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The reef fish assemblage of the Laje de Santos Marine State Park, Southwestern Atlantic: annotated checklist with comments on abundance, distribution, trophic structure, symbiotic associations, and conservation

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Abstract

A check-list containing 196 species of reef fishes recorded at the Laje de Santos Marine State Park is presented. Most of them occur along the tropical western Atlantic or occur on both sides of the Atlantic Ocean. A minor part ranges to the temperate rocky reefs of Patagonia or are endemics to southeastern Brazil. *Moringua edwardsi*, *Antennarius multiocellatus*, *Scorpaena dispar*, *Aulostomus strigosus*, *Lutjanus buccanella*, *Mulloidichthys martinicus* and *Halichoeres penrosei* have here their ranges extended southwards to the São Paulo coast. Basic data on species abundance at the study site, distribution of species between habitat types, trophic structure, feeding symbiotic associations, and conservation are commented upon.

Key words: Western South Atlantic, Brazil, rocky reefs, reef fishes, species list and distribution, zoogeography, conservation, trophic structure, feeding symbioses

Resumo

Uma lista com 196 espécies de peixes recifais registradas é apresentada para o Parque Estadual Marinho da Laje de Santos. A maioria das espécies tem ocorrência comum a todo o Atlântico Ocidental tropical ou ocorre nos dois lados do Oceano Atlântico. Uma parte menor das espécies tem distribuição em comum com os recifes rochosos temperados da Patagônia ou é endêmica ao Sudeste do Brasil. *Moringua edwardsi*, *Antennarius multiocellatus*, *Scorpaena dispar*, *Aulostomus strigosus*, *Lutjanus buccanella*, *Mulloidichthys martinicus* and *Halichoeres penrosei* tem aqui seu limite meridional de distribuição estendido ao Estado de São Paulo. Informações básicas sobre abundância das espécies no local de estudo e sua distribuição entre os diferentes tipos de habitats, estrutura trófica, associações alimentares simbióticas e conservação são aqui comentadas.

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Introduction

The Laje de Santos State Marine Park (*Parque Estadual Marinho da Laje de Santos - PEMLS*) is located on the southeastern coast of Brazil (24º15´S; 46º10´W), 36 km off the city of Santos, São Paulo State (Fig. 1). It consists of an uninhabited islet and several sparse rocky reefs with extensive intervening sand bottoms. The maximum depth is about 45 m. The subtidal substrate is composed of granitic boulders of varying sizes and shapes that delineate a steep profile (Fig. 2). The rocky substrate is mainly covered with patches of brown and red algae, the zoanthid *Palythoa caribeorum*, hydrozoans, ascidians, octocorals and sparse colonies of the scleractinian corals *Madracis decactis* and *Mussismilia hispida*. The local setting is a transitional tropical-subtropical environment that fits the definition of a high latitude 'marginal' reef site (Perry & Larcombe 2003) where hard corals may occur only as isolated colonies on the exposed bedrock.

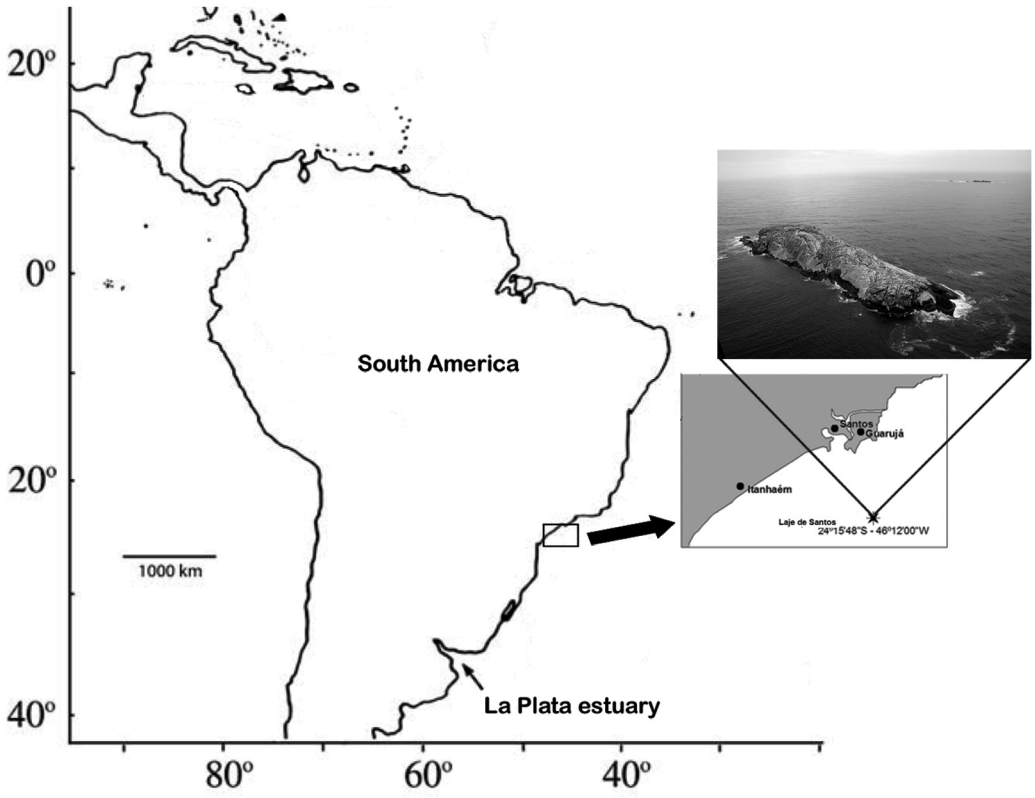

FIGURE 1. The Laje de Santos Marine State Park location in western South Atlantic. Photo: C.L.B. Francini.

The area is of particular interest as this is the only Marine Protected Area totally closed to fishing in the most populated and developed region of Brazil, allowing researchers to evaluate fishing impacts on local rocky reefs (Floeter *et al*. 2006). Since 1993 a 5,000 ha area around the Laje de Santos Island was declared a protected area. After some years as a "paper park" with low or even inexistent effective enforcement, the study site is experiencing a great increase in the effort to eradicate fishing in the last four years. Since 2003, a new official government management policy and the rise of an active NGO dedicated to protect the Park brought new boats, equipment and personnel (volunteer and staff) extensively engaged in the inspection of the Park boundaries. Recreational activities allowed in the Park include scuba diving and boating. Anchoring is not allowed anymore and mooring buoys have been used by dive boats.

Despite a few recent publications on reef fish taxonomy (Moura 1995), behavior (Sazima *et al*. 2000) and a species list of benthic algae (Amado-Filho *et al*. 2006), the Laje de Santos remains largely unknown biologically and a comprehensive list of reef fish species occurring in the Marine Park is still lacking. The knowl-

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edge of the species composition of a community is instrumental to provide a baseline for future management and a starting point to produce scientific information needed for the process of designing and evaluating Marine Protected Areas, such as biomass, dispersal patterns, recruitment dynamics, trophic interactions and habitat preferences of the resident organisms (Agardy 2000, Craig *et al.* 2004).

The present study provides the first comprehensive checklist of the reef fish species that occur at the Laje de Santos Marine State Park. In addition, patterns of species distribution, abundance, zoogeography, trophic types, representative symbiotic associations, and conservation issues are commented upon.

Material and methods

The species list results from fishes observed, photographed, and collected by the authors, as well as museums vouchers and reliable literature records. Bony fishes are listed in the phylogenetic order of families following Nelson (2006); elasmobranchs are listed following Compagno (1999). Species are organized in alphabetical order within families. Recent changes in the classification of the Serranidae as proposed by Craig and Hastings (2007) and Smith and Craig (2007) are adopted. Among these are the resurrection of the family Epinephelidae as distinct from Serranidae; the placement of the genus *Paranthias* within *Cephalopholis*; the change from genus *Epinephelus* to *Mycteroperca* for *M. marginata* (formerly *E. marginatus*) and the genus change of deep-bodied groupers of the *Epinephelus niveatus* complex to the resurrected genus *Hyporthodus.* In the list, we included the following information for each species:

Abundance. an indicator of the relative abundance in the last five years, period when the first author started quantitative visual censuses of fishes using SCUBA in the study area and in more than thirty years of observations on fishes, by SCUBA and fishing, done by the second author; this indicator is based on a diver's likelihood of recording a species in its normal habitat and depth range on any given dive (modified from Humann & DeLoach 2002, Feitoza *et al.* 2003), where: AB = abundant (several sightings of many individuals – at least 50 – are expected on nearly every dive), VC = very common (several sightings are expected on nearly every dive, but not necessarily of many individuals), CO = common (sights are frequent, but not necessarily expected on every dive), OC = occasional (sightings are not unusual, but are not expected on a regular basis), UN = unusual (sights occurs less than occasionally), and RA = rare (sights are exceptional).

Habitat and distribution. The particular place where a species has usually been found; we arbitrarily stipulated different habitats types based on physiographic factors like substrate type and depth (fig. 2), where: Sh = Shallow reef (rocky substrate from 0 to 12 m depth), RS = Reef slope (rocky substrate from 13 to 20 m depth), SB = Sand bottom (sandy substrate adjacent to the rocky reef slope), WC = Water column (pelagic environment from 0 to 10 m depth, adjacent to the rocky reef but distant at least ~3 m from the bottom), and DR = Deep reef (rocky substrate in the range of 30–45 m depth).

Geographic range of the species. namely: Br = Brazilian province (*sensu* Briggs 1974), CE = Central Atlantic (Islands of St. Helena and Ascension), CT = Circumtropical, EA= Eastern Atlantic, Pat = Patagonian (occur primarily in the temperate rocky reefs south to Argentina), SCa = Southern Caribbean (Coast of Venezuela, Trinidad and Tobago and other islands of the low lesser Antilles), SE = Southeastern Brazil (endemic from the region that encompass 20°S to 27S° in the Western Atlantic), TA = Trans-Atlantic (occur at both sides of the Atlantic Ocean), and WA = Western Atlantic (occur in Northern and Southern West Atlantic).

Trophic category. assessed from direct behavioral observations and from the literature (Randall 1967, 1996, Carvalho-Filho 1999, Ferreira *et al.* 2004), where: CAR = Carnivores (eat a variety of mobile organisms, including invertebrates and fishes), MIF = Mobile invertebrate feeders (feed primarily on small benthic mobile invertebrates like mollusks, crustaceans, worms, etc. associated to the hard- or nearby soft-substrate), OMN = Omnivores (feed on variety of organisms, including animal and vegetal), PIS = Piscivores (feed only or mostly on live fishes), PLK = Planktivores (feed primarily on macro- and micro-zooplankton), ROVH =

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Roving herbivores (non-territorial, large herbivores which includes in their diet a rich mass of detritus, turf algae and macroalgae), SIF = Sessile invertebrate feeders (feeds on a array of sessile benthic invertebrates like cnidarians, bryozoans, ascidians and sponges that are most associated to hard substrata), and TERH = Territorial herbivores (with a diet composed mainly by turf algae farmed within a vigorously defended territory).

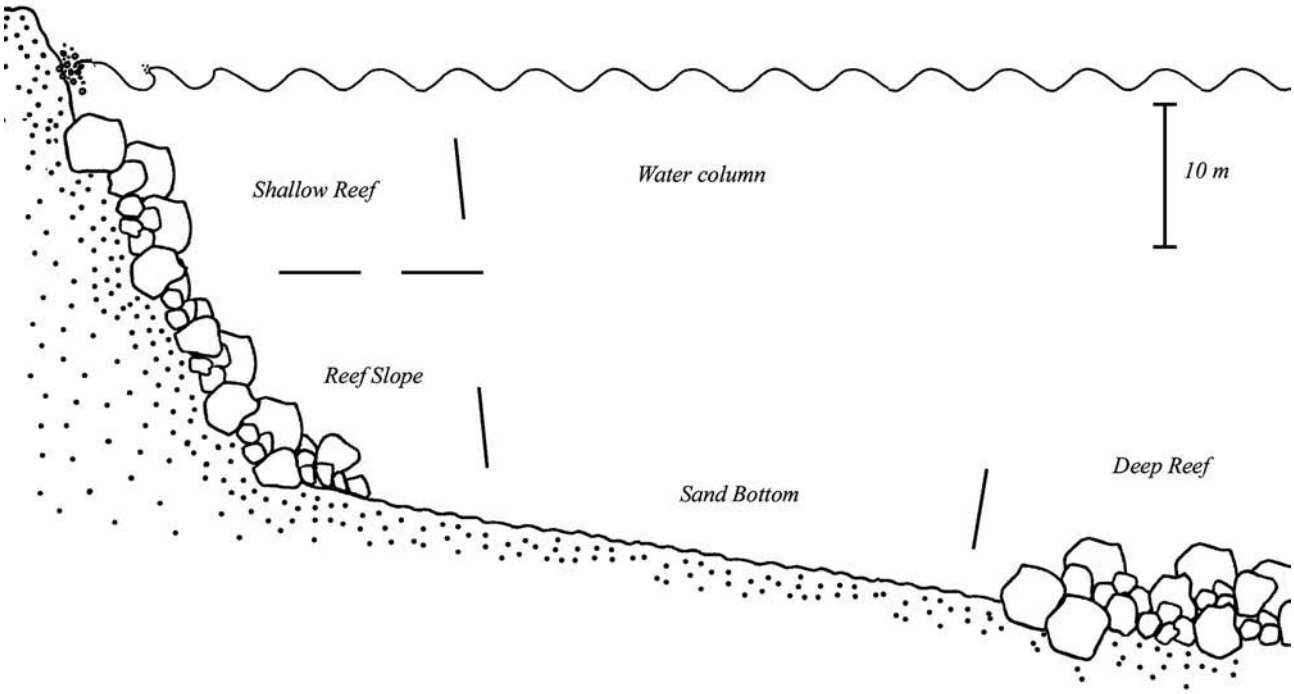

FIGURE 2. Habitat types found at the Laje de Santos Marine State Park.

Record type. how the species was recorded, where: COL = Collected, MUS = Museum voucher, LIT = Literature, PHO = Photograph, and SIG = Sighting. For specimens deposited in museum collections, the institution and voucher number are provided in the appendix.

We define reef fishes here as those species that are primarily associated with hard substrata, and which depend on the reef or it's immediate vicinity for shelter and food during any phase of its post-settlement life. We also consider as reef fishes the epipelagic species that regularly visit reefs in search of food, cleaning services, and reproduction. For the purpose of describing the occurrence patterns of fish species in the different habitats, a cluster analysis based on a species presence/absence matrix was performed. The Bray-Curtis dissimilarity index was used, and habitats were clustered according to the UPGMA method (Pielou 1984). The abundance patterns of reef fish in the different habitats, considering variables such as exposure degree, substrate complexity and depth will be presented elsewhere.

Results and discussion

Species composition

A total of 196 reef fish species in 124 genera in 66 families were recorded at the Laje de Santos (Table I). The most species rich families were Carangidae (16), Epinephelidae (12), Labridae (10), Pomacentridae (8) and Scaridae (8). *Caranx*, *Gymnothorax*, *Halichoeres*, *Mycteroperca* and *Sparisoma*, with 5 species each were the most species rich genera, followed by *Chromis*, *Haemulon*, and *Seriola* with 4 species. Twelve species were abundant (6%) (fig. 3), 26 (13%) were very common, 45 (23%) were common, 61 (32%) were occasional, 14 (7%) were unusual and 38 (19%) were rare.

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TABLE I. List of families and species, habitat, abundance, geographic range, trophic category and record status of the reef fishes recorded at the Laje de Santos Marine State Park. Families of elasmobranchs are arranged following Compagno (1999) and bony fishes are arranged according to Nelson (2006); genera and species are arranged in alphabetical order. **Habitat:** DR = Deep Reef; RS = Reef Slope; SB = Sand Bottom; SH = Shallow Reef; WC = Water Column. **Occurrence:** AB = Abundant; CO = Common; OC = Occasional; RA = Rare; UN = Unusual; VC = Very Common. **Geographic Range:** Br = Brazilian Province; CE = Central Atlantic; CT = Circumtropical. EA = Eastern Atlantic; SCa = Southern Caribbean; SE = Southeastern Brazil; TA = Trans-Atlantic; WA = Western Atlantic. **Trophic Category:** CAR = Carnivore; MIF = Mobile Invertebrate Feeder; OMN = Omnivore; PIS = Piscivore; PLK = Planktivore; ROVH = Roving Herbivore; SIF = Sessile Invertebrate Feeder; TERH = Territorial Herbivore. **Record Type:** COL = Collected; LIT = *in litteris*; MUS = Museum Voucher; PHO = Photograph; SIG = Sighting.

Family and species	Habitat	Occurrence	Geog. Range	Trophic Category	Record Type
ODONTASPIDIDAE					
Carcharias taurus Rafinesque, 1810	DR	UN	CT	PIS	SIG
ALOPIIDAE					
Alopias vulpinus (Bonaterre, 1788)	WC	RA	CT	PIS	SIG
CARCHARHINIDAE					
Carcharhinus brevipinna (Muller & Henle, 1839)	WC	RA	CT	PIS	COL, PHO
Carcharhinus falciformis (Bibron, 1839)	WC	RA	CT	PIS	COL, PHO
Carcharhinus limbatus (Muller & Henle, 1839)	WC	RA	CT	PIS	COL, PHO
Carcharhinus longimanus (Poey, 1861)	WC	RA	CT	PIS	PHO
RHINOBATIDAE					
Zapteryx brevirostris (Müller & Henle, 1841)	SB	RA	WA	MIF	SIG
GYMNURIDAE					
Gymnura altavela (L., 1758)	RS, SB	RA	TA	MIF	PHO
DASYATIDAE					
Dasyatis centroura (Mitchill, 1815)	RS, SB	OC	TA	MIF	PHO
Dasyatis hypostigma Santos & Carvalho, 2004	RS, SB	RA	SE	MIF	PHO
MYLIOBATIDAE					
Aetobatus narinari (Euphrasen, 1790)	WC	CO	CT	MIF	PHO
MOBULIDAE					
Manta birostris (Walbaum, 1792)	WC	OC	CT	PLK	PHO
Mobula hypostoma (Bancroft, 1831)	WC	RA	CT	PLK	MUS, SIG
Mobula japanica (Muller & Henle, 1841)	WC	RA	CT	PLK	SIG
Mobula tarapacana (Philippi, 1892)	WC	RA	CT	PLK	LIT*
* Gadig & Sampaio, 2002					
MORINGUIDAE					
Moringua edwardsi (Jordan & Bollman, 1889)	SH, RS	UN	WA	MIF	PHO
MURAENIDAE					
Gymnothorax funebris Ranzani, 1839	SH, RS	OC	WA	CAR	MUS, PHO
Gymnothorax miliaris (Kaup, 1856)	SH, RS	CO	TA	CAR	COL, PHO
Gymnothorax moringa (Cuvier, 1829)	SH, RS	CO	WA+CE	CAR	COL, PHO
Gymnothorax ocellatus Agassiz, 1831	SB	RA	WA	CAR	PHO
Gymnothorax vicinus (Castelnaul, 1855)	SH, RS	CO	TA	CAR	COL, PHO
Muraena retifera Goode & Bean, 1882	RS, DR	OC	WA	CAR	COL, PHO

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TABLE 1. (continued)

Family and species	Habitat	Occurrence	Geog. Range	Trophic Category	Record Type
OPHICHTHIDAE					
Ahlia egmontis (Jordan, 1884)	SH, RS	UN	WA	MIF	COL, PHO
Myrichthys ocellatus (LeSueur, 1825)	SH	CO	WA	MIF	PHO
Myrichthys breviceps (Richardson, 1848)	SH, RS	RA	WA	MIF	PHO
Ophichthus ophis (L., 1758)	SB	RA	TA	PIS	MUS
CLUPEIDAE					
Harengula clupeola (Cuvier, 1829)	WC	OC	WA	PLK	COL
Sardinella janeiro (Eingenmann, 1894)	WC	OC	WA	PLK	MUS
SYNODONTIDAE					
Synodus foetens (L., 1776)	SH, RS, SB	UN	WA	PIS	MUS
Synodus intermedius (Spix & Agassiz, 1829)	SH, RS, SB	VC	WA	PIS	MUS, COL, PHO
Synodus synodus (L., 1758)	SH, RS, SB	CO	TA	PIS	COL, PHO
BATRACHOIDIDAE					
Porichthys porosissimus (Cuvier, 1829)	SB	RA	SE+Pa	CAR	MUS
ANTENNARIIDAE					
Antennarius multiocellatus (Valenciennes, 1837)	SH	UN	WA	CAR	PHO
OGCOCEPHALIDAE					
Ogcocephalus vespertilio (L., 1758)	RS, SB	UN	WA	CAR	PHO
BELONIDAE					
Tylosurus acus (Lacepede, 1803)	WC	OC	CT	PIS	MUS, PHO
HEMIRAMPHIDAE					
Hemiramphus balao (Lesueur, 1821)	WC	OC	TA	OMN	SIG
Hemiramphus brasiliensis (L., 1758)	WC	OC	TA	OMN	SIG
HOLOCENTRIDAE					
Holocentrus adscensionis (Osbeck, 1765)	SH, RS	VC	TA	MIF	MUS, COL, PHO
Myripristis jacobus Cuvier, 1829	SH	CO	TA	PLK	MUS, COL, PHO
SYNGNATHIDAE					
Hippocampus reidi Ginsburg, 1933	RS	RA	WA	PLK	PHO
Micrognathus crinitus (Jenyns, 1842)	RS	OC	WA	PLK	PHO
AULOSTOMIDAE					
Aulostomus strigosus Wheeler, 1955	SH	RA	TA	CAR	PHO
FISTULARIIDAE					
Fistularia tabacaria L., 1758	RS, SB	OC	TA	PIS	SIG
DACTYLOPTERIDAE					
Dactylopterus volitans L., 1758	RS, SB	CO	TA	MIF	MUS, COL, PHO
SCORPAENIDAE					
Scorpaena dispar Longley & Hildebrand, 1940	SH, RS, DR	OC	WA	CAR	PHO
Scorpaena isthmensis Meek & Hildebrand, 1928	?	RA	WA	CAR	MUS
Scorpaena plumieri Bloch, 1789	SH, RS, DR	OC	WA+CA	CAR	COL, PHO
Scorpaenodes tredecimspinosus (Metzelaar, 1919)	SH, RS	CO	WA	CAR	COL, PHO

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TABLE 1. (continued)

Family and species	Habitat	Occurrence	Geog. Range	Trophic Category	Record Type
SERRANIDAE					
Acanthistius brasilianus (Cuvier, 1828)	RS, DR	CO	SE+Pat	CAR	MUS, COL, PHO
Acanthistius patachonicus (Jenyns, 1840)	DR	RA	SE+Pat	CAR	COL, PHO
Diplectrum formosum (L., 1766)	SB	UN	WA	CAR	PHO
Dules auriga Cuvier, 1829	DR	CO	SE+Pat	CAR	COL, PHO
Pronotogrammus martinicensis (Guichenot, 1868)	DR	UN	WA	PLK	SIG
Serranus baldwini (Evermann & Marsh, 1899)	SH, RS	CO	WA	CAR	MUS, PHO
EPINEPHELIDAE					
Cephalopholis fulva (L., 1758)	?	RA	WA	CAR	MUS
Cephalopholis furcifer (Valenciennes, 1828)	WC	CO	TA	PLK	MUS, COL, PHO
Epinephelus adscensionis (Osbeck, 1765)	SH, RS	RA	TA	CAR	MUS, COL, PHO
Epinephelus itajara Lichtenstein, 1822	SH, RS	OC	TA	CAR	PHO
Epinephelus morio (Valenciennes, 1828)	RS	UN	WA	CAR	COL, PHO
Hyporthodus flavolimbatus (Poey, 1865)	DR	OC	WA	CAR	COL, PHO
Hyporthodus niveatus (Valenciennes, 1828)	SH, RS, DR	CO	WA	CAR	MUS, COL, PHO
Mycteroperca acutirostris (Valenciennes, 1828)	SH, RS	VC	WA	PIS	MUS, COL, PHO
Mycteroperca bonaci (Poey, 1860)	SH, RS	RA	WA	PIS	COL, PHO
Mycteroperca interstitialis (Poey, 1860)	SH, RS	CO	WA	PIS	MUS, COL, PHO
Mycteroperca marginata (Lowe, 1834)	SH, SB, RS, DR	VC	SE+Pat+ EA	CAR	MUS, COL, PHO
Mycteroperca venenosa (L., 1758)	SH, RS, DR	RA	WA	PIS	COL, PHO
PRIACANTHIDAE					
Cookeolus japonicus (Cuvier, 1829)	DR	OC	CT	PLK	COL, PHO
Heteropriacanthus cruentatus (Lacepède, 1801)	SH, RS	OC	CT	PLK	COL, PHO
Priacanthus arenatus Cuvier, 1829	SH, RS, DR	OC	TA	MIF	COL, PHO
APOGONIDAE					
Apogon americanus Castelnau, 1855	SH, RS	CO	Br	PLK	MUS, COL, PHO
Apogon pseudomaculatus Longley, 1932	SH, RS	CO	TA	PLK	MUS, COL, PHO
MALACANTHIDAE					
Caulolatilus chrysops (Valenciennes, 1833)	SB	RA	WA	CAR	MUS
Malacanthus plumieri (Bloch, 1786)	SB	CO	WA+CE	CAR	MUS, PHO
POMATOMIDAE					
Pomatomus saltatrix (L., 1766)	WC	OC	CT	CAR	COL, PHO
ECHENEIDAE					
Echeneis naucrates (L., 1758)	WC	OC	CT	CAR	COL, PHO
Remora albescens (Temminck & Schlegel, 1845)	WC	OC	CT	CAR	PHO
Remora remora (L., 1758)	WC	OC	CT	MIF	PHO
RACHYCENTRIDAE					
Rachycentron canadum (L., 1766)	SB	OC	CT	CAR	COL, PHO

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Family and species	Habitat	Occurrence	Geog. Range	Trophic Category	Record Type
CORYPHAENIDAE					
Coryphaena hippurus L., 1758	WC	RA	CT	CAR	COL
CARANGIDAE			CT		
Alectis ciliaris (Bloch, 1787)	WC	CO	CT	CAR	COL, PHO
Caranx bartholomaei (Cuvier, 1833)	WC	OC	WA	PIS	COL, PHO
Caranx crysos (Mitchill, 1815)	WC	OC	TA	CAR	COL, PHO
Caranx hippos (L., 1766)	WC	RA	TA	CAR	COL, PHO
Caranx latus Agassiz, 1831	WC	OC	TA	CAR	MUS, PHO
Caranx ruber (Bloch, 1793)	WC	OC	WA	CAR	PHO
Decapterus macarellus (Cuvier, 1833)	WC	OC	CT	PLK	COL, PHO
Decapterus punctatus (Cuvier,1829)	WC	UN	TA	PLK	COL, PHO
Pseudocaranx dentex (Bloch & Schneider, 1801)	WC, SH, RS, SB, DR	VC	CT	MIF, PLK	MUS, COL, PHO
Seriola dumerilli (Risso, 1810)	WC	CO	CT	CAR	MUS, COL, PHO
Seriola fasciata (Bloch, 1793)	WC	UN	TA	CAR	COL, PHO
Seriola lalandi Valenciennes, 1833	WC	OC	CT	CAR	COL, PHO
Seriola rivoliana (Valenciennes, 1833)	WC	OC	CT	PIS	COL, PHO
Trachinotus falcatus (L.,758)	WC	OC	WA	CAR	PHO
Trachinotus goodei Jordan & Evermann,1896	WC	VC	WA	CAR	PHO
Uraspis secunda (Poey, 1860)	WC	OC	CT	CAR	COL, PHO
LUTJANIDAE					
Lutjanus analis (Cuvier, 1828)	SH, RS	VC	WA	CAR	PHO
Lutjanus buccanella (Cuvier, 1828)	DR	RA	WA	CAR	COL, PHO
Lutjanus cyanopterus (Cuvier,1828)	SH, RS, DR	OC	WA	CAR	PHO
Ocyurus chrysurus (Bloch, 1791)	WC	RA	WA	CAR	COL, PHO
Pristipomoides aquilonaris Goode & Bean, 1896)	DR	OC	WA	PIS	COL, PHO
Rhomboplites aurorubens (Cuvier, 1829)	WC	CO	WA	CAR, PLK	MUS, COL, PHO
LOBOTIDAE					
Lobotes surinamensis (Bloch, 1790)	WC	OC	CT	CAR	COL, PHO
HAEMULIDAE					
Anisotremus surinamensis (Bloch, 1791)	SH, RS	VC	WA	MIF	COL, PHO
Anisotremus virginicus (L., 1758)	SH, RS, WC, DR	AB	WA	MIF	COL, PHO
Haemulon aurolineatum Cuvier, 1830	SH, RS, WC, DR	AB	WA	MIF	COL, PHO
Haemulon parra (Desmarest, 1823)	RS	OC	WA	MIF	COL, PHO
Haemulon plumierii (Lacepède, 1801)	RS	CO	WA	MIF	COL, PHO
Haemulon steindachneri (Jordan & Gilbert, 1882)	RS	CO	WA	MIF	COL, PHO
SPARIDAE					
Calamus bajonado (Bloch & Schneider, 1801)	RS	RA	WA	MIF	COL, PHO
Calamus mu Randall & Caldwell, 1966	RS, SB	RA	SE	MIF	MUS

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Family and species	Habitat	Occurrence	Geog. Range	Trophic Category	Record Type
Calamus pennatula Guichenot, 1868	SB	CO	WA	MIF	COL, PHO
Diplodus argenteus (Valenciennes, 1830)	WC, SH, RS	AB	WA	OMN	COL, PHO
Pagrus pagrus (L., 1758)	SB, DR	VC	TA	MIF	MUS, COL, PHO
SCIAENIDAE					
Odontoscion dentex (Cuvier, 1830)	SH, RS	CO	WA	CAR	PHO
Pareques acuminatus (Bloch & Schneider, 1801)	SH, RS	CO	WA	CAR	MUS, PHO
MULLIDAE					
Mulloidichthys martinicus (Cuvier, 1829)	RS, SB	RA	TA	MIF	PHO
Pseudupeneus maculatus (Bloch, 1793)	RS, SB	VC	WA	MIF	MUS, COL, PHO
PEMPHERIDAE					
Pempheris schomburgki Müller & Troschel, 1848	SH	VC	WA	PLK	MUS, PHO
CHAETODONTIDAE					
Chaetodon sedentarius Poey, 1860	SH, RS	UN	WA	MIF	MUS, PHO
Chaetodon striatus L., 1758	SH, RS	VC	WA	SIF	MUS, PHO
Prognathodes brasiliensis Burgess, 2001	DR	OC	Br	MIF	PHO
Prognathodes guyanensis (Durand, 1960)	DR	RA	WA	MIF	PHO
POMACANTHIDAE					
Centropyge aurantonotus Burgess, 1974	SH, RS	OC	TA	TERH	SIG
Holacanthus ciliaris (L., 1758)	SH, RS	OC	WA	SIF	PHO
Holacanthus tricolor (Bloch, 1795)	SH	OC	WA	SIF	PHO
Pomacanthus paru (Bloch, 1787)	SH, RS, WC	VC	WA	OMN	PHO
KYPHOSIDAE					
Kyphosus incisor (Cuvier, 1831)	SH, RS, WC	AB	TA	ROVH	MUS, COL, PHO
Kyphosus sectator (L., 1766)	SH, RS, WC	AB	TA	ROVH	COL, PHO
POMACENTRIDAE					
Abudefduf saxatilis (L., 1758)	SH, WC	AB	CT	OMN	COL, PHO
Chromis cf. *enchrysura* Jordan & Gilbert, 1882	RS, DR	OC	WA	MIF	PHO
Chromis flavicauda (Günther, 1880)	RS	CO	Br	PLK	MUS, COL, PHO
Chromis jubauna Moura, 1995	RS, DR	AB	Br+SCa	PLK	MUS, COL, PHO
Chromis multilineata (Guichenot, 1853)	WC, SH	AB	TA	PLK	MUS, COL, PHO
Stegastes fuscus (Cuvier, 1830)	SH, RS	AB	Br	TERH	COL, PHO
Stegastes pictus (Castelnau, 1855)	RS	CO	Br+SCa	TERH	COL, PHO
Stegastes cf. *variabilis* (Castelnau, 1855)	SH, RS	CO	WA	TERH	COL, PHO
LABRIDAE					
Bodianus pulchellus (Poey, 1860)	SH, RS, DR	VC	TA	MIF	MUS, COL, PHO
Bodianus rufus (L., 1758)	SH, RS	VC	WA	MIF	MUS, COL, PHO
Clepticus brasiliensis Heiser, Moura & Robertson, 2000	WC	OC	Br	PLK	MUS, COL, PHO
Doratonotus megalepis Günther, 1862	RS	RA	TA	MIF	PHO
Halichoeres **sp n.**	SB, DR	CO	SE	MIF	COL, PHO

to be continued.

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TABLE 1. (continued)

Family and species	Habitat	Occurrence	Geog. Range	Trophic Category	Record Type
Halichoeres brasiliensis (Bloch, 1791)	SH, RS, SB	CO	Br	MIF	COL, PHO
Halichoeres dimidiatus (Agassiz, 1831)	RS	VC	Br	MIF	COL, PHO
Halichoeres penrosei (Starks, 1913)	SH, RS	OC	Br	MIF	SIG
Halichoeres poeyi (Steindachner, 1867)	SH, RS	AB	WA	MIF	MUS, COL, PHO
Thalassoma noronhanum (Boulenger, 1890)	WC, SH	OC	Br	PLK	MUS, PHO
SCARIDAE					
Cryptotomus roseus Cope, 1871	RS	CO	WA	ROVH	PHO
Scarus trispinosus Valenciennes, 1840	SH	RA	Br	ROVH	PHO
Scarus zelindae Moura, Figueiredo & Sazima, 2001	SH, RS	CO	Br	ROVH	PHO
Sparisoma amplum (Ranzani, 1842)	SH, RS	CO	Br	ROVH	PHO
Sparisoma axillare (Steindachner, 1878)	SH, RS	VC	Br	ROVH	COL, PHO
Sparisoma frondosum (Agassiz 1831)	SH, RS	VC	Br+SCa	ROVH	PHO
Sparisoma radians (Valenciennes, 1840)	RS	CO	WA	ROVH	MUS, SIG
Sparisoma tuiupiranga Gasparini, Joyeux & Floeter, 2003	RS	VC	SE	ROVH	PHO
PINGUIPEDIDAE					
Pinguipes brasilianus Cuvier, 1829	DR	OC	SE+Pat	CAR	PHO
TRIPTERYGIIDAE					
Enneanectes altivelis Rosenblatt, 1960	SH, RS	CO	WA	MIF	COL
LABRISOMIDAE					
Labrisomus nuchipinnis (Quoy & Gaimard, 1824)	SH	VC	TA	MIF	MUS, COL, PHO
Labrisomus kalisherae (Jordan, 1904)	SH	OC	WA	MIF	PHO
Malacoctenus delalandii (Valenciennes, 1836)	SH	CO	WA	MIF	PHO
Starksia brasiliensis (Gilbert, 1900)	SH	CO	Br	MIF	PHO
CHAENOPSIDAE					
Emblemariopsis signifera (Ginsburg, 1942)	SH, RS	VC	WA	MIF	MUS, COL, PHO
BLENNIIDAE					
Hypleurochilus fissicornis (Quoy & Gaimard,1824)	SH	OC	Br	MIF	PHO
Hypsoblennius invemar Smith-Vaniz & Acero, 1980	SH	CO	WA	MIF	PHO
Ophioblennius trinitatis Miranda-Ribeiro,1919	SH	RA	Br	TERH	MUS, SIG
Parablennius marmoreus (Poey, 1876)	SH	VC	WA	MIF	PHO
Parablennius pilicornis (Cuvier, 1829)	SH, RS, DR	AB	TA	MIF	MUS, COL, PHO
Scartella cristata (L., 1758)	SH	OC	CT	TERH	MUS, COL, PHO
CALLYONIMIDAE					
Callionymus bairdi Jordan, 1887	SH,, RS	CO	WA	MIF	COL
GOBIIDAE					
Coryphopterus glaucofraenum Gill, 1863	RS, SB	VC	WA	OMN	COL, PHO
Ctenogobius saepepallens (Gilbert & Randall, 1968)	RS, SB	OC	WA	OMN	SIG
Elacatinus figaro Sazima, Moura & Rosa, 1997	SH, RS	VC	Br	MIF	COL, PHO

to be continued.

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TABLE 1. (continued)

Family and species	Habitat	Occurrence	Geog. Range	Trophic Category	Record Type
Gnatholepis thompsoni Jordan, 1902	RS, SB	OC	TA	OMN	SIG
MICRODESMIDAE					
Ptereleotris randalli Gasparini, Rocha & Floeter, 2001	SB	CO	Br+SCa	MIF	PHO
EPHIPPIDAE					
Chaetodipterus faber (Broussonet, 1782)	WC	CO	WA	SIF	COL, PHO
ACANTHURIDAE					
Acanthurus bahianus Castelnau, 1855	SH	CO	WA	ROVH	COL, PHO
Acanthurus coeruleus Bloch & Schneider, 1801	SH	RA	WA	ROVH	PHO
Acanthurus chirurgus (Bloch, 1787)	SH, RS	AB	TA	ROVH	COL, PHO
Acanthurus monroviae Steindachner, 1876	SH, RS	OC	SE+EA	ROVH	PHO
SPHYRAENIDAE					
Sphyraena barracuda (Edwards, 1771)	WC	RA	CT	PIS	PHO
Sphyraena tome Fowler, 1903	WC	OC	SE	PIS	PHO
SCOMBRIDAE					
Euthynnus alleteratus (Rafinesque, 1810)	WC	OC	TA	CAR	PHO
BOTHIDAE					
Bothus maculiferus (Poey, 1860)	SB	OC	WA	CAR	PHO
Bothus ocellatus (Agassiz, 1831)	SB	CO	WA	CAR	PHO
BALISTIDAE					
Balistes vetula L., 1758	SH, RS	OC	TA	MIF	PHO
Melichthys niger (Bloch, 1786)	WC	RA	CT	OMN	SIG
MONACANTHIDAE					
Aluterus monoceros (L., 1758)	SH, RS, WC	UN	CT	CAR	PHO
Aluterus scriptus (Osbeck, 1765)	SH, RS	OC	CT	SIF	SIG
Cantherhines macrocerus (Hollard, 1853)	SH, RS	OC	WA	SIF	PHO
Cantherhines pullus (Ranzani, 1842)	SH	UN	TA	OMN	MUS, SIG
Stephanolepis hispidus (L., 1766)	SH, RS	UN	TA	MIF	SIG
OSTRACIIDAE					
Acanthostracion polygonius Poey, 1876	RS	CO	WA	SIF	PHO
TETRAODONTIDAE					
Canthigaster figueiredoi Moura & Castro, 2002	SH, RS	VC	Br+SCa	MIF	MUS, PHO
Sphoeroides spengleri (Bloch, 1785)	SH, RS	VC	WA	MIF	MUS, COL, PHO
DIODONTIDAE					
Chilomycterus spinosus (L., 1758)	SH, RS	OC	WA	MIF	MUS, SIG
Diodon hystrix L., 1758	RS	OC	CT	MIF	SIG
MOLIDAE					
Mola mola (L., 1758)	WC	RA	CT	CAR	PHO

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FIGURE 3. Some abundant fish species at the Laje de Santos Marine State Park. The tomtate grunt *Haemulon aurolineatum* (a); adult and juvenile sergeant major *Abudefduf saxatilis* (b); the brown chromis *Chromis multilineata* (c); juvenile dusky damselfish *Stegastes fuscus* (d); intermediate individual of the jubauna reeffish *Chromis jubauna* (e); the silver porgy *Diplodus argenteus* (f); juvenile porkfish *Anisotremus virginicus* (g); the ringneck blenny *Parablennius pilicornis* (h). Photos: O.J. Luiz Jr, except (e) by L.F. Cassino.

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Geographical Distributions and Zoogeography

The relative proportion of geographic distribution types is shown on Fig.4. Forty two percent of the species (86) occur in the entire Western Atlantic, 19% (40) are trans-Atlantic, 18% (37) are circumtropical, and 12% (22) are endemic to the Brazilian coast (Fig. 5), 3% (6) are distributed southwards to temperate Patagonia, 2% (3) are found in the Western Atlantic and the islands of the mid-Atlantic (Ascension and Sta. Helena) and 1% (2) are found in the eastern Atlantic and southeastern coast of Brazil but neither reach northern sites of Brazil and the Northwestern Atlantic. Five species (3%) present a curious distribution pattern: they occur along the Brazilian coast but are limited to the Southern Caribbean in the Northwest Atlantic (coast of Venezuela, Trinidad & Tobago, Barbados and Curacao). It has been hypothesized that these five species have a Brazilian origin and only recently crossed to the north of the Amazon Barrier (Joyeux *et al.* 2001, Rocha 2003).

Perhaps the most surprising and unexpected finding at the Laje the Santos Marine State Park was the occurrence of *Acanthurus monroviae* individuals (fig. 7a), a surgeonfish thought to be restricted to the Eastern Atlantic. This record was described in detail by Luiz Jr. *et al*. (2004).

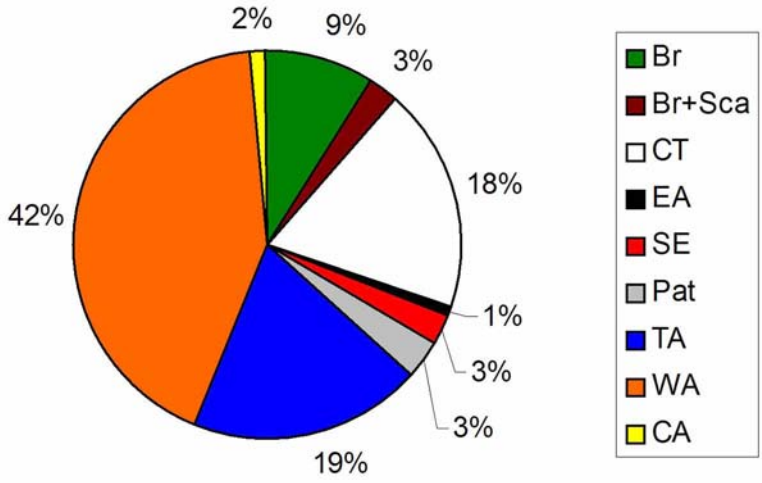

FIGURE 4. Relative proportions of geographic distribution types of the species observed at the Laje de Santos Marine State Park. Br = Brazilian Province; CE = Central Atlantic; CT = Circumtropical. EA = Eastern Atlantic; SCa = Southern Caribbean; SE = Southeastern Brazil; TA = Trans-Atlantic; WA = Western Atlantic.

Despite the position of the study site at subtropical latitudes, the local reef fish fauna more closely resembles that of the tropical Western Atlantic and Northeastern Brazilian coast than that of the southern temperate reefs (Floeter *et al.* 2008). Due to the prevailing Brazil Current, which flows southwards from low latitudes, superficial warm waters continuously reach the Laje de Santos Marine Park, providing larval supply and a suitable thermal range for tropical reef species. Colder waters are also present at the study site due to a seasonal upwelling that brings cold (14-18ºC) deep waters from the shelf slope (Campos *et al.* 1995). Cold waters are usually restricted to the deepest parts of the reefs, providing a suitable environment for temperate species (fig. 6). Thus, the species that range south to Patagonia and the subtropical endemics were observed mostly on, or are even restricted to the deep reefs at our study site.

The mixture of different conditions in ecological transitional areas is regarded as a major factor for a high diversity in SE Brazilian reef systems (Floeter *et al.* 2001). Why are there many more tropical than subtropical/temperate species is a subject of future research. One possible cause is that the deep reefs were poorly sampled and an increase in the sampling effort could result in additional new records of cold water species for the region. Few studies with the use of SCUBA were done by biologists at depths greater than 30 m, but on

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the other hand commercial and recreational fisheries were present for many decades in the surrounding areas of the study site, providing a fairly good assessment of fish species from all depths over the study area. Thus, we could expect to find some unrecorded species in the deep reefs that could only be found by SCUBA and not by conventional fishing gear, however, this is not expected to significantly change the zoogeographical affinities presented here.

An alternative explanation to poor sampling may be that the larval input from the southern temperate reefs is limited. Waters from Patagonia are known to reach the southeastern coast of Brazil through the Malvinas current, which flows northward from the coast of Argentina and can carry larvae from temperate reefs to the study site (Pereira 1989, Campos *et al.* 1996). However, dispersal via Malvinas Current may be restricted to species with some tolerance to low salinity waters. The high freshwater outflow from La Plata River and Patos Lake may extend for a great distance offshore (Piola *et al.* 2000, Pimenta *et al.* 2005) and can act as a barrier to larval dispersal in the same way as the Amazon River does between the Caribbean and Brazil (Floeter & Gasparini 2000, Rocha *et al.* 2003).

Range Extensions

We consider here only species previously unrecorded for the coast of São Paulo State. We use this unnatural, political division because most books and species accounts of fishes in Brazil usually determine the limits of species' ranges this way. Additionally, we feel that species whose recorded range limits lie only a few kilometers north or south of our study site do not represent an actual range increase. Thus, the Laje de Santos Marine Park position, approximately in the middle of São Paulo's coast, distant 171 km from Rio de Janeiro State to the north and 215 km from Paraná State to the south, provides a convenient 'buffer' distance for range extensions. Species whose ranges are extended in this paper are listed below.

Moringua edwardsi: Previously recorded for Trindade Island (Gasparini & Floeter 2001) and on the continental coast south to the State of Bahia (Menezes *et al.* 2003). Our record is based on a photograph made in July 2006 by Armando de Luca Jr. (fig. 7b).

Antennarius multiocellatus: Previous southernmost record is at Arraial do Cabo, Rio de Janeiro State (Carvalho-Filho 1999, Ferreira *et al*. 2001). Our record is based on a photograph made in November 2004 by Robson Leite (fig. 7c).

Scorpaena dispar: Southernmost occurrence previously recorded for the State of Rio de Janeiro (Menezes *et al.* 2003). Our record is based on a photograph made in July 2001 by Osmar J. Luiz Jr. (fig. 7d).

Aulostomus strigosus: Previous southernmost record is the state of Rio de Janeiro (Carvalho-Filho 1999). Our record is based on a photograph made in January 2004 by Renata Linger (fig. 7e).

Lutjanus buccanella: Previous southernmost record is Ilhéus, State of Bahia (Carvalho-Filho 1999, Menezes *et al*. 2003). Our record is based on a specimen 42 cm SL collected in October 1987 by Alfredo Carvalho-Filho (fig. 7f).

Mulloidichthys martinicus: Previous southernmost record is the state of Rio de Janeiro (Carvalho-Filho 1999, Menezes *et al*. 2003). Our record is based on a photograph made in June 2002 by Osmar J. Luiz Jr. (fig. 7g).

Halichoeres penrosei: Previous southernmost record is the state of Rio de Janeiro (Carvalho-Filho 1999, Menezes *et al.* 2003). Our record of this species is based on sightings of several individuals in January 2006 and 2007 by Alfredo Carvalho-Filho.

These previously unrecorded species were stray individuals that were seen once or twice at the study site and do not seem to represent resident populations. This reflects the high potential for dispersal among reef fishes and their ability to reach distant areas when associated with spatially and temporally unusual currents. When they do reach new areas, site specific ecological factors and occurrence of competitors or predators could prevent the establishment of new populations, and in our case cold waters seem to prevent the establishment of the above mentioned species.

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FIGURE 5. Selected Brazilian endemic reef fish species that occur at the Laje de Santos Marine State Park. The barber goby *Elacatinus figaro* (a); the Brazilian yellowcheek wrasse *Halichoeres dimidiatus*, initial phase (b); the Brazilian wrasse *Halichoeres brasiliensis*, intermediate phase (c); the Noronha wrasse *Thalassoma noronhanum*, terminal male (d); the tuiupiranga parrotfish *Sparisoma tuiupiranga*, initial phase (e); Zelinda's parrotfish *Scarus zelindae*, initial phase (f); the reef parrotfish *Sparisoma amplum*, initial phase (g); the gray parrotfish *Sparisoma axillare*, terminal male (h). Photos: O.J. Luiz Jr, except (d) by I. Cavas.

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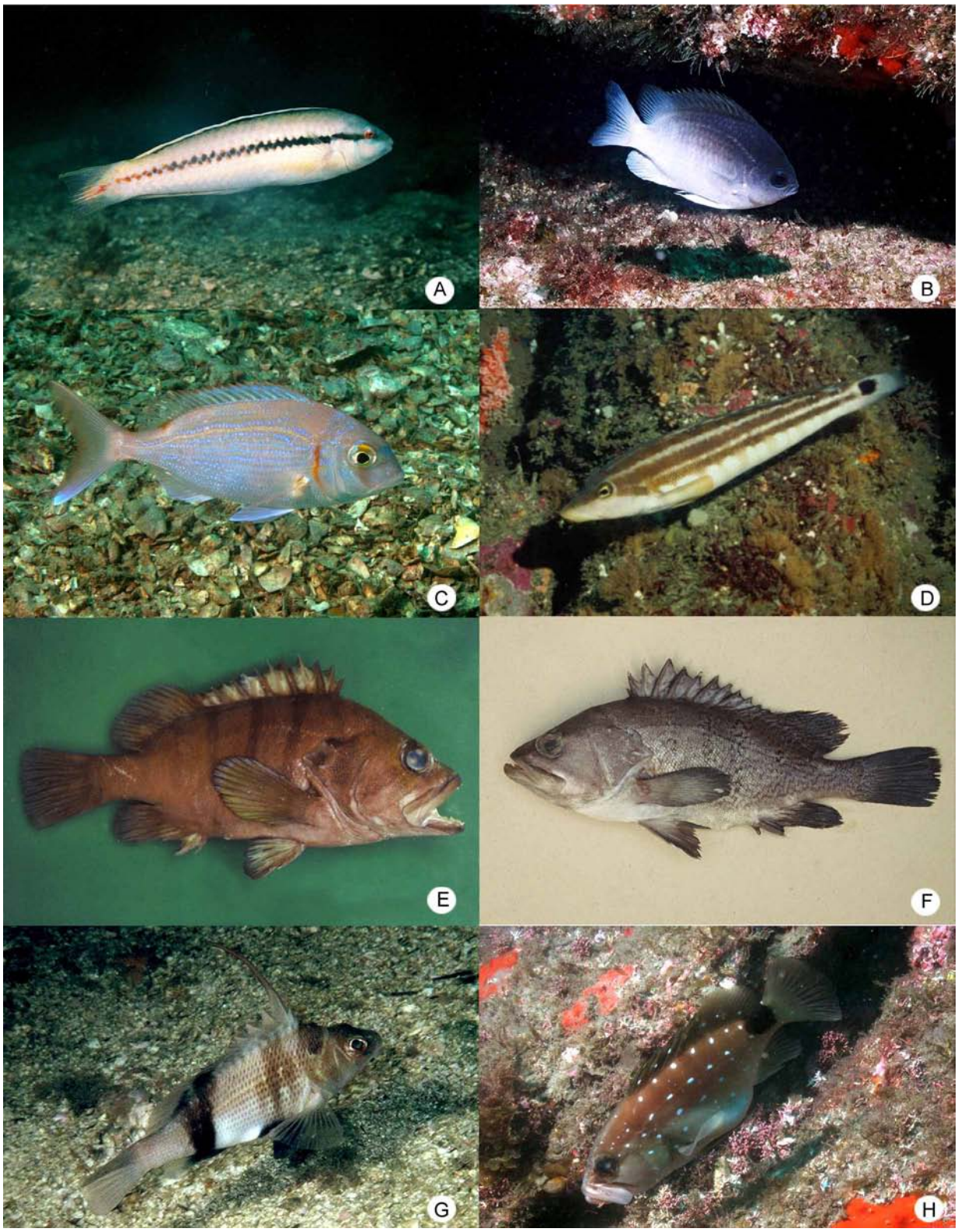

FIGURE 6. Selected fish species that dwell in the deep reef (30-45 m) community at the Laje de Santos State Marine Park. The deep-reef wrasse *Halichoeres* sp.n. (a); the reeffish *Chromis* cf. *enchrysura* (b); the red porgy *Pagrus pagrus* (c); the Brazilian sandperch *Pinguipes brasilianus* (d); the sea basses *Acanthistius brasilianus* (e), *A. patachonicus* (f) and *Dules auriga* (g); the snowy grouper *Hyporthodus niveatus* (h). The former species (a) is probably a Brazilian endemic, closely related to the Northwestern Atlantic species *H. bathyphilus*. The distinctive status from its sister species is supported by molecular mtDNA analysis (L.A. Rocha pers. comm.).The last six species (c-h) ranges southward to temperate Patagonian rocky reefs. Photos: A. Carvalho-Filho (e-g); O.J. Luiz Jr. (a-d, h).

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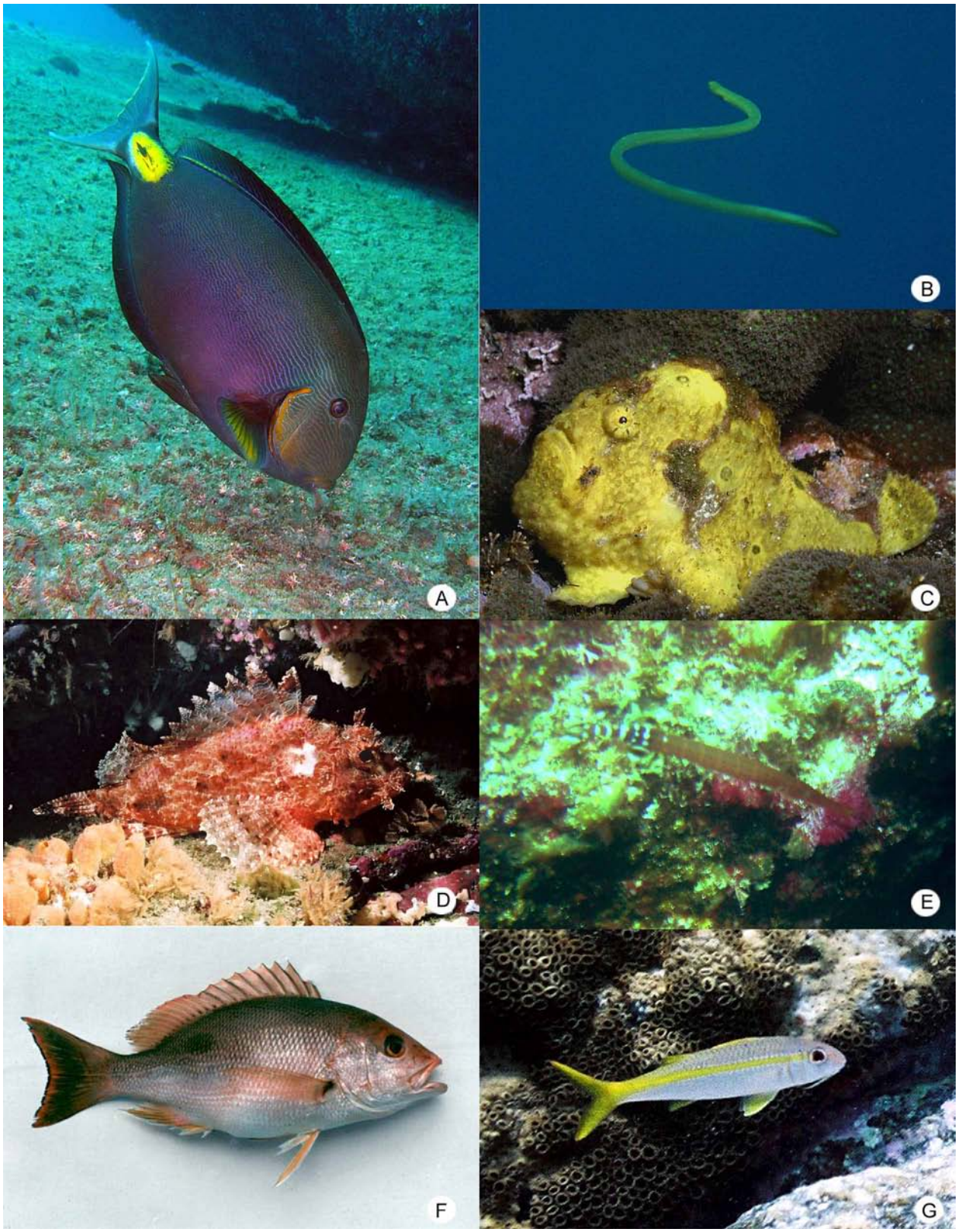

FIGURE 7. Unusual records of reef fish species for the State of São Paulo. The African surgeonfish *Acanthurus monroviae* (a), which record was dealt in details by Luiz Jr. *et al.* (2004) and the previously unrecorded species: the eel *Moringua edwardsi* (b); the frogfish *Antennarius multiocellatus* (c); the scorpionfish *Scorpaena dispar* (d); the trumpetfish *Aulostomus strigosus* (e); the blackfin snapper *Lutjanus buccanella* (f); the yellow goatfish *Mulloidichthys martinicus* (g). Except for (a), all records are southward extensions for these species' ranges in the West Atlantic. Photos: A. Carvalho-Filho (f); R. Leite (c); R. Linger (e); A. de Luca Jr. (a, b); O.J. Luiz Jr. (d, g).

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Trophic Structure

More than a half of the species at the study site are carnivores and mobile invertebrate feeders, 28% of the species belonging in each of these categories, followed by planktivores (13%), piscivores (11%), roving herbivores (8%), omnivores (5%), sessile invertebrate feeders (4%), and territorial herbivores (3%). Mobile invertebrate feeders are expected to be the most species-rich trophic category on reef fish assemblages along the Brazilian coast due mostly to their diverse morphology and variety of prey items (Ferreira *et al*. 2004). Carnivores are mostly epinephelids, carangids and muraenids, three diverse families at the study site. The relatively high proportion of planktivores and piscivores may be attributed to the mid-shelf location of the study site. Distance from the coast is regarded as a good predictor for the occurrence and abundance of planktivorous reef fishes in southwestern Atlantic rocky reef system (Floeter *et al.* 2007).

Most piscivores belong to epipelagic families (carangids, scombrids, pomatomids, sphyraenids) that usually are found far offshore, but this category also includes many species that dwell on sandy bottom, an extensive habitat at the study site. These patterns, however, were not consistent between the different zones of the study site. Habitat specific trophic structure was reflected in the similarity of clusters of species recorded for each habitat (fig. 8). The shallow reef and reef slope zones were almost identical and matched best for the whole assemblage at the study site. However, as expected, in the water column zone, planktivore and carnivore categories are better represented. The deep reef and the sand bottom habitats were similar in trophic structure patterns; both have no herbivores and no sessile invertebrate feeders, probably a result of the reduced algal coverage due to low light levels in the deep reef, and the lack of suitable substrate for attachment of algae.

Symbiotic feeding associations

As most reef assemblages in tropical or temperate regions (e.g., Fricke 1975, Strand 1988, Côté 2000, Grutter 2005, Sazima *et al*. 2007), the Laje de Santos has its share of symbiotic feeding relationships (see Losey 1978 for an instrumental definition and examples of symbiotic behavior). One such feeding association is cleaning symbiosis, in which a fish species (the cleaner) remove parasites, necrotic tissue, and mucus from a variety of fishes (the clients) that seek the cleaner's services (reviews in Côté 2000, Grutter 2005).

An obligate cleaner recorded at our study site is the barber goby *Elacatinus figaro*, which maintains well defined cleaning stations on prominent points of the reef and services a diverse and species-rich fish assemblage (see Sazima *et al*. 2000). The goby is a bottom-dweller but moves towards mid-water clients that hovers near the cleaning station (fig. 9a). Since cleaning symbiosis between fishes is a strictly diurnal activity, nocturnal species leave their shelters to seek cleaning (fig. 9b). Other cleaners recorded at the Laje de Santos are facultative and clean mostly as juveniles (Côté 2000), such as the porkfish *Anisotremus virginicus* and the spotfin hogfish *Bodianus pulchellus* (fig. 9c); this latter, however, occasionally cleans as a small adult as well (fig. 9d). Although occasionally recorded at the Laje de Santos, the versatile Noronha wrasse *Thalassoma noronhanum* was never recorded as a cleaner there, a role it apparently plays in Brazil's oceanic islands only (e.g., Gasparini & Floeter 2001, Sazima *et al* 2005). Two common fishes at our study site, the silver porgy *Diplodus argenteus* and the sergeant major *Abudefduf saxatilis*, also remain to be recorded as cleaners there, although they occasionally clean at other coastal sites in southern and southeastern Brazil (Sazima 1986, Krajewski 2007). Apparently, the rarity or even absence of cleaning by these two latter species is related to the presence of more colorful and efficient cleaners such as the goby *E. figaro* and the wrasse *B. pulchellus*. The "weak" cleaning role of *D. argenteus* in southern Brazil seems related to its unattractiveness as compared to more specialized and colorful cleaners there (Krajewski 2007), and a similar idea may be applied to the cleaner guild of the Laje de Santos.

Another conspicuous symbiotic association in reef assemblages is following behavior (revision in Sazima *et al.* 2007). In this association type, a benthic species (the nuclear) attracts other, opportunistic and mostly carnivorous species (the followers) during its feeding activity. Small animals exposed by the substrate-dis-

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turbing activity of the nuclear fish and not taken by it may be preyed upon by the follower fish. Substrate feeders that dig into sandy bottoms are very prone to attract followers, as the sediment clouds are a clue to the latter (see Sazima *et al*. 2006). The best known and studied example are the goatfishes, family Mullidae, which are regarded as nuclear fishes *par* excellence (Sazima *et al*. 2006). Less studied in the following symbiosis is the role of jacks, family Carangidae, which may act both as nuclear and followers (Sazima 1988, Sazima *et al*. 2007). At our study site, the white trevally *Pseudocaranx dentex* (fig. 9e) acts as a nuclear species and attracts mostly wrasses, which are known for their follower role (Sazima *et al*. 2007). Morays and other eels are another fish group that is readily followed during foraging activity (Diamant & Shpigel 1985, Gerhardinger *et al*. 2006), and attracts mostly groupers (fig. 9f). Less important are several fishes that forage on sandy bottoms but need not raise sediment to attract followers. One such example is the flying gurnard *Dactylopterus volitans* (fig. 9g) whose moving close to the bottom disturb small fishes and other animals that are preyed upon by the followers (Sazima & Grossman 2005).

The hitch-hiking remoras (Echeneididae) exemplify still another type of feeding association. Although widely known as hitch-hikers on larger fishes and other marine vertebrates, and feeding on scraps left by their hosts or cleaning them of parasites (review in O'Toole 2002), there is a less known feeding activity of remoras on their hosts. While attached near the mouth of a filter-feeding, large fish such as the Atlantic manta (fig. 9h) or a whale shark, the remoras engage in filter-feeding (Clarke & Nelson 1997), a role recorded for other species in the family (e.g., Sazima *et al*. 2006).

Conservation Remarks

With 196 recorded species, the reef fish assemblage of the Laje de Santos Marine State Park has a relatively high richness when compared to other localities along the Brazilian coast. Despite its higher latitude position (*i.e.*, subtropical), our study site has an equal or even a larger number of species than similarly-sized tropical reefs of Northeastern Brazil (Rosa & Moura 1997, Feitoza 2001, Ferreira & Cava 2001, Rocha & Rosa 2001, Souza *et al.* 2007). This is probably due to the co-occurrence of tropical and subtropical/temperate species on Brazil's southeastern coast. Additionally, there are more species at the Laje de Santos than at other similarly-sized coastal reef sites in southeastern and south Brazil (Ferreira *et al.* 2001, Hostim-Silva *et al.* 2006, Rangel *et al.* 2007), which could be explained by the off-shore, mid-shelf location of the Laje de Santos reefs and the consequent occurrence of a relatively large number of epipelagic species.

Unlike coral reefs, rocky reefs are highly restricted to the shores of continents and islands (Ebeling & Hixon 1991) with few patchily distributed rocky bottoms at the mid-shelf. Thus, the Laje de Santos Marine State Park is to be regarded as an important biodiversity hot-spot for Brazilian reef fishes. Some species that are targeted and highly prized by spear-fishermen occasionally attain large sizes at the Laje de Santos (fig. 10). However, it would be premature to say that the occurrence of these endangered species is directly related with the protection conferred to the Laje de Santos without further investigation.

Acknowledgements

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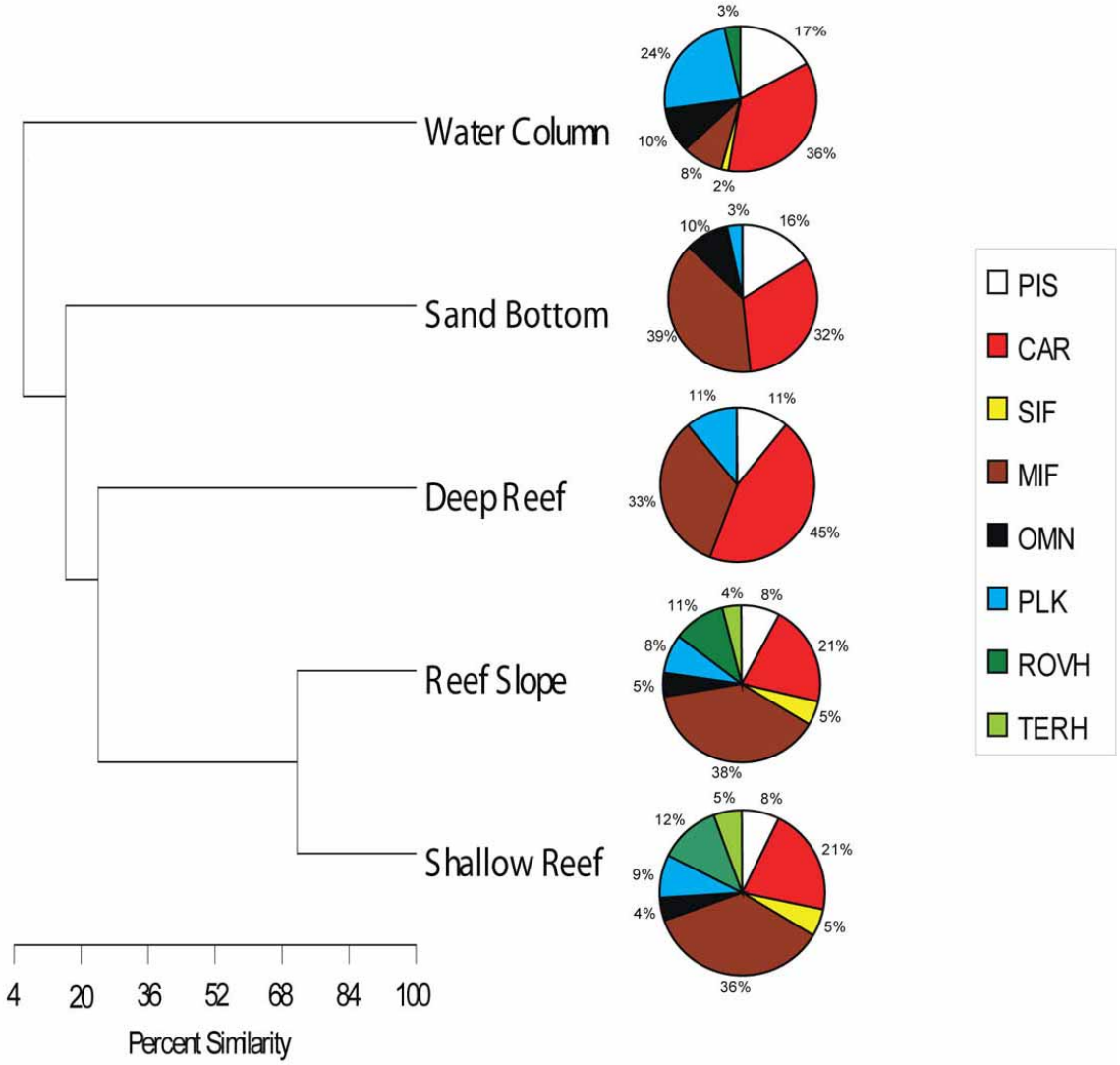

FIGURE 8. Cluster analysis of habitat types at the Laje de Santos Marine State Park based on the similarity of species composition. The relative distribution of trophic categories in each habitat is shown in the graphs. CAR = Carnivore; MIF = Mobile Invertebrate Feeder; OMN = Omnivore; PIS = Piscivore; PLK = Planktivore; ROVH = Roving Herbivore; SIF = Sessile Invertebrate Feeder; TERH = Territorial Herbivore.

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FIGURE 9. Selected examples of symbiotic associations between reef fishes recorded at the Laje de Santos Marine State Park. The barber goby *Elacatinus figaro* cleans the head of the jubauna reeffish *Chromis jubauna* hovering close to the goby's cleaning station (a); the same cleaner species inspects the back of the nocturnal squirrelfish *Holocentrus adscensionis* that approached its cleaning station (b); juvenile spotfin hogfish *Bodianus pulchellus* cleans the mouth of the spotted moray *Gymnothorax moringa* (c); adult of the same hogfish species cleans the head of the jubauna reeffish (d); the wrasse *Halichoeres* sp. n. follows a group of the white trevally *Pseudocaranx dentex*, which stir sediment clouds while feeding on the sandy bottom (e); the dusky grouper *Mycteroperca marginata* closely follows the goldspotted snake eel *Myrichthys ocellatus* that nudges its head in rocky crevices (f); the spotfin hogfish follows the flying gurnard *Dactylopterus volitans* moving close to the bottom (g); two diskfish *Remora remora* attached near the mouth of the Atlantic manta *Manta birostris* (h).Photos: M. Andrade (h); A. Carvalho Filho (e-f); J. P. Krajewski (a); O.J. Luiz Jr. (c-d, g); A. de Luca Jr. (b).

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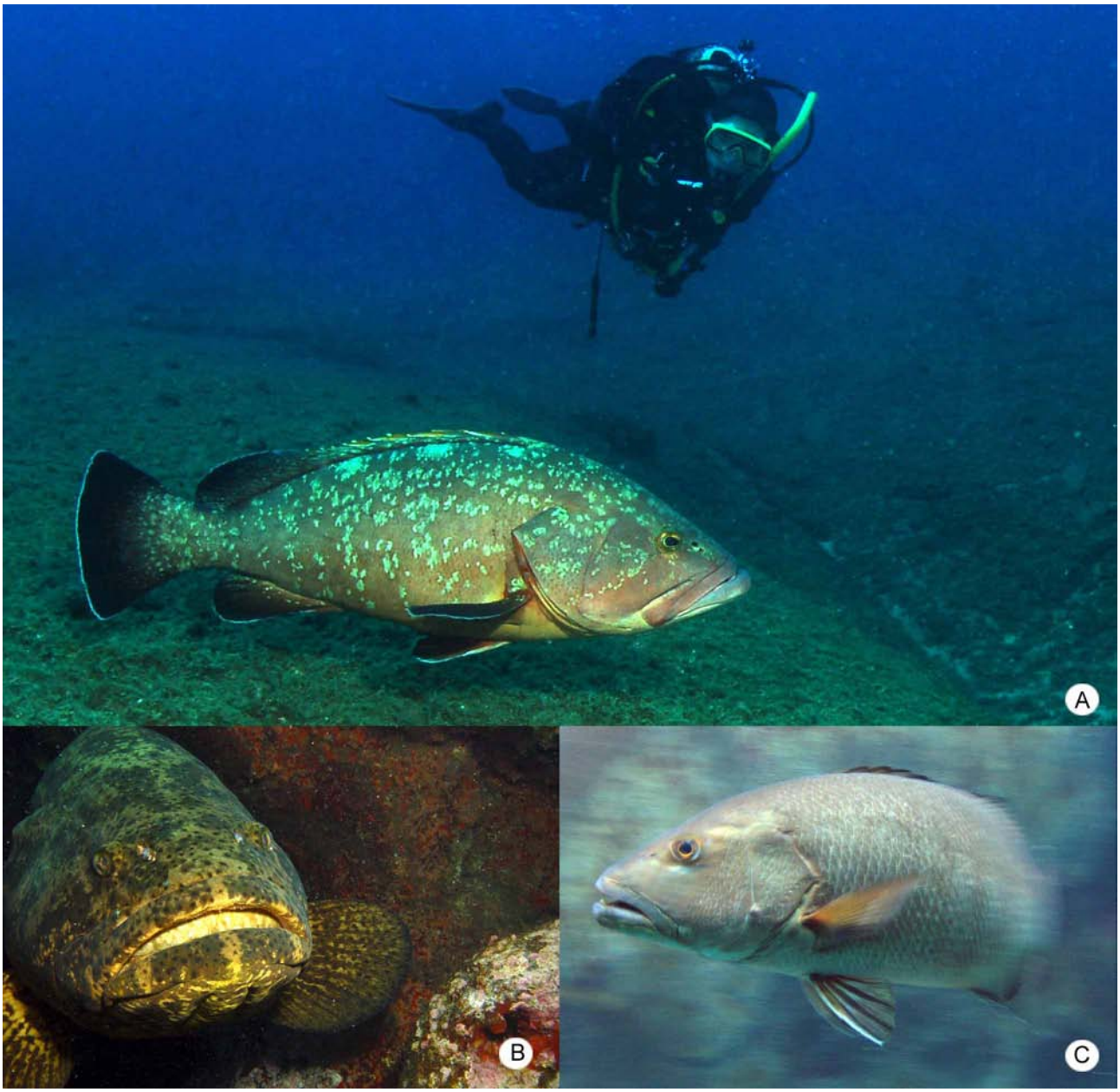

FIGURE 10. Targeted and endangered top-predators recorded at the Laje de Santos Marine State Park. The dusky groupers *Mycteroperca marginata* are very common in the area, but attain unusual large size and are largely unafraid of divers, contrarily to what happens at other unprotected sites (a); the goliath grouper *Epinephelus itajara* (b) and the cubera snapper *Lutjanus cyanopterus* (c). Several individuals of these two latter species have been seen at in the Laje de Santos in the last two years, after a period of more than ten years over which they remained unrecorded at the site.
Photos: A. Carvalho-Filho (c); L. Cheidde (b); A. Valente (a).

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Appendix

Museum vouchers of specimens from the Laje de Santos Marine State Park. Species arranged in alphabetical order. Institutions names and acronyms are the follow: California Academy of Sciences (CAS); Museu de Zoologia, Universidade de São Paulo (MZUSP); National Museum of Natural History, Smithsonian Institution (USNM); Museu de História Natural, Universidade Estadual de Campinas (ZUEC).

Abudefduf saxatilis—MZUSP 50989; *Acanthistius brasilianus*—MZUSP 14890, 70738, 70743; *Acanthurus bahianus*— MZUSP 45659; *Acanturus chirurgus*—MZUSP 45661; *Anisotrenus virginicus*—MZUSP 45662, 67870, 67873; *Apogon americanus*—MZUSP 45641; *Apogon pseudomaculatus*—MZUSP 45635, 45643; *Bodianus pulchellus*— MZUSP 44589, 66230, 66238, 66242; ZUEC 3394, 4255, 4427; *Bodianus rufus*—MZUSP 44596, 66240; *Calamus mu*—MZUSP 69958, 70039; *Calamus penna*—MZUSP 14891, 14892; *Cantherhines pullus*—MZUSP 44658, 44660, 72924; *Canthigaster figueiredoi*—MZUSP 44594 (paratype), 44595; USNM 357498 (paratype); *Caranx latus*—MZUSP 43487; *Caulolatilus chrysops*—MZUSP 14878, 44650; *Cephalopholis fulva*—MZUSP 47436; *Chaetodon sedentarius*—MZUSP 45654; *Chaetodon striatus*—MZUSP 45644, 45649; *Chilomycterus spinosus*— MZUSP 5246, 5247, 5248, 5249, 71370; *Chromis flavicauda* MZUSP 44624, 44625, 44626; *Chromis jubauna*— MZUSP 44631 (holotype), 44632- 44635 (paratypes); ZUEC 4331, 4426; *Chromis multilineata*—MZUSP 44619, 44620; ZUEC 3916, 6310; *Clepticus brasiliensis*—CAS 99821-99822 (paratypes); MZUSP 44590, 44644, 44657, 47151 (paratype), 53271, 99821-99822 (paratypes); *Dactylopterus volitans*—MZUSP 46986; *Diplodus argenteus*— MZUSP 45651; *Dules auriga*—MZUSP 70845; *Elacatinus figaro*—ZUEC 3898, 3902, 3903, 3911, 3912, 3914, 3915; *Emblemariopsis signifera*—MZUSP 44608; *Epinephelus adscensionis*—MZUSP 47440; *Epinephelus morio* – MZUSP 71106; *Gymnothorax funebris* - MZUSP 14877*; Halichoeres* sp n.—MZUSP 46825, 47152; *Halichoeres poeyi*—MZUSP 44584, 44585, 44586, 47435; *Halichoeres brasiliensis*—MZUSP 47437, 47438, 47441; *Holocentrus adscensionis*—MZUSP 43489, 47434, 45657, 47434; *Hyporthodus niveatus*—MZUSP 43490, 70937, 70949; *Kyphosus incisor*—43495, 44656; *Labrisomus nuchipinnis*—MZUSP 44614, 44615, 44616, 44617, 44618, 66796; ZUEC 6309; *Lobotes surinamensis*—MZUSP 72733; *Malacanthus plumieri*—MZUSP 14870; *Mobula hypostoma* – 13402 (head); *Mycteroperca acutirostris*—MZUSP 43494; *Mycteroperca interstitialis*—MZUSP 43497; 47150, 70975, 70976; *Mycteroperca marginatus*—MZUSP 43491, 51248, 70913; *Myripristis jacobus*—MZUSP 43488, 44645; *Ophichthus ophis*—MZUSP 44649; *Ophioblennius trinitatis*—MZUSP 44607; *Pagrus pagrus*—MZUSP 45647, 70094; *Parablennius pilicornis*—MZUSP 44599, 44601, 63869; *Paranthias furcifer*—MZUSP 43496, 71045, 71046; *Pareques acuminatus*—MZUSP 43493, 44647; *Pempheris schomburgki*—MZUSP 43492, 45645; *Porichthys porosissimus*—MZUSP 44651; *Priacanthus arenatus*—MZUSP 69931; *Pseudocaranx dentex*—MZUSP 14871, 45655; *Pseudupeneus maculatus*—MZUSP 41992, 43486; *Remora albescens*—MZUSP 69754; *Rhomboplites aurorubens*—MZUSP 44582; *Sardinella janeiro*—MZUSP 11411; *Scartella cristata*—MZUSP 44602; *Scarus zelindae*—USNM 357500 (paratype); *Scorpaena isthmensis*—MZUSP 43481; *Serranus baldwini*—MZUSP 43478, 43479; *Seriola dumerili*—MZUSP 14880, 46989; *Seriola fasciata*—MZUSP 46990; *Sparisoma amplum*— MZUSP 46444; *Sparisoma axillare*—MZUSP 46817; *Sparisoma frondosum*—MZUSP 46802, 46818; *Sparisoma radians* – MZUSP 46440; *Sparisoma tuipiranga*—MZUSP 46441, 46442, 46443; *Sphoeroides spengleri*—MZUSP 44579; *Stegastes fuscus*—MZUSP 45775, 45780, 45782, 45784, 45787, 45789, 49065; ZUEC 6309; *Stegastes pictus*—MZUSP 45786; *Stegastes variabilis*—MZUSP 45776, 45779, 45781, 45783, 45791; *Synodus foetens*— MZUSP 43483; *Synodus intermedius*—MZUSP 43484; *Thalassoma noronhanum*—MZUSP 45633, 45639; ZUEC 3146; *Tylosurus acus*- MZUSP 14879; *Uraspis secunda*—MZUSP 65901.