Synopsis of the knowledge on the Brazilian estuarine fishes

Ciro Colodetti Vilar[1*], Jean-Christophe Joyeux[1,2]

[1]*Programa de Pós-Graduação em Oceanografia Ambiental, Universidade Federal do Espírito Santo, Rod. ES 10, km 16, 565, Aracruz, ES, Brazil.*

[2]*Departamento de Oceanografia e Ecologia, Universidade Federal do Espírito Santo, Av. Fernando Ferrari, 514, 29075-910, Vitória, ES, Brazil.*

*Corresponding author:

Ciro Colodetti Vilar[1]

Email address: cirovilar@hotmail.com

Abstract

A substantial amount of information on the Brazilian estuarine fishes has been collected, but is still largely fragmented into different sources. This study presents a summary of the available knowledge on the biodiversity of estuarine fishes in Brazil, a brief analysis of the historical development of estuarine ichthyology and identifies current research gaps in the country. A total of 796 fish species were inventoried, representing about 2.3% of current valid fish species and about 17.6% of the Brazilian fish fauna. Data evidenced the existence of large coastal stretches inadequately sampled and a lack of human resources and infrastructure in parts of the coast. Large gaps in basic knowledge about the biology and ecology of the species were also detected. Reducing these deficiencies is of utmost importance for the study, documentation and conservation of the Brazilian biodiversity.

Keywords: Sisbiota-Mar, fish fauna, estuaries, biodiversity, Brazil, South West Atlantic.

Introduction

The term "fish" has been used to describe a wide array of chordates, represented by organisms highly diverse such as hagfishes, lampreys, sharks and rays, lungfishes, coelacanths, ray-finned bony fishes, among others. It is most often employed for convenience, i.e. to refer to the animals studied by ichthyologists and addressed in ichthyology courses rather than to a *stricto sensu* taxonomic category (e.g. Nelson 2006). Despite representing independent evolutionary lineages, fishes can be inclusively defined as: "aquatic vertebrates that have gills throughout life and limbs, if any, in the shape of fins" (Nelson 2006).

In light of this definition, fishes are a paraphyletic assemblage comprising more than half of the 55,000 species of living vertebrates (Helfman et al. 2009). Currently, 515 families, 62 orders and 5 classes are recognized – Myxini, Petromyzontida, Chondrichthyes, Actinopterygii e Sarcopterygii (Nelson 2006). The fossil record indicates that fishes exist at least since the Lower Cambrian, approximately 530 million years ago (Shu et al. 1999) and have evolved to conquer a large variety of aquatic environments. It is estimated that about 58% of the living fish species are marine, 41% live in freshwater and 1% are diadromous – i.e. migrate regularly between marine and freshwater environments during their life cycle (Helfman et al. 2009). Many marine species and a smaller number of freshwater species also occur in estuarine environments, but relatively few can complete their entire life cycle in these ecosystems (McLusky & Elliott 2004). The co-occurrence of these three species groups in estuaries composes a peculiar fish assemblage, which is the central theme of this study.

Until the 90s, the knowledge on the Brazilian estuarine fishes was still incipient compared to other regions of the world, mainly in the southern hemisphere (e.g. Australia and South Africa, see Potter & Hyndes 1999 and Whitfield 1999). However, there has been considerable progress in recent years, with an increase in the number of ichthyologists and the publication of new information on systematics (e.g. Marceniuk & Menezes 2007), taxonomy (e.g. Ramos et al. 2009), trophic ecology (Pimentel & Joyeux 2010, Contente et al. 2012), reproduction (e.g. Albieri & Araújo 2010, Oliveira & Fávaro 2011), ontogenetic migration (e.g. Oliveira et al. 2016) and, in particular, on the taxonomic composition of assemblages and their spatial and temporal variations (e.g. Garcia et al. 2001, Barletta et al.

2005, Chagas et al. 2006, Vilar et al. 2011a,b). Although Brazil's coastline extends for more than 37° of latitude, such studies have been conducted primarily within a local geographic context (for exceptions, see Andrade-Tubino et al. 2008, Paiva et al. 2013, Vilar et al. 2013). At present, there is a large amount of data scattered in dozens of sources, many of them in Portuguese and difficult to access. This hinders the identification of collection gaps and regions whose fauna is relatively well known, for instance. In the present work an extensive (but not exhaustive) literature review was conducted to presents a synopsis of the available knowledge on the biodiversity of estuarine fishes on the Brazilian coast, along with a brief analysis of the historical development of estuarine ichthyology and existing research gaps in the country.

Historic of studies in Brazil

Many people helped to forge the available knowledge on estuarine fishes in Brazil, and the effort of these persons should be fully acknowledged. Nevertheless, the historic account presented here does not intend, in any way, to be exhaustive but only to provide a chronological narrative of some researchers and facts relevant to the development of national estuarine ichthyology.

The arrival of the German naturalist Georg Macgrave (1610–1644) in Brazil during the XVIIth century, associated with the occupation of the northeastern region of Brazil by the Dutch, marked the beginning of ichthyology in the country. Earliest researches on the fauna and flora of the New World conducted by Macgrave were published posthumously in 1648, in an iconic work entitled "*Historia Naturalis Brasiliae*". This document contains detailed depictions of more than 100 fish species, among which some are found in estuaries: e.g., *Epinephelus itajara* (Lichtenstein 1822), *Lile piquitinga* (Schreiner & Miranda Ribeiro 1903), *Fistularia tabacaria* Linnaeus 1758 and *Archosargus rhomboidalis* (Linnaeus 1758). For about 150 years after his publication, Macgrave´s book remained the main source of knowledge about hundreds of animals and plants of the country, including fish. More than a century later, the renowned zoologist – also German – Johann Baptist von Spix (1781–1826) was responsible for planning and coordinating a scientific expedition to Brazil, between 1817 and 1820, which he undertook along with the botanist von Martius (Fittkau 2001). Part of the discoveries made by Spix during this trip was published in 1829

with Louis Agassiz in "*Selecta genera et species Piscium quos in itinere per Brasiliam*". Later, Brazilian fish fauna was also studied by Francis Laporte de Castelnau (1810–1880) (Castelnau 1855) and Edwin Chapin Starks (1867–1932) (Starks 1913), among other scientists who visited the country.

In the second half of the XIXth century began studies on estuarine and coastal fishes conducted by researchers born or living in Brazil. The German naturalized Brazilian Hermann von Ihering (1850–1930) was one of these pioneers. Among his many publications (338 are listed in Nomura 2012), is "*Os peixes da costa do mar no estado do Rio Grande do Sul*" (Ihering 1896, 1897). Posteriorly the Brazilian Alípio Ribeiro de Miranda (1874–1939) published his most illustrious work, "*Fauna brasiliensis: peixes*", whose first volume was released in 1907 (Miranda-Ribeiro 1907) and the last (vol. V) in 1918 (Miranda-Ribeiro 1918). Sixteen years later, Alberto Vasconcellos would bring the first, and extensive, contribution to the knowledge of estuarine and marine fishes of the state of Pernambuco (Vasconcellos, 1934).

In the 1950s and 1960s, João de Paiva Carvalho (1903–1961), former head of the Division of Biological Oceanography of the current "*Instituto de Oceanografia*" of "*Universidade de São Paulo*", would publish, among other works, records of the occurrence of *Xenomelaniris brasiliensis* [= *Atherinella brasiliensis* (Quoy & Gaimard 1825)] for the state of São Paulo (Carvalho 1954) and a taxonomic list of flatfishes found in Brazil (Carvalho et al. 1968). In the late 60s and the following decade, Aída Maria Eskinazi de Oliveira published manuscripts on the estuarine fishes of the Brazilian Northeast (e.g. Eskinazi 1969, 1972, Oliveira 1972). Some of these works remain valuable sources of information for coastal areas still poorly explored, such as the Parnaíba river estuary (Figure 1; Oliveira 1974). In 1977 was launched the first volume of José Lima de Figueiredo and Naércio Aquino Menezes' seminal work, "*Manual de peixes marinhos do sudeste do Brasil*", the most comprehensive key for fish species identification published in the country until today. The guide has marked the course of the Brazilian ichthyology and is still widely used by contemporary researchers.

In the 80s, Ning Labbish Chao and collaborators began the description of the estuarine and coastal fish fauna of southernmost Brazil, more precisely of the Patos lagoon and the marine adjacent region, in the state of Rio Grande do Sul (Figure 1; Chao et al.

1982). In the same period, Francisco Gerson Araújo, then a Master's student, began researching the biology of catfishes in the Patos lagoon (Araújo 1984, 1988), Marco Fábio Maia Corrêa wrote his first reports on the biology of the fish fauna in the Paranaguá Estuarine Complex, state of Paraná (Figure 1;. e.g. Corrêa et al. 1984) and José Vanderli Andreata initiated his ichthyological surveys in estuaries of the state of Rio de Janeiro (Volcker & Andreata 1982, Andreata et al. 1989).

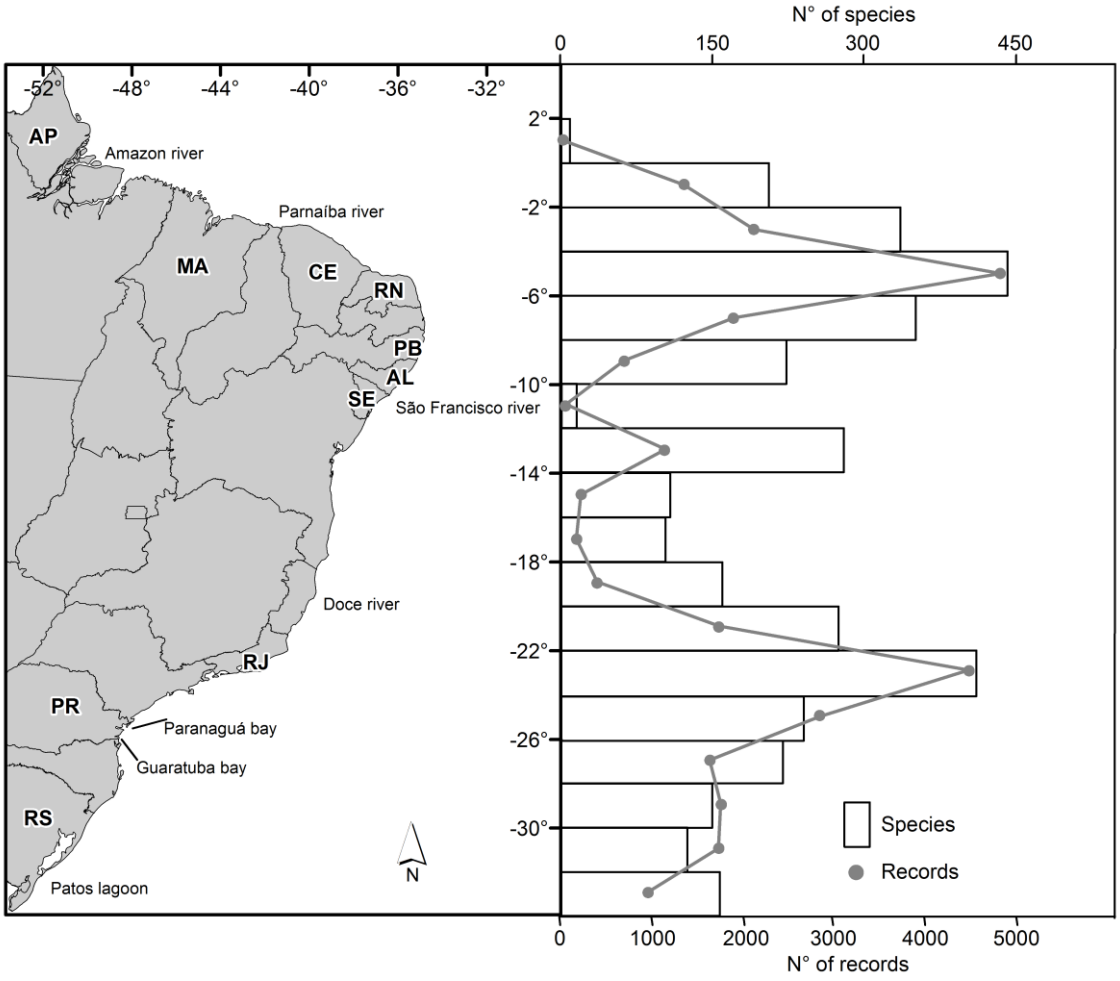

Figure 1. Number of species (bars) and independent occurrence records (line) of estuarine fishes along the Brazilian coast, by 2-degree-class of latitude. States mentioned in the text are indicated: AP, Amapá; MA, Maranhão; CE, Ceará; RN, Rio Grande do Norte; PB, Paraíba; AL, Alagoas; SE, Sergipe; BA, Bahia; RJ, Rio de Janeiro; PR, Paraná; RS, Rio Grande do Sul.

The following decade saw a large expansion in the number of ichthyologists and works on estuarine fishes in southeastern and southern Brazil. Mário Barletta and Marco Fábio Maia Corrêa released the guide for identification of Brazilian estuarine and marine

fish families (Barletta & Corrêa 1992). Still in the 90s, Paulo de Tarso da Cunha Chaves and Henry Louis Spach started their studies on the fish fauna of the Baía de Guaratuba (Figure 1; e.g. Chaves 1994, Chaves & Corrêa 1998), Baía de Paranaguá and adjacent marine areas (e.g. Almeida & Spach 1992, Godefroid et al. 1998) of the state of Paraná. Also in this decade, João Paes Vieira Sobrinho published emblematic studies on the biogeography of estuarine fishes in the Western Atlantic (Vieira & Musick 1993, 1994) and his prolific former student, Alexandre Miranda Garcia, began working on estuarine ichthyology (Garcia & Vieira 1997).

The cooperation agreement between the Centre for Tropical Marine Ecology, in Germany, the "*Universidade Federal do Pará*" and the "*Museu Paraense Emílio Goeldi*" for the project Mangrove Dynamics and Management – MADAM (Saint-Paul & Schneider 2016), boosted estuarine ichthyology in an undersampled region near and south of the Amazon river mouth, between the 1990s and 2000. As a result, several studies addressing not only the spatial and temporal dynamics, but also other aspects of fish assemblages from estuaries in northern Brazil were published (e.g. Barletta et al. 2003, 2005, Giarrizzo & Krumme 2007, Giarrizzo & Saint-Paul 2008), filling a notable gap on the coast. In 2003–2004, the project "*Uso e Apropriação de Recursos Costeiros – RECOS*", a partnership between researchers from five Brazilian universities enabled the first large-scale comparisons of the fish fauna between estuaries on the Brazilian coast using data collected with standardized methods (Joyeux et al. 2009, Vilar et al. 2013). In recent years, a significant advance in estuarine ichthyology in the country has been noticeable as a consequence of the formation of human resources, international collaboration and the application of modern techniques involving stable isotopes, microchemistry, genetics or GIS in taxonomic (e.g. Menezes et al. 2015), biological (e.g. Mai et al. 2014) and ecological (e.g. Albuquerque et al. 2012) studies.

Methods

Data were obtained through an extensive survey of literature, including peer-reviewed articles, books, master´s and PhD theses, conference proceedings and technical reports, as well as from scientific collections in Brazil and abroad (see Appendix 1) via the databases *SpeciesLink* (http://splink.cria.org.br) and *Global Biodiversity Information*

Facility (http://data.gbif.org/welcome.htm). We recorded basic information from the source (authors, year, title, journal/publisher, volume/edition and pages or catalog number and collection's name), taxonomic data (class, order, family, genus, species) and the geographical location (latitude, longitude, locality, municipality and state) of each occurrence record. Here an occurrence record represents one or more individuals of a given fish species sampled at a particular locality and study. Duplicate records of a given species at a given locality coming from works built on the same dataset were removed. The taxonomic classification and nomenclature of species were reviewed using the tool *match taxon* of *World Register of Marine Species* (WoRMS Editorial Board 2015). For those taxa missing in *WoRMS* the taxonomy was based on Eschmeyer (2015). Only estuarine and marine fish were considered. Species of primary freshwater families (*sensu* Berra 2007) or belonging to the superorder Ostariophysi were excluded from the analysis, except all Ariidae and the estuarine species of Aspredinidae (*sensu* Barletta & Blaber 2007). The references used to compile the data presented in this study are listed in Appendix 2. Any interested person can contact the authors to discuss future uses of this database.

Biodiversity of estuarine fishes in Brazil

This review assembled 27,891 unique records of 796 estuarine fish species sampled along the Brazilian coast (Table A1). Data were extracted from 154 references and 25 fish collections spanning from 1908 to 2013. The fish species documented belong to 425 genera, 144 families and 36 orders (Table A1). Chondrichthyes were represented by 89 species, 45 genera, 24 families and 11 orders. At least five non-native fish species were found in the country – *Butis koilomatodon* (Bleeker 1849), *Coptodon rendalli* (Boulenger 1897), *Omobranchus punctatus* (Valenciennes 1836), *Opsanus beta* (Goode & Bean 1880) and *Oreochromis niloticus* (Linnaeus 1758). Perciformes was the richest order (385 species), followed by Clupeiformes (42), Anguiliformes (39), Pleuronectiformes (39), Tetraodontiformes (37) and Carcharhiniformes (30). The most species-rich families were Sciaenidae (38), Carangidae (36), Serranidae (31), Cichlidae (29), Gobiidae (28) and Engraulidae (23), corresponding together to 23.2% of the total species richness.

The number of species and families surveyed was 1.7–4.3 and 1.3–2.5 times, respectively, higher than observed in previous studies on the Brazilian estuarine fish fauna

(Andrade-Tubino et al. 2008, Paiva et al. 2013, Vilar et al. 2013). Since the number of taxa is positively correlated with the area and the number of sampled habitats, such difference could have derived from the inclusion of shallow coastal environments besides estuaries (i.e. sandy beaches and soft-bottom areas of the inner shelf near to estuaries). These environments are often inhabited by estuarine species, but were not considered in aforementioned studies. The number of species inventoried represents about 2.3% of the valid fish species currently known in the world (about 33,536 species; Eschmeyer & Fong 2015), and about 17.6% of the total diversity of fish species known in Brazil, considering both those living in marine (about 1,393 species; ICMBio 2015) and in continental environments (about 3,114 species; ICMBio 2015).

The species richness showed a peak between latitudes 4° and 5°S and another between 22° and 23°S (Figure 1). This result is similar to that found in a previous study using extent-of-occurrence maps, in which the (*lato sensu*) estuarine fish species richness was also higher near latitude 23°S (Vilar et al. 2017). Sampling effort also varied widely along the coast, with species richness strongly and positively correlated to the number of records (Figure 1). This geographical pattern of species richness should, therefore, be viewed with caution.

In terms of composition, the Brazilian fauna of estuarine and coastal fishes differs geographically in parallel with the geomorphological, climatic and oceanographic characteristics of the littoral (Vilar et al. 2013). Species typically associated with temperate waters, such as *Paralichthys patagonicus* Jordan 1889, *P. orbignyanus* (Valenciennes 1839), *Anchoa marinii* Hildebrand 1943 and *Pinguipes brasilianus* Cuvier 1829 were more common or occurred exclusively in the southern and southeastern regions. Those associated with tropical waters, such as *Cathorops agassizii* (Eigenmann & Eigenmann 1888), *Stellifer naso* (Jordan 1889), *Sciades herzbergii* (Bloch 1794) and *Colomesus psittacus* (Bloch & Schneider 1801), were more frequent or found only in the northern and northeastern regions.

Knowledge gaps about Brazilian estuarine fishes

Despite recent advances in knowledge about the Brazilian estuarine fishes, long stretches of the coast still remain inadequately sampled, especially in the North and

Northeast regions. Among them are the coast of Amapá, parts of the coast of Maranhão, Ceará, Rio Grande do Norte, Paraíba, Alagoas and Sergipe. Even for some of the large estuaries of Brazil, such as those of Parnaíba, São Francisco and Doce rivers (Figure 1), basic information about fish assemblages are scarce, non-existent or in documents difficult to access. Other estuaries, located in metropolitan areas and near research centers, such as Baía da Guanabara in the state of Rio de Janeiro, were deeply degraded before being properly studied.

In addition to the collection gaps, many crucial research questions remain unanswered at the regional scale, three of which are highlighted below. One of the major questions is related to the degree of fish dependence on estuaries. Improving knowledge in this aspect is essential to support management strategies, especially for threatened, endemic or commercially targeted species. Addressing this issue is also fundamental to understand the role of estuaries in the functioning of adjacent ecosystems and in the provision of food and income. Another question, no less important and closely associated with the first, relates to the level of significance of estuaries for the maintenance of many coastal fisheries. This is due to the fact that some species of fish commercially caught offshore presumably depend upon estuaries at some stage of their life. Finally, the old and widespread hypothesis that the risk of predation in estuaries is lower than in adjacent ecosystems still remains to be adequately tested.

The high number of open questions indicates a lack of studies on estuarine fish ecology in the country and means that there is a huge potential of development for this area in the coming years. For a long time, estuarine fish studies were largely clustered in south-southeastern Brazil from the Patos Lagoon (state of Rio Grande do Sul), Guaratuba and Paranaguá Bays (state of Paraná) to Sepetiba Bay (state of Rio de Janeiro). Biology and ecology of the species are certainly better understood in this region as a result of years of activity of researchers linked to FURG, UFPR and UFRRJ. More recently, studies have been published on the estuarine fish fauna in northern Brazil and areas hitherto unexplored in the northeast of the country (e.g. Barletta et al. 2005, Giarrizzo & Krumme 2007, Ramos et al. 2011), after the settlement of ichthyologists at universities in these regions and also as a result of projects developed in partnership with foreign researchers. Currently, the deficit of ichthyologists devoted to estuarine fishes is declining as a consequence of the constant

training of human resources and their integration into new university centers scattered along the Brazilian coast.

As part of this process, some existing fish collections (e.g. CIUFES – "*Coleção Ictiológica da Universidade Federal do Espírito Santo*", 20°16'S 40°18'W) have been improved as well as new collections (e.g. CZNC – "*Coleção Zoológica Norte Capixaba*", 18°40'S 39°51'W) have been created. However, the number of fish collections, their structure and their accessibility are, generally, deficient, with many regionally-important collections without Internet interface or remote search capabilities. Another bottleneck is the scarcity of professionals dedicated to taxonomy and systematics of mostly estuarine fish groups. Finally, the need to encourage the training of qualified human resources for the curatorship of zoological collections should be emphasized, as well as the expansion and structuring of collections reinforced to provide better conditions for the study, documentation and conservation of the Brazilian estuarine fish fauna.

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Table A1. Number of genera and species for each family of fish inventoried along the Brazilian coast.

Class	Order	Family	Genus	Species
Chondrichthyes	Carcharhiniformes	Carcharhinidae	6	19
		Sphyrnidae	1	6
		Triakidae	2	5
	Chimaeriformes	Callorhynchidae	1	1
	Hexanchiformes	Hexanchidae	3	3
	Lamniformes	Alopiidae	1	1
		Lamnidae	2	3
		Odontaspididae	1	1
		Pseudocarchariidae	1	1
	Myliobatiformes	Gymnuridae	1	2
		Myliobatidae	5	8
		Potamotrygonidae	1	1
		Urotrygonidae	1	1
	Orectolobiformes	Ginglymostomatidae	1	1
		Rhincodontidae	1	1
	Pristiformes	Pristidae	1	2
	Rajiformes	Arhynchobatidae	2	5
		Dasyatidae	2	9
		Rajidae	2	2
		Rhinobatidae	2	3
	Squaliformes	Etmopteridae	1	2
		Squalidae	2	4
	Squatiniformes	Squatinidae	1	4
	Torpediniformes	Narcinidae	4	4
Actinopterygii	Albuliformes	Albulidae	1	2
	Anguilliformes	Chlopsidae	1	1
		Congridae	4	5
		Moringuidae	1	1
		Muraenesocidae	1	1
		Muraenidae	5	12
		Nettastomatidae	1	1
		Ophichthidae	11	18
	Atheriniformes	Atherinopsidae	4	14
	Aulopiformes	Chlorophthalmidae	1	1
		Paralepididae	1	1
		Synodontidae	3	5
	Batrachoidiformes	Batrachoididae	5	9
	Beloniformes	Belonidae	3	5
		Exocoetidae	4	7
		Hemiramphidae	3	7
	Beryciformes	Holocentridae	3	3
	Clupeiformes	Clupeidae	10	14
		Engraulidae	7	23
		Pristigasteridae	3	5
	Cyprinodontiformes	Anablepidae	2	5
		Poeciliidae	6	12
		Rivulidae	5	7
	Elopiformes	Elopidae	1	2

	Megalopidae	1	1
Gadiformes	Merlucciidae	1	1
	Moridae	2	2
	Phycidae	1	1
Gobiesociformes	Gobiesocidae	3	3
Lampriformes	Lampridae	1	1
	Trachipteridae	1	1
Lophiiformes	Antennariidae	2	3
	Ogcocephalidae	1	3
Mugiliformes	Mugilidae	1	5
Ophidiiformes	Bythitidae	1	1
	Carapidae	1	1
	Ophidiidae	4	4
Perciformes	Acanthuridae	1	3
	Acropomatidae	1	1
	Apogonidae	3	7
	Blenniidae	8	13
	Bramidae	1	1
	Callionymidae	2	2
	Caproidae	1	1
	Carangidae	17	36
	Centropomidae	1	5
	Chaenopsidae	1	1
	Chaetodontidae	1	3
	Cichlidae	14	29
	Cirrhitidae	1	1
	Clinidae	1	1
	Coryphaenidae	1	2
	Dactyloscopidae	3	5
	Echeneidae	3	4
	Eleotridae	5	6
	Ephippidae	1	1
	Gempylidae	2	2
	Gerreidae	5	12
	Gobiidae	17	28
	Grammatidae	1	1
	Haemulidae	7	22
	Istiophoridae	4	4
	Kyphosidae	1	2
	Labridae	6	14
	Labrisomidae	4	10
	Lobotidae	1	1
	Lophiidae	1	1
	Lutjanidae	5	12
	Malacanthidae	1	1
	Microdesmidae	2	3
	Mullidae	4	5
	Opistognathidae	2	3
	Osphronemidae	1	1
	Pempheridae	1	1

Table 1. (Continued)

Class	Order	Family	Genus	Species
		Percophidae	1	1
		Pinguipedidae	1	1
		Polynemidae	1	2
		Polyprionidae	1	1
		Pomacanthidae	3	5
		Priacanthidae	4	4
		Ptereleotridae	1	1
		Rachycentridae	1	1
		Scaridae	4	10
		Sciaenidae	21	38
		Scombridae	8	15
		Serranidae	13	31
		Sparidae	4	7
		Sphyraenidae	1	6
		Stromateidae	2	2
		Trichiuridae	1	1
		Tripterygiidae	1	1
		Uranoscopidae	1	2
		Xiphiidae	1	1
	Pleuronectiformes	Achiridae	5	10
		Bothidae	2	5
		Cynoglossidae	1	5
		Paralichthyidae	5	17
		Pleuronectidae	2	2
	Polymixiiformes	Polymixiidae	1	1
	Scorpaeniformes	Congiopodidae	1	1
		Dactylopteridae	1	1
		Peristediidae	1	1
		Scorpaenidae	3	7
		Sebastidae	1	1
		Triglidae	3	4
	Siluriformes	Ariidae	8	20
		Aspredinidae	2	3
	Synbranchiformes	Synbranchidae	2	2
	Syngnathiformes	Aulostomidae	1	1
		Fistulariidae	1	2
		Syngnathidae	8	13
	Tetraodontiformes	Balistidae	5	6
		Diodontidae	2	4
		Molidae	1	1
		Monacanthidae	4	9
		Ostraciidae	3	4
		Tetraodontidae	4	13
	Zeiformes	Zeidae	1	1
Total	36	144	425	796

Appendix 1. Name (according to Sabaj Pérez 2014) of collections used to construct the database.

California Academy of Sciences, San Francisco, California

Coleção de Peixes da Universidade Federal de Mato Grosso, Cuiabá, Mato Grosso

Coleção Ictiológica [or Laboratório de Ictiologia], Departamento de Ecologia e Recursos Naturais, Universidade Federal do Espírito Santo, Vitória, Espírito Santo

Colección Ictiológica del Centro Nacional Patagónico, Centro Nacional Patagónico - Consejo Nacional de Investigaciones Científicas y Técnicas, Puerto Madryn, Chubut

Colección Nacional de Peces, Instituto de Biología, Universidad Nacional Autónoma de México (UNAM), Mexico City

Field Museum of Natural History, Zoology Department, Chicago

Københavns Universitet, Zoologisk Museum [Zoological Museum, University of Copenhagen], Vertebrater, Fiskesamlingen, Copenhagen

Laboratório de Ictiologia de Ribeirão Preto, Departamento de Biologia, Faculdade de Filosofia, Ciências e Letras, Universidade de São Paulo, São Paulo

Museu de Biologia Professor Mello Leitão, Coleção Zoológica, Santa Tereza, Espírito Santo

Museu de Ciências e Tecnologia, Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre, Rio Grande do Sul

Museu de História Natural Capão da Imbuia, Curitiba, Paraná

Museu de Zoologia da Universidade de São Paulo, São Paulo

Museu de Zoologia da Universidade Estadual de Campinas "Adão José Cardoso", Campinas, São Paulo

Museu de Zoologia, Universidade Estadual de Londrina, Londrina, Paraná

National Museum of Natural History, Smithsonian Institution, Department of Vertebrate Zoology, Washington D.C.

National Museum of Nature and Science, Shinjuku-ku, Tokyo

Naturhistoriska riksmuseet [Swedish Museum of Natural History], Department of Vertebrate Zoology, Stockholm

Paleobiology database

Royal Ontario Museum, Department of Natural History, Toronto, Ontario

Senckenberg Forschungsinstitut und Naturmuseum [alternatively Senckenberg Research Institute and Natural History Museum], Frankfurt am Main, Hesse

South African Institute for Aquatic Biodiversity, Grahamstown

Universidade Federal do Rio Grande do Sul, Departamento de Zoologia

University of Florida, Florida Museum of Natural History, Gainesville, Florida

Appendix 2. List of references used to compile the dataset presented in this paper.

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