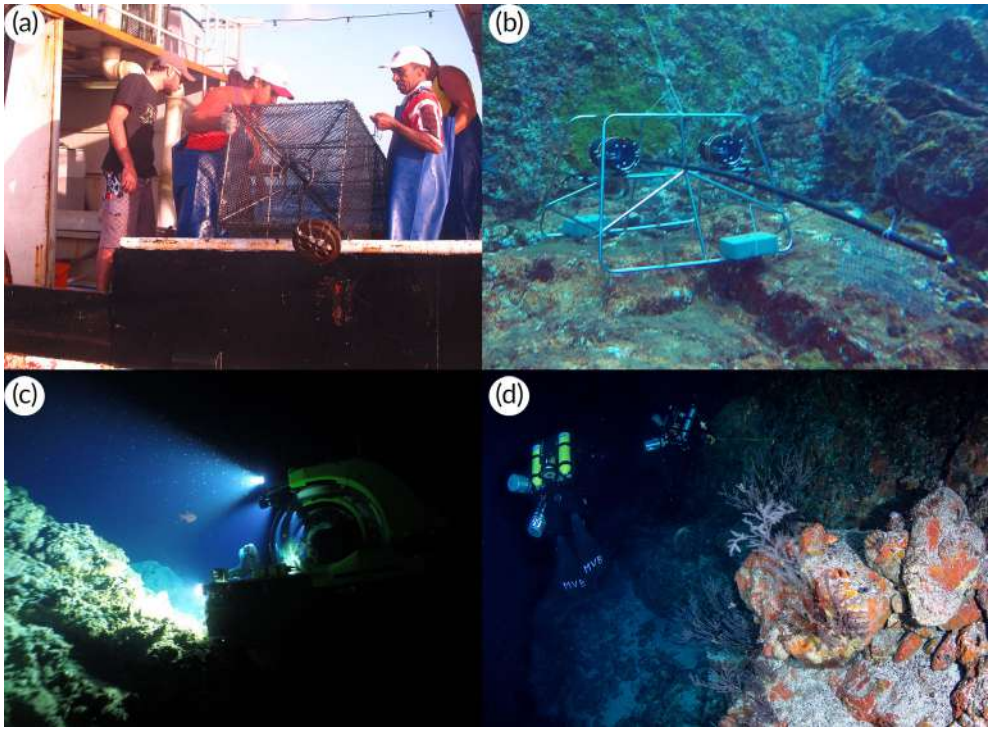

FIGURE 3 Sampling methods used to study the fish biodiversity in Saint Peter and Saint Paul's Archipelago, Mid-Atlantic Ridge: (a) fishing bottom traps, (b) baited remote underwater stereo-videos, (c) manned submersible dives and (d) closed-circuit rebreathers

gears down to 1050 m depth (Nunes *et al*., 2016) (Figure 3a), and a collation of new occurrences of fish species recorded by still pictures and video footage (including stereo-BRUVs; Figure 3b) and/or recorded/collected during scientific surveys carried out between 2009 and 2018. During one expedition to SPSPA between 21 June and 4 July 2017, six manned submersible dives (MSD) were performed, with two submersibles (Deep Rover 2 and the Nadir) operating simultaneously, to explore waters between 150 and 600 m depth (Figure 3c). Still pictures and video footage were obtained by cameras mounted on the submersibles (benthic video cameras, HD video camera and GoPro still cameras) for imaging the environment and associated biodiversity. Each MSD lasted an average of 6 h,

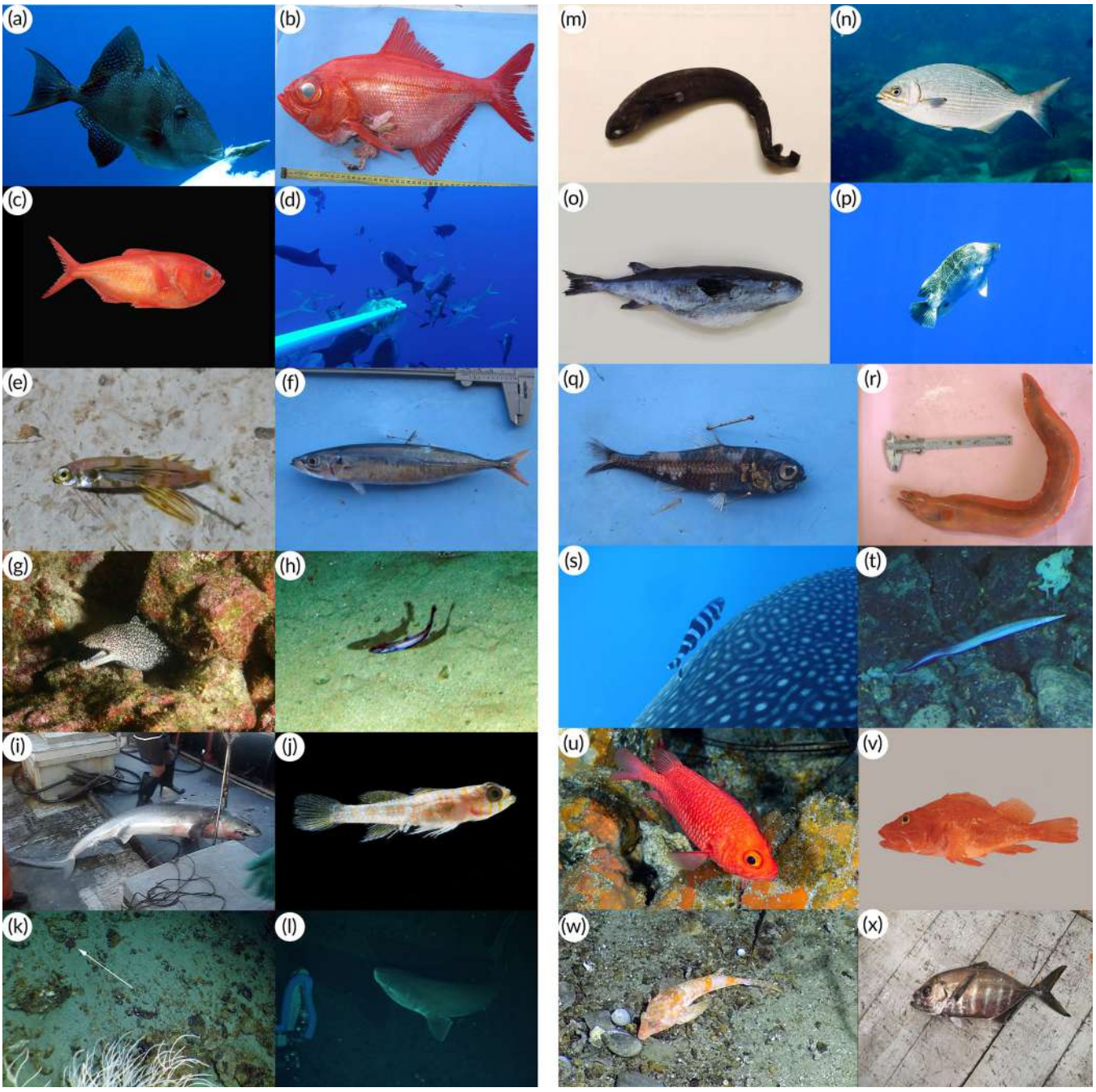

FIGURE 4 Fishes recorded for the first time in Saint Peter and Saint Paul's Archipelago, Mid-Atlantic Ridge (MAR), Brazil: (a) *Balistes capriscus*, (b) *Beryx decadactylus*, (c) *Beryx splendens*, (d) *Canthidermis maculata*, (e) *Cypselurus comatus*, (f) *Decapterus macarellus*, (g) *Enchelycore* sp., (h) *Etmopterus* sp., (i) *Galeocerdo cuvier*, (j) Gobiidae gen.n. sp. nov., (k) *Halieutichthys* sp., (l) *Hexanchus griseus*, (m) *Isistius brasiliensis*, (n) *Kyphosus vaigiensis*, (o) *Lagocephalus lagocephalus*, (p) *Lobotes surinamensis*, (q) *Myctophum obtusirostre*, (r) *Myroconger compressus*, (s) *Naucrates ductor*, (t) *Nettastoma melanurum*, (u) *Corniger spinosus*, (v) *Pontinus castor*, (w) *Synchiropus dagmarae* and (x) *Uraspis secunda*

totalling 36.8 h of sampling. Also 11 closed-circuit rebreather dives were performed, where two ichthyologists (Hudson T. Pinheiro and Luiz A. Rocha) recorded (videos and photos) and collected samples (hand nets and spears) between 2 and 135 m depth, totalling 42 h of diving by each person (Figure 3d). Shallow waters from 2 to 30 m were surveyed by two scientists recording videos and photos in about 20 open-circuit scuba dives (*ca*. 25 h of sampling per diver). A total of 14 demersal stereo-BRUVs deployments (1 h each), between 30 and 85 m depth, and 5 deployments of pelagic stereo-BRUVs (2 h each), at 20 and 30 m depth, were performed in September 2018, using 500 g of sardines as bait in each session (Pimentel *et al*., 2020). Fish larvae records were compiled from the literature (Lima *et al*., 2016; Macedo-Soares *et al*., 2012).

Orders, families and species nomenclature follow Eschmeyer's Catalogue of Fishes (Fricke *et al*., 2019, 2020), except for Labridae, which includes Scarinae (Westneat & Alfaro, 2005). Genera and

species are listed in alphabetical order. Species records were categorized by (a) life stage (adult, larvae or both); (b) habitat [shallow reef shorefishes (shallow and mesophotic habitats: 0–150 m depth), deep-reef shorefishes (rariphotic and disphotic habitats: >150 m) and pelagic fishes (open water and migratory species recorded in a 20 nm radius of SPSPA)]; (c) geographical distribution [SPSPA Endemics, Oceanic Islands Endemics, Brazilian Coast Endemics, Oceanic Islands of Brazil, SA, western Atlantic (WA), MAR, eastern Atlantic (EA), eastern Pacific, circumtropical (CT)]; (d) fishery importance [important targets, new targets (species with a recent focus due to overexploitation of important targets and by-catch)]; and (e) extinction risk [IUCN and Brazilian Red List categories (vulnerable – VU, endangered – EN and critically endangered – CR)]. Although a list of species not confirmed in the database were presented, the number of species reported in the manuscript consists exclusively of confirmed species (column "Species Confirmation" in the database). The accumulation curves of fishes were calculated using the combination of confirmed adults and larvae records per habitat (pelagic, shallow and deep reefs) through the years.

Collecting permits were granted by Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio; SISBIO 17081 and 58069), and specimens were deposited at the Ichthyological Collection of the Universidade Federal do Espírito Santo (CIUFES) and the Coleção de Cordados Marinhos (CHORDATAMAR) of the Museu de Oceanografia Professor Petrônio Coelho at the Universidade Federal de Pernambuco (MOUFPE).

3 | RESULTS

3.1 | New records

A total of 41 new records of fishes in adult stages were obtained: 18 shorefishes from shallow and mesophotic ecosystems (8 recorded only on mesophotic reefs), 14 from deeper habitats (rariphotic and disphotic) and 9 in open waters (Supporting Information S2; Figure 4). These records represent 35 teleosts and 6 elasmobranchs. The species are distributed in 27 families, with Tetraodontiformes and Anguilliformes as the orders with most members (6 species each), followed by Perciformes (5) and Carangiformes (4). Five species were identified only at the genus level, and one is likely a new species. About 57% of the new records identified at species level (36 species) have a global distribution, 11.4% occur in both the WA and EA (*i.e.*, amphi-Atlantic), 22.8% are restricted to the WA and 8.6% are possibly endemics. The potential new species is from the family Gobiidae and probably represents an undescribed genus (L. Tornabene, pers. comm.). Of the new records, only *Dermatolepis inermis* (Valenciennes, 1833) and *Galeocerdo cuvier* (Péron & Lesueur, 1822) seem to be vagrant at SPSPA, with only a single individual sighted for each species. Hybrids of *Cephalopholis fulva* (Linnaeus, 1758) and *Paranthias furcifer* (Valenciennes, 1828) were recorded in two occasions.

3.2 | Larval records

Records of fish larvae are also presented to provide a more comprehensive list of the fish diversity in SPSPA. Excluding doubtful records and not-confirmed species, the larvae diversity consists of 79 confirmed species that were compiled from the literature and includes one new record (*Ariosoma* sp.). The fish larval assemblage is distributed in 12 orders and 33 families (Supporting Information S2). Sixteen species were identified to the family level and another 37 to the genus level, with Myctophiformes comprising most of the assemblage (37.5%) followed by Stomiiformes (13.8%) and Scombriformes (7.5%). Most species are diel vertical migrators with pelagic habitats (72.0%), whereas 23.0% are shorefishes from shallow reef habitats and 5% from deep reefs (Supporting Information S2). Two records are of threatened species, *Thunnus obesus* (Lowe, 1839), vulnerable according to the IUCN, and *Stegastes sanctipauli* Lubbock & Edwards, 1981, vulnerable according to the Brazilian Red List. Fifty-seven larval records are not found in adult stages, consisting mostly of pelagic species (51) followed by deep (4) and shallow (2) reef species (Supporting Information S2).

3.3 | Fish database

The primary data and literature review revealed 169 species recorded in adult stages for SPSPA (Supporting Information S2). Pooling the checklists of adults and larvae, 225 different species were reported for SPSPA (169 species represented by adults and 79 by larvae, with 23 species recorded in both stages) (Supporting Information S2; Figure 5). Most species are pelagic (112 species) followed by shallow (86 species) and deep (27 species) reef shorefishes (Supporting Information S2). The checklist consists of 202 Teleostei distributed in 16 orders and 23 Elasmobranchii in 6 orders. Myctophiformes accounted for 13.3% of the species (30) followed by Perciformes with 9.7% (22), Anguilliformes with 8% (18) and Tetraodontiformes and Carangiformes with 7.1% (16) each. A total of 78 families were recorded, with Myctophidae being the richest with 13.3% of the species (30) followed by Carangidae at 4.4% (10), Exocoetidae and Muraenidae at 4.0% (9) each (Supporting Information S2).

Eighty-three species are considered commercially important (36.8%), 18 considered threatened (vulnerable – VU, endangered – EN or critically endangered – CR) following IUCN categories and 23 following the Brazilian Red List (Supporting Information S2), totalling 29 endangered species considering both lists. Twenty-one species have restricted distribution (*i.e.*, endemic to SPSPA and other Atlantic Oceanic islands). Of these, 10 are endemic to SPSPA, 6 are shared with Fernando de Noronha Archipelago and Rocas Atoll only and 5 shared with St. Helena and/or Ascension Island. The species accumulation curves show that the number of fishes recorded in SPSPA is increasing through time, including fishes found in shallow and deep reefs, as well as the pelagic environment (Figure 5).

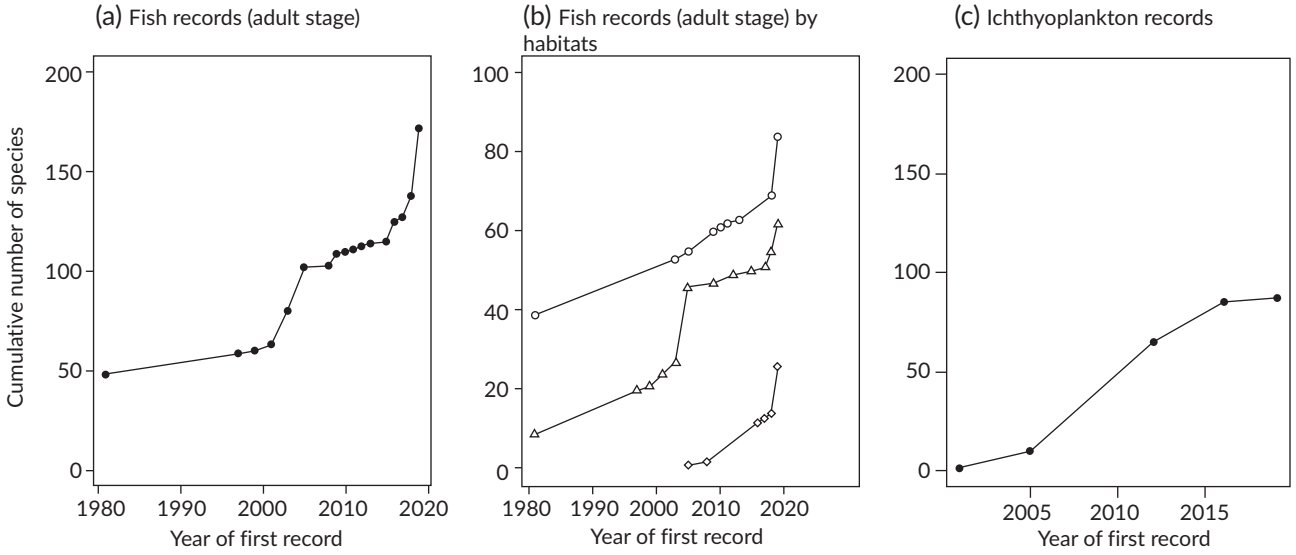

FIGURE 5 Species accumulation curve for the fishes recorded in Saint Peter and Saint Paul's Archipelago, Mid-Atlantic Ridge, Brazil. (a) Fish records (adult stage), (b) fish records (adult stage) by habitat (circle = shallow reefs, triangle = pelagic, diamond = deep reefs) and (c) Ichthyoplankton records

3.4 | Natural history notes

The whale-shark *Rhincodon typus* (Smith, 1828) and groups of devil rays *Mobula tarapacana* (Philippi, 1892) were occasionally sighted near or inside the bay and consistently recorded along the expeditions performed. These filter-feeding elasmobranchs likely visit SPSPA for feeding and/or reproduction, with greater abundance from January to June (Macena & Hazin, 2016; Mendonça *et al*., 2018), when the waters are enriched with plankton (Macedo-Soares *et al*., 2012).

Underwater observations of other shark species, reef or pelagic, in shallow waters around SPSPA reefs are rare. Some of the sharks observed included the dusky *Carcharhinus obscurus* (Lesueur, 1818), hammerheads *Sphyrna* spp. and silky sharks *C. falciformis*. Nevertheless, many sharks were observed in scientific longline and handline fishing captures during recent expeditions organized by some of the authors (Bruno C. L. Macena and Natalia P. A. Bezerra), including some of the new records presented here, such as *C. obscurus*, *G. cuvier*, *Hexanchus griseus* (Bonnaterre, 1788) and *Sphyrna zygaena* (Linnaeus, 1758) (Bezerra *et al*., 2017). The cookie cutter shark *Isistius brasiliensis* (Quoy & Gaimard, 1824) was recorded attached to a yellowfin tuna *Thunnus albacares* (Bonnaterre, 1788) caught with handline. *Carcharhinus limbatus* (Müller & Henle, 1839), which was documented over 20 years ago (Oliveira *et al*., 1997), was not recorded again. On the contrary, *C. galapagensis*, considered locally extinct, was recently recorded with BRUVs (Pimentel *et al*., 2020) and tagged with acoustic transmitters (Hazin *et al*., 2018). According to Hazin *et al*. (2018), the detection rate of *C. galapagensis* was high, demonstrating its close association with the insular ecosystem.

SPSPA is also known for the high abundances of unusual colour morphs of the Queen angelfish *Holacanthus ciliaris* (Linnaeus, 1758), which include predominantly golden, blue, white and other variations of these colours (Feitoza *et al*., 2003; Luiz, 2003). Despite the relatively high abundance of typical *H. ciliaris* at SPSPA, only a few individuals of the blue colour morphs were recorded during the expeditions in 2017 and 2018 (Figure 6), and no other unusual morphs have been observed since 2009. Besides *H. ciliaris*, unusual colour patterns were recorded for other species [*e.g*., *Chromis multilineata* (Guichenot, 1853)]. All non-cryptic and shallow-water endemic species were seen in relatively high abundances.

Two of the most abundant mesophotic reef fishes of SPSPA, *Chromis* aff. *enchrysura* Jordan & Gilbert, 1882, and *Prognathodes obliquus* (Lubbock & Edwards, 1980), live in areas dominated by branching black corals, which are used as shelter (Figure 6). Agonistic interactions between these two species are common. Groups of 2–4 individuals of the endemic butterflyfish *P. obliquus* are usually seen between 30 and 50 m, with larger groups (up to 20 individuals) in depths between 80 and 100 m (Francini-Filho *et al*., 2019; Rosa *et al*., 2016). The endemic *Choranthias salmopunctatus* (Lubbock & Edwards, 1981) was recorded along the steep wall just in front of the cove (same area sampled by Edwards and Lubbock, 1983, and Luiz *et al*., 2007), in groups of 10–25 individuals between 45 and 65 m depth (Figure 6). The grey triggerfish *Balistes capriscus* Gmelin, 1789, was recorded only in the mesophotic zone and in groups of up to four individuals.

3.5 | Taxonomic notes

Three of the four species of Anthiadinae (subfamily of Serranidae) that occur in SPSPA are endemic (*C. salmopunctatus*, *Odontanthias cauoh* Carvalho-Filho *et al*., 2016, and *Tosanoides aphrodite* Pinheiro, Rocha & Rocha, 2018), and two (*O. cauoh* and *T. aphrodite*) are the only representatives of their genera in the Atlantic (Carvalho-Filho *et al*., 2016; Pinheiro *et al*., 2018). The fourth species, *Anthias asperilinguis* Günther, 1859, seems to have distinct populations: genetic analyses of the

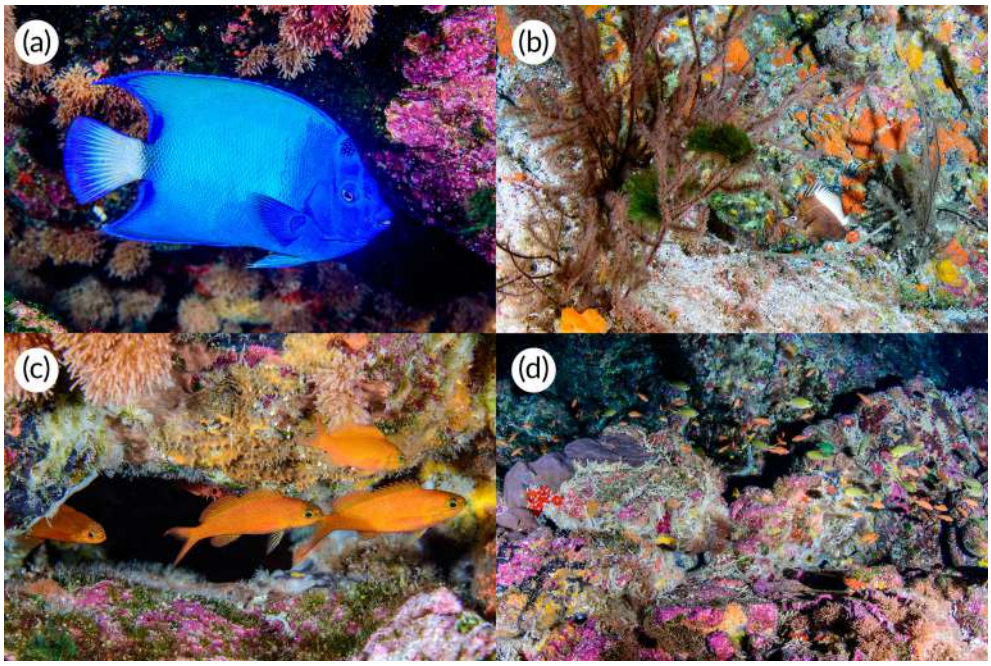

FIGURE 6 Endemic colour morphs and species in Saint Peter and Saint Paul's Archipelago: (a) Queen angelfish *Holacanthus ciliaris*, (b) oblique butterflyfish *Prognathodes obliquus*, (c) salmon-spotted jewelfish *Choranthias salmopunctatus* and (d) school of *Choranthias salmopunctatus* mixed with brown *chromis Chromis multilineata* fish

samples from SPSPA are very similar to those from the Caribbean, but morphometric data split them apart (Anderson *et al*., 2017). A similar pattern (*i.e*., morphologically different but genetically similar populations) was recorded for another Anthiadinae species, *Pronotogrammus martinicensis* (Guichenot, 1868), while comparing populations in Brazil and the Caribbean (Carvalho-Filho *et al*., 2009).

Among the scorpaenid fishes recorded in SPSPA, the deep-reef *Pontinus nigropunctatus* (Günther, 1868) seems to be the most abundant species (15 specimens analysed by this study) of the family and its congener, *Pontinus castor* Poey, 1860, one of the rarest; *Scorpaenodes insularis* Eschmeyer, 1971, is a relatively common shallow-reef fish. *P. nigropunctatus* and *S. insularis* also occur at St. Helena Island (Edwards & Glass, 1987). A third species, *Scorpaena laevis* Troschel, 1866, occurs in SPSPA and was previously known from East Africa only. A fifth species, tentatively identified as *Scorpaena mellissi* Günther, 1868 (endemic to St. Helena Island), is a new species and is currently being described (ACF, pers. comm.).

Muraenidae are well represented in SPSPA with 4 genera and 10 species, but two records are doubtful. *Channomuraena vittata* (Richardson, 1845), *Enchelycore nigricans* (Bonnaterre, 1788), *Enchelycore* sp. nov., *Gymnothorax funebris* Ranzani, 1839, *Gymnothorax maderensis* (Johnson, 1862), *Gymnothorax miliaris* (Kaup, 1856), *Muraena melanotis* (Kaup, 1859) and *Muraenapavonina* Richardson, 1845, had their occurrence confirmed here. Nonetheless, *Enchelycore anatina* (Lowe, 1838), reported only by Feitoza *et al*. (2003), might be a misidentification of an undescribed species of the same genus which, pending further studies, might also occur in Brazilian continental waters (ACF, pers. comm.). *Gymnothorax* sp., reported by Nunes *et al*. (2016), has no voucher specimen and, due to the depth of its capture, could be the deep-water *G. maderensis*, not reported from Brazilian waters at the time of their publication, which occurs in the Brazilian mainland and in SPSPA (Carvalho Filho & Paiva, 2017, and this study).

4 | DISCUSSION

In this study, the combination of different observational and fishing techniques allowed the scientific exploration of shallow and deep reefs of SPSPA, as well as its surrounding pelagic environment, revealing new fish records and new species. Mesophotic and rariphotic exploration around the world have resulted in new records and discoveries (Baldwin *et al*., 2018; Kane *et al*., 2014; Pinheiro *et al*., 2019; Rocha *et al*., 2018; Wagner *et al*., 2014), including in the SA (Feitoza *et al*., 2005; Francini-Filho *et al*., 2019; Pinheiro *et al*., 2015; Rosa *et al*., 2016; Simon *et al*., 2016). The increase in the depth range of scientific exploration is contributing to a better understanding of the distribution of the world's marine biodiversity and accelerating the rate of knowledge acquisition about the distributions and biogeographical patterns of marine organisms. For instance, despite being considered a cosmopolitan species, there were few records for the chondrichthyan *Odontaspis ferox* (Risso, 1810) in the southwestern (Fergusson *et al*., 2008; Graham *et al*., 2016; Long *et al*., 2014) and equatorial Atlantic (present study). Moreover, the recent research effort in the deep waters at SPSPA resulted in the description of new teleost species such as *Physiculus cirm* Carvalho-Filho & Pires, 2019, *O. cauoh* and *T. aphrodite*. Many species recorded in the deep and pelagic ecosystems of SPSPA remain identified only at the family or genus level, with possible new species yet to be described.

Despite the isolation and small area of SPSPA, the richness of the fish species is similar to that recorded for other larger islands of the SA (Pinheiro *et al*., 2015; Quimbayo *et al*., 2019; Soto, 2001) and MAR (Wirtz *et al*., 2017), and should keep increasing with further studies, based on the species accumulation curves and low overlap between adults and larvae records (Figure 5). This relatively high fish richness level recorded for SPSPA is a consequence of extensive sampling on

habitats other than shallow reefs (*i.e.*, pelagic and deep habitats, which contain about 50% of SPSPA fish species), most of which are still unexplored in other islands. Records of mesopelagic and bathypelagic species based on larvae (51 species), however, need to be considered carefully, because they involve species that are difficult to identify and could be related to distant populations. For shorefishes (down to 150 m), richness remains low (86 species), but the endemism level of SPSPA (9.3% – eight species, Supporting Information S2) stands out as the third highest in the Atlantic, after St. Helena and Ascension, also situated on the MAR (Floeter *et al*., 2008; Wirtz *et al*., 2017). If it is added to that species shared only with other oceanic islands, 20.9% (18 species, Supporting Information S2) of the shorefishes have a restricted geographical range. Because there are no oceanic currents directly connecting those islands, stochastic and ecological factors (due to the remarkable habitat similarity in terms of temperature, productivity and water transparency) might drive the distribution of these insular species (Pinheiro *et al*., 2018).

Deep benthic fishes (deeper than 150 m) seem to follow the same biogeographical pattern as the shallow-water fauna, displaying low richness (24 species) and high endemism (8.3% – 2 species, Supporting Information S2). The limited information about fishes from deep habitats is probably due to the low sampling effort caused by the difficulty for manned submersibles or remote-operated vehicles to spot and collect mobile fishes and collections in deep habitats relying on fishing gears that usually select large-bodied carnivorous species. Thus, it is believed that additional deep exploration and sampling effort in SPSPA might reveal more endemic and undescribed deep-sea species. Also, more scientific investigation is needed to assess cryptic species, in terms of collection using both anaesthetics (*e.g.*, Baldwin *et al*., 2018; Luiz & Mccosker, 2018) and genetics to disclose possible endemic lineages (*e.g.*, Anderson *et al*., 2017).

The observations made about the fish biodiversity and its natural history in SPSPA call attention to the need for additional conservation measures in this unique ecosystem. The recent efforts to create a no-take zone around SPSPA failed due to political and economic interests (Giglio *et al*., 2018; Pereira, 2019). Before the establishment of a large marine-protected area around SPSPA in March 2018 (Giglio *et al*., 2018), a working group composed of scientists, the Brazilian environmental agency (ICMBio), the Brazilian Navy (represented by the SECIRM) and representatives of several ministries discussed the closure of reef fish exploitation in an area of 1 nautical mile radius around the islands or, alternatively, an area with a border at the 1000 m isobath, allowing the capture of only migratory pelagic species that are not suitably managed by MPAs. Nonetheless, because these MPAs were created, the working group was dissolved and bottom fishing is currently allowed, even on shallow reefs inside the strictest protection zone (SPSPA's natural monument – MONA). Moreover, the vessels that transport the researchers to SPSPA routinely engage in commercial fishing. Although such activities are not illegal, the boats involved in the transport of researchers should be dedicated exclusively for that purpose, engaging in fishing only for scientific purposes. Meanwhile, because the fishing vessels associated with the SECIRM research programme are the only fleet that operates in the region, fishing agreements based on co-management (Almeida *et al*., 2009; Nobre *et al*., 2017) could address the lack of regulations until a management plan is prepared by the government.

SPSPA has the highest number of endangered fish species recorded for an oceanic island in Brazil, thus clearly deserving full protection encompassing the entire archipelago. Even though there is evidence for the recent recovery of pelagic sharks, the scarcity of underwater shark observations around the islands' reefs, which were abundant in the past (Edwards & Lubbock, 1982), reinforces the need for fishing regulations that allow shark populations to fully re-establish. Sharks, as top predators, perform critical roles controlling prey and influencing energy flux, having important impacts on reef ecosystem dynamics (Roff *et al*., 2016). Because the commercial fleet acts in pelagic waters around SPSPA, a fishery closure for reef-associated fishes would not stop pelagic fisheries, avoiding socio-economic impacts on this activity (Viana *et al*., 2015). Sustainable management of pelagic fisheries around SPSPA and full protection of its reefs are necessary to protect not only top predators but also the unique species and genetic diversity of the region.

The effective conservation of the biodiversity in SPSPA requires the Brazilian government to ban fishing activities from the reefs where known endemics are concentrated, allowing the capture of only sustainably managed migratory pelagic species, such as tunas, bonitos, dolphinfish and mackerels. This protection could be achieved stipulating a genuine no-take zone with border following the 1000 m isobath around the SPSPA.

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AUTHOR CONTRIBUTIONS

H.T.P. and B.C.L.M. worked on the first drafts of the database and manuscript. All authors contributed sampling data in the field and reviewed the database and manuscript.

ORCID

Hudson T. Pinheiro https://orcid.org/0000-0002-3143-1474
Luiz A. Rocha https://orcid.org/0000-0003-4011-569X

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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