Fish biodiversity and conservation in South America

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The freshwater and marine fish faunas of South America are the most diverse on Earth, with current species richness estimates standing above 9100 species. In addition, over the last decade at least 100 species were described every year. There are currently about 5160 freshwater fish species, and the estimate for the freshwater fish fauna alone points to a final diversity between 8000 and 9000 species. South America also has *c.* 4000 species of marine fishes. The mega-diverse fish faunas of South America evolved over a period of >100 million years, with most lineages tracing origins to Gondwana and the adjacent Tethys Sea. This high diversity was in part maintained by escaping the mass extinctions and biotic turnovers associated with Cenozoic climate cooling, the formation of boreal and temperate zones at high latitudes and aridification in many places at equatorial latitudes. The fresh waters of the continent are divided into 13 basin complexes, large basins consolidated as a single unit plus historically connected adjacent coastal drainages, and smaller coastal basins grouped together on the basis of biogeographic criteria. Species diversity, endemism, noteworthy groups and state of knowledge of each basin complex are described. Marine habitats around South America, both coastal and oceanic, are also described in terms of fish diversity, endemism and state of knowledge. Because of extensive land use changes, hydroelectric damming, water divergence for irrigation, urbanization, sedimentation and overfishing 4–10% of all fish species in South America face some degree of extinction risk, mainly due to habitat loss and degradation. These figures suggest that the conservation status of South American freshwater fish faunas is better than in most other regions of the world, but the marine fishes are as threatened as elsewhere. Conserving the remarkable aquatic habitats and fishes of South America is a growing challenge in face of the rapid anthropogenic changes of the 21st century, and deserves attention from conservationists and policy makers.

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INTRODUCTION

The fish faunas of South America are the most diverse on Earth, with current estimates standing above 9100 species for continental fresh waters and nearshore marine waters combined, or *c.* 27% of all fishes worldwide. In addition, over the last decade, >100

additional species have been described every year. There are currently *c.* 5160 freshwater fish species described for the continent, allotted to 739 genera, 69 families and 20 orders. This number represents about one-third of all freshwater fishes worldwide, compressed into *c.* 12% of the total continental surface area of the Earth. The marine fish fauna includes > 4000 species, representing 23% of the *c.* 17 300 current valid species of marine fishes worldwide, distributed across *c.* 30 000 km of South American coastline ranging from *c.* 12°N to 55°S, and from 34° to 81°W (Miloslavich *et al.*, 2011), or *c.* 8·8% of the world's total continental coastline.

South American fish faunas formed over a lengthy period of > 100 million years, with most lineages tracing origins to Gondwana and the adjacent Tethys Sea during the formation of tropical rainforest and coral reef ecosystems (Albert *et al.*, 2011; Bowen *et al.*, 2013; Bellwood *et al.*, 2015). Tropical South America is the only region on Earth that escaped the mass extinctions and biotic turnovers associated with Cenozoic climate cooling, the formation of boreal and temperate zones at high latitudes, and aridification in many places at equatorial latitudes (Hoorn *et al.*, 2010; Bush *et al.*, 2011; Kristiansen *et al.*, 2011; Morley, 2012). Partly as a result, tropical South America has the highest diversity of any region of comparable area on Earth, for terrestrial vertebrates (Jetz & Fine, 2012), vascular plants (Kreft & Jetz, 2007), ants (Jenkins *et al.*, 2013) and many freshwater taxa (Tisseuil *et al.*, 2013). Conserving the remarkable aquatic habitats and fishes of South America is a growing challenge in the face of rapid anthropogenic changes of the 21st century. Continued habitat loss through land use changes, hydroelectric damming, water pollution, mining, urbanization and poor agricultural practices, in addition to overfishing, are causing rapid declines and threatening the extinction of many fish species in South America (Reis *et al.,* 2003; Allan *et al.*, 2005; Barletta *et al.*, 2010).

In this article a summary of the evolutionary history of the region and its fish faunas and an updated estimate for the diversity of freshwater fishes in the continent is presented. The main habitats and major river basins and marine ecosystems are also described, and the main threats to the fishes and their habitats discussed.

SPECIES RICHNESS ESTIMATES

Since the publication of the *Check List of the Freshwater Fishes of South and Central America* (CLOFFSCA) (Reis *et al.*, 2003), which listed 4475 valid species in the neotropical region, an average of 104 new species have been described every year for South America, or about two new species per week, totalling 1142 new species. In other words, *c.* 28% of the known fauna was described in just the past 11 years. Further, this rapid pace of species description is not slowing, and most reasonable estimates for the actual total number of freshwater fishes in the neotropical region exceed 8000 species (Fig. 1; Schaefer, 1998; Lundberg *et al.*, 2000; Reis *et al.*, 2003; Albert & Reis, 2011*a*; Reis, 2013). All estimates of actual species richness, however, are accompanied by broad uncertainties. Species-discovery curves usually do not contain sufficient information to reliably estimate the total richness of a biota, unless the curve has been approaching an asymptotic value for some time (Bebber *et al.*, 2007). Extrapolations based on existing data have very large error margins, unless an inventory is close to complete (*e.g.* >90% complete for birds). Synonymies and changing species concepts add additional uncertainty to species richness estimates, even for relatively well-known
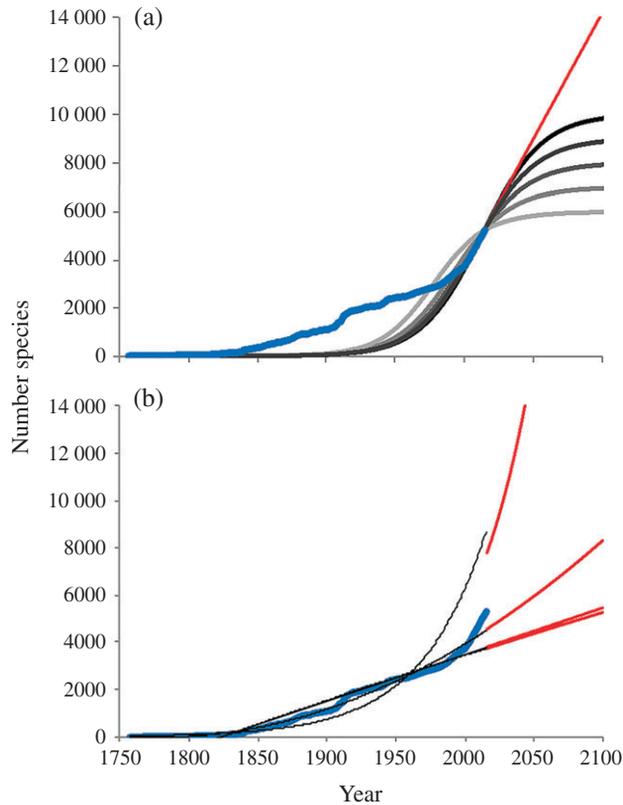
FIG. 1. Species richness projections for Neotropical freshwater fishes. Empirical data (——) for the period 1758–2015. (a). Projected estimates for 2100 for five logistic growth models, with K (carrying capacity) values varying from 6000 to 10 000 species, and r (growth) values for each model fitted to the K and 2015 species totals. Models from top (——) to bottom (——); $K = 10\,000$ species, $r = 0.059$; $K = 9000$ species, $r = 0.060$; $K = 8000$ species, $r = 0.061$; $K = 7000$ species, $r = 0.063$; $K = 6000$ species, $r = 0.068$. ——, projected species numbers assuming a constant 104 new species per year (the average for 2005–2014). (b). Projected estimates assuming growth according to four regression models (polynomial, exponential, log and linear), each fitted to the empirical data. Four curves from top to bottom are a polynomial ($y = 0.0792x^2 - 281.33x + 24984$; $r^2 = 0.98037$), exponential ($y = 2E-15e^{0.0213x}$; $r^2 = 0.88815$), log ($y = 37435\ln x - 281083$; $r^2 = 0.90642$) and linear ($y = 19.804x - 36111$; $r^2 = 0.91531$). These best-fit estimates to either equilibrium (a) or non-equilibrium (b) models indicate the fauna to be in the range 8000 to 9000 species. According to this estimate, *c.* 34–42% of the Neotropical freshwater fish fauna currently remains undescribed.

taxa such as birds and flowering plants (Scotland & Wortley, 2003; Wortley & Scotland, 2004). Extrapolating from existing data is also sensitive to idiosyncrasies of the discovery process in different taxa through time, and to the proportion of the biota used in making the extrapolation. Unfortunately, the completeness of an inventory cannot be known until all species have been described. The shape of species-discovery curves is strongly affected by both the number of species remaining to be discovered, and the vagaries of discovery effort.

Nonetheless, estimates can be made (Mora *et al.*, 2011), and based on historical trends in rates of species discovery and description, it is anticipated that the total

number of neotropical freshwater fish species is *c.* 8000–9000 (Fig. 2). As expected, the range of estimates from different models varies widely. Both equilibrium and non-equilibrium growth models with species richness values of 8000 or 9000 species, however, best fit the historical data. Among the models examined, an equilibrium logistic growth curve with asymptotic values of $K = 8000$ or 9000 species [Fig. 2(a)], and a non-equilibrium exponential model [Fig. 2(b)], best fit the historical data. A final estimate of 8000–9000 species is consistent with the recent acceleration in rates of species description, knowledge within the community regarding numbers of undescribed species for each taxonomic group and under-explored regions, and rates of synonymization. If validated by future discoveries these results mean that, as of 2015, 34–42% of neotropical freshwater fishes remain undescribed.

Numbers of marine fish diversity in South America are also impressive: about 4000 species of marine fishes are reported in the shelf, slope and deep-sea habitats in the Exclusive Economic Zone (EEZ) of the 10 countries that have coastlines in the continent (Miloslavich *et al.*, 2011). This represents about 23% of the *c.* 17 300 current valid species of marine fishes of the world (Eschmeyer, 2015). As is the case for freshwater fishes, numbers of species descriptions and of new records for South American marine waters have increased consistently in the last decades. The number of currently active marine fish taxonomists in the continent, however, is markedly lower than the number of freshwater taxonomists, a situation that naturally causes a slower pace of marine fish descriptions. With 7500 km of coastline, Brazil stands out as the most taxonomically active country in the region when marine fishes are considered, with > 40 species described since the turn of the century in groups as taxonomically and ecologically distinct as the Myxinidae (Mincarone, 2000, 2001), Elasmobranchii (Soares *et al.*, 2015), Labrisomidae (Sazima *et al.*, 2009), Serranidae (Carvalho-Filho & Ferreira, 2013) and Ophidiiformes (Nielsen *et al.*, 2015), to name just a few examples (Eschmeyer *et al.*, 2010). More than 15 species of marine fishes have also been described from Chilean waters in the last decades, most of them based on specimens collected, as expected, in regions previously insufficiently explored such as deep-sea habitats and oceanic islands (Meléndez, 2008).

Recent revisionary studies also revealed an unexpectedly hidden diversity among coastal marine South American fishes. Several reef fishes previously reported as co-occurring in both the Caribbean (central Atlantic Ocean) and Brazilian biogeographic provinces, for example, are now conclusively regarded as distinct species (Rocha, 2004), lending extra support to the hypothesis that the combined freshwater and sediment discharge of the Amazon and Orinoco River basins act together as a major biogeographic barrier for shallow reef-fish species (Collette & Rützler, 1977; Floeter *et al.*, 2008). Application of DNA barcoding and similar techniques have also increased in the last decades, most notably in countries such as Argentina and Brazil (Mabragaña *et al.*, 2012; Ribeiro *et al.*, 2012; Silveira *et al.*, 2014), but large portions of the South American coast are still virtually unexplored, especially in deep-sea habitats. Active research on marine biodiversity is also imbalanced between countries, due mostly to constraints related to different scientific traditions and, as expected, funding opportunities. Therefore, any reasonable estimate on the real diversity of marine fishes in the region cannot be made at the moment. As an example, only in 2009 it was concluded that the eastern Pacific and western Atlantic populations of the goliath grouper (genus *Epinephelus*), one of the most emblematic and large inhabitants of the New World's reef fish communities, actually belong to two distinct species, *E.*
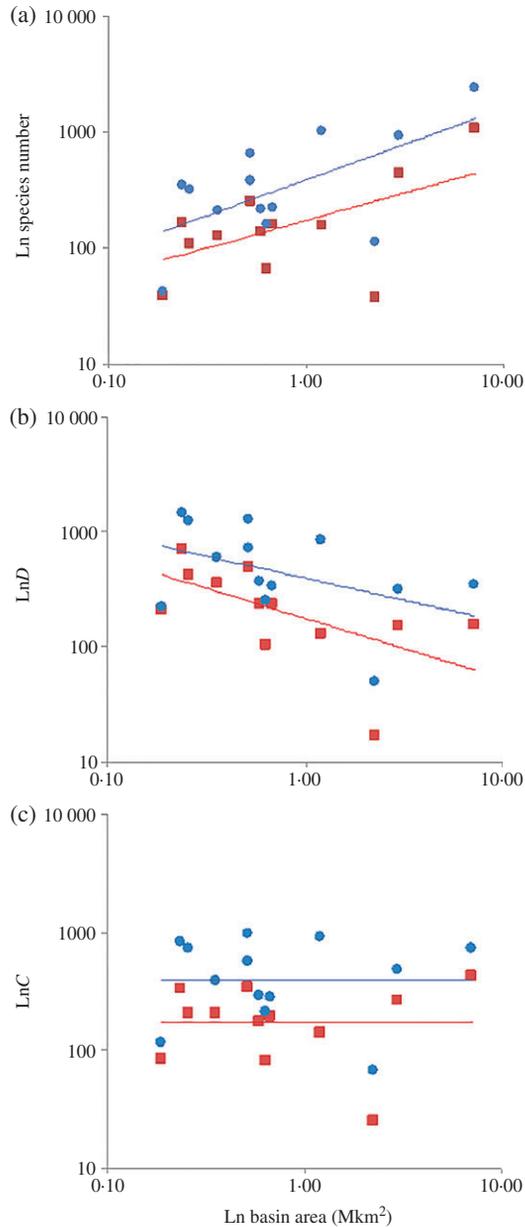
Fig. 2. Species-area relationships (SAR; ln scale) for freshwater fishes among 12 principal river basins of South America (see Fig. 3) [numbers of endemic species (■); total number of species (●)]. (a). SAR for all species ($y = 390\cdot35x^{0\cdot6174}$) and endemic species ($y = 174\cdot26x^{0\cdot476}$). Note high b-values indicate that the major river basins of South America behave more like separate biogeographic provinces than as an archipelago of islands, where speciation contributes more than dispersal to high species richness levels (Albert et al., 2011). (b). Species density (D) calculated as $D = SA^{-1}$, where S is species number and A is area, showing negative relationships, highlighting the error of this method for estimating species density (Rosenzweig, 2004) {total species ($r^2 = 0\cdot3411$), endemics ($r^2 = 0\cdot19646$)}. (c). Species density calculated from the SAR as $C = S(A^b)^{-1}$. Note when calculated this way species density is not significantly correlated with basin area (total species $r^2 = 3E-09$, endemic species $r^2 = 9\cdot6E-10$).

itajara (Lichtenstein 1822) in the Atlantic Ocean, and *E. quinquefasciatus* (Bocourt 1868) in the Pacific Ocean (Craig *et al.*, 2009).

BRIEF SUMMARY OF EVOLUTIONARY HISTORY OF THE REGION AND FAUNA

CONTINENTAL FISHES

The species rich neotropical freshwater fish fauna (NFF) evolved over $> 100 \times 10^6$ years, under the influence of numerous geological and climatic changes, involving the formation and evolution of hydrogeographic basins and other large-scale landscape formations, as well under humid tropical conditions that prevailed throughout this long interval (Albert & Reis, 2011*b*). Freshwater fishes are restricted by their physiology to rivers and lakes, and generally possess limited capacities to disperse across terrestrial or marine barriers (Albert & Carvalho, 2011). As a result there is often a close match between the evolutionary history of river basins and the fish lineages that inhabit them. The evolution of the main neotropical drainage axis (Orinoco, Amazon, Paraná-Paraguay basins) was strongly constrained by several prominent geological structures such as the South American Platform, Guyana and Brazilian Shields, Southern, Central and Northern Andes, Sub-Andean foreland, Southern and Nuclear Central America. The formation of the modern NFF was also influenced by global climate and eustatic sea-level changes (from the Upper Cretaceous and early Cenozoic greenhouse to the Late Neogene icehouse), and by global and regional tectonics (*e.g.* Lower Cretaceous Peruvian, Paleogene Incaic and Neogene Quechua 1–4 phase orogenies). Finally, regional landscape and ecological features, like altitude, stream gradient, rainfall, temperature, forest cover and water chemistry also affect the diversity of local assemblages.

Understanding the causes of species richness requires detailed species-level knowledge of geographic distributions and phylogenetic relationships. For freshwater fishes this biological information must be interpreted in the context of the geological and geographic histories of river basins. Many patterns of biodiversity and biogeography in the NFF are universal (*e.g.* latitudinal and altitudinal species gradients, species-area and species-river discharge relationships), typical of continental taxa (*e.g.* core *v.* periphery arrangement of species richness and endemism, respectively), or distinct for fishes (*e.g.* lineages generally constrained to individual basins; maximum diversity at lowest elevations). Yet other patterns emerge from the unique geographic history of the region (*e.g.* western Amazon as the area of highest diversity). Species richness and endemism are spatially heterogeneous, with highest species richness in the Amazon-Orinoco-Guyana (AOG) Core, and highest species endemism in the Continental Periphery (Albert *et al.*, 2011). The species-area relationship is more pronounced in drainage basins of the AOG Core than the Continental Periphery, indicating more within-basin diversification in the Core, and a greater influence of basin boundaries on species accumulations in the Periphery. Most species have small geographic ranges, with more than half restricted to a single ecoregion, and there is a high gamma diversity of species turnover across the landscape. These patterns result from both dispersal limitation relative to historical events (isolation across basin boundaries) and environmental (*i.e.* habitat) filtering.

In terms of species richness and total abundance, the NFF is dominated by three clades of obligate freshwater fishes, characiforms, siluriforms and cichlids, all of which originated in Gondwana during the Lower Cretaceous (145–100 million year ago, Ma), and all of which underwent evolutionary radiations during the Paleogene (66–23 Ma; López-Fernández & Albert, 2011). Palaeontological evidence from at least two modern freshwater families, Callichthyidae and Cichlidae, suggests that these teleost groups did not diversify into forms recognized as modern families and genera until the Upper Cretaceous or Lower Paleogene (Reis, 1998; Malabarba *et al.*, 2006; Malabarba *et al.*, 2010). Palaeontological and phylogenetic data suggest that the Paleocene (*c.* 65–56 Ma) radiations of freshwater teleosts filled the newly emerged proto Amazon-Orinoco river valley that drained the Sub-Andean foreland. At its maximum this basin extended over 4000 km, from headwaters in the area of the modern Pantanal in northern Paraguay or even modern Patagonia, to a mouth, which depending on sea-level stand, was located in the area of the modern llanos of south-western Venezuela or eastern Colombia (Mora *et al.*, 2010). This foreland basin may have been significantly depleted of Mesozoic fishes by a succession of marine transgressions during the Lower Cretaceous-Upper Paleocene (*c.* 80–58 Ma) and by the K/T impact (*c.* 65 Ma), and may have served as an important cradle for the diversification of basal lineages of the modern NFF.

The Upper Cretaceous and Paleogene origins of lineages and phenotypes in most modern Amazonian fishes means that these taxa are much older than the late Cenozoic formation of the modern Amazon basin *c.* 10 Ma. The rise of the Michicola Arch in the Oligocene, and of the Fitzcarrald and Vaupes Arches in the Neogene, fragmented the Sub-Andean Foreland, reorganizing the drainage network of northern South America, and establishing the great river systems of the modern continent (Hoorn *et al.*, 1995; Lundberg *et al.*, 1998; Albert & Carvalho, 2011). These hydrogeographic events sub-divided and mixed the pre-existing aquatic faunas, resulting in a complex history of speciation within and between basins, extinction and geodispersal (*i.e.* basin coalescence or range expansion) from which the modern basin-wide species pools came to be assembled. Patterns of drainage isolation and coalescence across catchments have been linked to speciation and range expansion, respectively, in many groups of freshwater fishes from tropical South America. Vicariance and geodispersal are complimentary earth history processes, each resulting in concordant biogeographic patterns among the multiple lineages that constitute a regional biota (Lieberman, 2003; Albert & Crampton, 2010). Headwater stream capture across a catchment divide involves both geodispersal and vicariance, connecting and severing portions of adjacent basins, forming routes of dispersal for some aquatic taxa and barriers to dispersal in others. Such hydrogeographic changes across catchment divides contribute to the assembly of basin-wide faunas, and also to the formation of new species.

Continental fishes are commonly classified in three divisions (Myers, 1949, 1966). The primary division includes the Ostariophysi and four additional small teleost families that originated and diversified in freshwater habitats, and were trapped in South America on its final separation from the remainder of Gondwana. The Ostariophysi comprises *c.* 30% of all living fishes and 70% of all freshwater fishes in all continents except Australia. In South America, the tetras and their allies or Characiformes (*c.* 1700 spp.), electric eels and knife fishes, or Gymnotiformes (*c.* 212 spp.), and catfishes or Siluriformes (*c.* 1915 spp.), represent 74% of all fishes in the continent. In addition to the Ostariophysi, the primary division includes three to five species of pirarucus,

including the largest freshwater fish in the continent (Arapaimidae), two species of arowanas (Osteoglossidae), six to eight species of leaf-fishes (Polycentridae) and one species of lungfish (Lepidosirenidae).

The secondary division is composed of freshwater fish families that are closely related to marine groups, but are entirely confined to continental habitats. Families in this division have also been trapped on the continent by the Gondwana break-up, and include the Cichlidae (*c.* 480 spp.), the highly threatened annual fishes (Rivulidae, *c.* 270 spp.) and the Andean Cyprinodontidae (59 spp.), and the livebearers of the families Anablepidae (17 spp.) and Poeciliidae (*c.* 250 spp.).

Completing the South American continental ichthyofauna is the peripheral division, an assemblage of mostly unrelated representatives of 28 marine teleost and elasmobranch families that have invaded fresh waters at different times during the history of the continent (Albert *et al.*, 2011; Bloom & Lovejoy, 2011). Most of these groups include one or a few species, although some can reach around 100 species, as in the silversides (Atherinidae and Atherinopsidae). Other peripheral freshwater fish groups include anchovies (Engraulidae), drums (Sciaenidae), eels (Anguillidae), flatfishes (Achiridae), gobies (Gobiidae), mullets (Mugilidae), needlefishes (Belonidae), pipefishes (Syngnathidae), puffers (Tetraodontidae), sardines (Clupeidae and Pristigasteridae), stingrays (Potamotrygonidae) and others.

MARINE FISHES

Whereas allopatry is regarded as the prevalent mode of speciation and clade diversification in freshwater fishes, parapatric or sympatric speciation driven by ecological adaptation to semi-permeable barriers may be the most common mode of speciation in marine fishes. This view, which at first seems to represent a shift from the prevailing vicariance paradigm of the 1980s and early 1990s back to the classical centre of origin and dispersion scenario of pre-cladistic times, is actually based on a host of empirical and theoretical evidence, and seems to be particularly valid for the highly diversified tropical reef-fish biota (Rocha & Bowen, 2008; Bowen *et al.*, 2013). The acknowledgement of non-vicariant processes and of dispersal and ecology as the main forces driving species diversification in marine systems also partially answers what was dubbed as 'the enigma of speciation in the sea', where physical barriers are absent or semi-permeable, and where population connectivity and dispersal through larval stages is much more widespread (Bowen *et al.*, 2013).

The South American marine fish fauna is also clearly distinct from continental waters in the sense that it has a compound macro-biogeographic origin that differs markedly in the western Atlantic and eastern Pacific coasts. That situation results from the fact that the Pacific and Atlantic Oceans are highly distinct in terms of geological history and taxonomic composition, particularly at the species level. The rise of the Panama isthmus and the consequent isolation between the Pacific and Atlantic Oceans in the northern portion of South America during the Plio-Pleistocene (*c.* 9–3 Ma; Leigh *et al.*, 2013; Montes *et al.*, 2012) also has obvious consequences for the diversification of the South American marine fish fauna. The Caribbean region is considered a hotspot of reef-fish diversity whose influence extends to the subtropical portion of the south-western Atlantic Ocean (Floeter *et al.*, 2008). Another major biogeographic component of the north Atlantic portion of South America is the combined discharge of fresh waters carried by the Amazon and Orinoco Rivers into the ocean.

The Amazon-Orinoco plume is actually one of the few relatively well-understood biogeographic barriers in the western Atlantic Ocean, acting as a filter to several coastal fishes, especially those associated with shallow reef environments (Rocha, 2003). The astonishing amount of sediment deposited by those river basins in the coastal shelf of the region also has a strong relevance on the local composition of the non-reef marine fish fauna of northern South America (Marceniuk *et al.*, 2013).

Oceanographic currents act differently on the Pacific and Atlantic coasts, and strongly influence the large-scale composition of the South American marine fish fauna. As a result of the Coriolis effect and atmospheric circulation, orientation of the Ekman spiral in both the southern Pacific and Atlantic Oceans is counter clockwise. Therefore, whereas on the Atlantic coast of South America, superficial waters (up to *c*. 100 m deep) are warm and mostly carried in a western- to southern-bound direction, on the Pacific coast the much colder Antarctic waters flow in a northerly direction along the coast, forming most of the temperate Humboldt Current. Deflection of the Humboldt Current in a westerly direction occurs approximately at the Peruvian coast, and the South American Pacific coast north of this point is basically tropical. The number of marine species in each of those regions also reflects the influence of those two distinct water masses: between 1100 and 1200 species of marine fishes are reported from both the tropical and temperate portions of the South American Pacific coast, even though the coast length of the former is about one-third shorter than the other (5100 *v*. 7800 km, respectively; Miloslavich *et al.*, 2011).

In the Atlantic, the separation of the warm tropical current (usually referred to as the Southern Equatorial Current) on the north-eastern coast of Brazil forms both the North Brazil Current, which flows mostly in a westerly direction towards the Caribbean, and the Brazil Current, which flows southward along the coast. In the southern portion of the eastern South American coast, the warm Brazil Current meets the colder, mostly sub-antarctic, Malvinas (Falklands) Current at the subtropical Atlantic convergence. A Patagonian, Argentinian, or Temperate region, mostly under the influence of the Malvinas Current, is recognizable on the southern coast of South America based on the distribution of several marine organisms, even though its northern limit might not be clear. Only *c*. 540 marine species of fishes are recorded in the temperate portion of the Atlantic coast of South America, in contrast with the *c*. 1300 species reported only for the mostly tropical Brazilian coast (Miloslavich *et al.*, 2011).

Most biogeographic studies on South American marine fishes have focused on coastal shelf waters, which presumably holds a larger biodiversity, and for which distributional and taxonomic information are much more reliable. The oceanographic and historic (geological) features described above, associated with general patterns of endemism and distributions of marine fishes and other organisms, were considered by Ekman (1953) and Briggs (1974), who provided the first modern biogeographic schemes for coastal marine regions of the world. A more recent general biogeographic and ecological scheme for coastal regions was proposed by Spalding *et al.* (2007) who summarized the distribution of benthic and pelagic biotas into a system in which South America is included in the Tropical Eastern Pacific, the Tropical Atlantic, and the Temperate South America realms. Those realms are further divided into provinces, including four in the Pacific (Tropical East Pacific, Galapagos, Juan Fernández and Desventuradas, and the Warm Temperate South-eastern Pacific) and four in the Atlantic (Tropical North-western Atlantic, North Brazil Shelf, Tropical South-western Atlantic and the Warm Temperate South-western Atlantic) coasts of South America, with the addition of

another province (the Magellanic or Magellan) that includes both the western and eastern coasts of the southern temperate tip of the continent. Briggs & Bowen (2012) further divided the Magellanic province into four distinct provinces [southern Chile, Tierra del Fuego, southern Argentina and Falkland (Malvinas) Islands] based mostly on the high endemism rates for invertebrates. They also noted a sharp distinction between a southern cold-temperate and a northern warm-temperate fauna near the Valdes Peninsula, Argentina (42°S), with five fish families (Bovichtidae, Eleginopidae, Nototheniidae, Congiopodidae and Moridae) not occurring north of this point. Similar arrangements were more recently proposed by Kulbicki *et al.* (2013), based on quantitative analyses of the global distribution of reef fishes.

In summary, biogeographic studies on South American marine fishes have so far recovered similar results in terms of broad areas, a situation that reflects a combination of historical events and the strong influence of the major oceanographic features acting in the region. One particular aspect that might still require further corroborative evidence is the relatively recent proposal, based mostly on reef-fish distributions, that the southern limit of the 'Brazilian Province' should be extended to *c.* 28°S (Floeter *et al.*, 2001, 2008; Briggs & Bowen, 2012; Kulbicki *et al.*, 2013), contrary to the more traditional hypothesis that indicates that the austral limit of the tropical western Atlantic is located at *c.* 22°S Briggs, 1974, 1995; Boschi, 2000; Menni *et al.,* 2010; Di Dario *et al.*, 2011). A more comprehensive understanding of the possible biogeographic patterns of fish distribution in the deepest parts of the marine shelf and slope off South America is also needed.

HABITATS

South America includes many of the largest rivers and river basins in the world. Three of these rivers (Amazon, Orinoco and Paraná) discharge a combined 269 000 m^3 s^{-1} into the Atlantic Ocean, or >25% of all the Earth's free flowing surface fresh waters (Allan, 1995; Vari & Malabarba, 1998). The Amazon River alone (214 000 m^3 s^{-1}) has by far the largest water discharge in the world, and the Orinoco River (33 000 m^3 s^{-1}) the third largest discharge after the Amazon and the Congo Rivers. Neotropical freshwater fishes inhabit a broad range of continental aquatic habitats, from alpine lakes and torrential rapids of the Andes, broad lowland river floodplains and seasonally flooded savannahs and estuaries, to flooded forests and deep channels of large lowland rivers and underground waterways and caverns of karst landscapes on the Brazilian Shield.

Some of the major faunal assemblages of neotropical fishes are associated with water chemistry, influenced especially by the substratum geochemistry of headwater sources, dominant vegetation cover and soil types. Sediment-rich white-water rivers originate in the Andes (*e.g.* Madeira, Marañon, Meta and Napo). Tannin-rich (tea-coloured) black-water rivers (*e.g.* Atabapo, Japurá, Negro and Tefé) originate in forested lowlands, have very low sediment loads and can have very low pH values (<4). Clear-water rivers drain the ancient and well-weathered crystalline rocks of the Guyana and Brazilian Shields (*e.g.* Tapajós, Tocantins, Ventuari and Xingu), and have low sediment loads and high transparency (Albert & Reis, 2011b; Crampton, 2011). Regional differences in water quality are also based on the chemical composition of soils and bedrock. Large zones of the Paraná and Paraguay basins drain a limestone karst platform, and these waters can be very hard with a high pH. Some lagoons in the Pantanal, locally called

baias, have high salt concentrations, and the Salado River and some tributaries of the Mar Chiquita in north-central Argentina also have brackish water.

Seasonally flooded wetlands of South America harbour an enormous diversity of specialized fishes. The Amazon Basin encompasses >300 000 km^2 of seasonal floodplains known as várzeas for white-water rivers and igapós for black-water rivers. Seasonally flooded savannahs include the llanos of the Orinoco Basin in Colombia and Venezuela with *c.* 450 000 km^2, and the Pantanal of the upper Paraguay River in border areas of Brazil, Bolivia and Paraguay, with *c.* 195 000 km^2. The drainage density in most of South America is very high with an immense diversity of small-bodied fishes inhabiting low-order terra-firme (non-floodplain) creeks and small rivers covering 98% of the landscape. The headwater tributaries of terra-firme waterways are frequently isolated from one another across low-lying catchments, reducing gene flow among populations and contributing to high levels of basin-wide endemism. Some aquatic habitats peculiar to South America do not have many species, but rather specialized and endemic species. Fishes inhabiting high altitude rivers and lakes of the Andes are highly specialized for life in fast-flowing, well-oxygenated, cold waters. The endorheic river basins of the southern cone of the continent harbour a depauperate fish fauna specialized to high salt content and frequent desiccation. Specialists can also be diverse, like the *c.* 170 species of annual fishes of the family Rivulidae that inhabit the coastal drainages of eastern South America and the São Francisco River basin. These species live in shallow, temporary habitats that dry every year, the fish spawning in the substratum before it dries completely. Early in the next rainy season the eggs hatch and the fish repopulate the water body.

SOUTH AMERICA FRESHWATER BASINS

The basin complexes included here are based on the Freshwater Ecoregion of the World (FEOW) (Abell *et al.*, 2008) grouped by hydrologic and biogeographic units (Fig. 3). All large basins were consolidated as a single basin unit in addition to adjacent coastal drainages historically connected, whereas smaller coastal basins were grouped together based on proximity and biogeographic criteria. The boundaries between the coastal units were determined based on faunal composition using shared assemblages and the presence or absence of key taxa as criteria. River basin areas were calculated using the Shuttle Radar Topography Mission (SRTM) data with flow accumulation and flow direction on a hydrologic conditioned Digital Elevation Model (DEM). For basin complexes including multiple ecoregions the sum of the areas of the ecoregions was used to calculate the total basin area.

Three large freshwater basins dominate the South American continent: the Amazon, Orinoco and Paraná-Paraguay (also called La Plata), which together encompass 11 300 000 km^2 and 3599 fish species. The Amazon Basin is the largest and most diverse freshwater basin in the world (FEOW 312, 313, 314, 315, 316, 317, 318, 319, 320, 321, 322, 323 and 324). It has 7 130 000 km^2 and discharges 214 000 m^3 s^{-1} on average (Goulding *et al.*, 2003) to the Atlantic Ocean, comprising 15–17% of the total river water on Earth. This basin drains territories of Colombia, Ecuador, Peru and Bolivia, and has its most spectacular floodplains in Brazil. Diversity of fish species in the Amazon Basin is equally impressive, as 57 families, 525 genera and 2411 species occur there. Of these, 111 genera (21%) and 1089 species (45%) are endemic to the basin. As in most of South America, the fish fauna of the Amazon

FIG. 3. Major river basins and basin complexes of South America. ▇, Amazon; ▢, East Atlantic; ▇, Guianas; ▇, Magdalena; ▇, Maracaibo-Carribean; ▇, North-east Atlantic; ▇, North-west Pacific; ▇, Orinoco; ▇, Parana-Paraguay; ▇, South-east Atlantic; ▇, Southern Cone; ▇, São Francisco; ▇, Titicaca.

Basin is dominated by several groups of ostariophysans and cichlids. Several other fish groups are also emblematic for the basin. The freshwater stingrays are not restricted to the Amazon, but their greatest diversity occurs there. The Amazon and Paraguay basins share the only South American sarcopterygian (lobed-fin) fish, the lungfish *Lepidosiren paradoxa* Fitzinger 1837, locally called pirambóia. Also very important, both evolutionarily and economically, is the pirarucu *Arapaima gigas* (Schinz 1822), the largest freshwater fish in South America. Along with the pirarucu, two species of aruanã (*Osteoglossum* spp.) represent the primitive order Osteoglossiformes in the

continent. The electric eel or poraquê *Electrophorus electricus* (L. 1766), together with the infamous piranhas, are among the most feared fishes in the basin. Finally, long-range migratory catfishes of the genera *Brachyplatystoma*, some migrating 3000–4000 km between the lower Amazon and its upper tributaries in Bolivia, Peru and Colombia to spawn, are noteworthy fishes in the Amazon Basin. The Amazon estuary and small coastal basins both south and north of the mouth have extensive areas of brackish water mangrove swamps, where banjo-catfishes of the genera *Aspredo* and *Aspredinichthys* (Aspredinidae) can be found. Large areas of the Amazon Basin, both north and south of the main river channel, are severely under sampled and will reveal a large number of undescribed species when properly sampled. Considering the proportional distribution of the different families of fishes in the basin, most of the unknown diversity will probably be found in the family Characidae and among the small-sized catfishes, especially of the families Loricariidae and Heptapteridae.

The second most diverse freshwater basin in South America is the Orinoco River (FEOW 305, 306, 307, 308 and 309). It has 1 212 000 km^2 and discharges 33 000 m^3 s^{-1} (García & Mechoso, 2005; Ffield, 2007) on average to the Atlantic Ocean, being the third largest river discharge volume in the world. This basin encompasses areas of Colombia and Venezuela, having the largest wetland in South America, the llanos with 450 000 km^2 of flooded area. Diversity in the Orinoco Basin includes 53 families, 363 genera and 1002 species of fishes. Of these, 14 genera (3·8%) and 153 species (15%) are endemic to the basin. Many fish genera and species are shared with the Amazon Basin, resulting in a comparatively lower number of endemic groups. Among the endemics, *c.* 40% are loricariid catfishes, especially of the tribe Ancistrini, like the distinctive *Neblinichthys roraima* Provenzano, Lasso & Ponte 1995 from the Neblina Mountain Range, or the recently described *Micracanthicus vandragti* Lujan & Armbruster 2011, *Soromonichthys stearleyi* Lujan & Armbruster 2011 and *Pseudolithoxus kelsorum* Lujan & Birindelli 2011. Other examples of endemics are the primitive *Lithogenes wahari* Schaefer & Provenzano 2008 (Loricariidae), the monotypic *Acanthobunocephalus nicoi* Friel 1995 (Aspredinidae) and *Ammoglanis pulex* de Pinna & Winemiller 2000 (Trichomycteridae), a tiny catfish that attains maturity at *c.* 10 mm standard length (L_S), being one of the smallest vertebrates (de Pinna & Winemiller, 2000). In the llanos there are some monotypic genera, such as the specialized killifishes *Terranatos dolichopterus* (Weitzman & Wourms 1967) and *Llanolebias stellifer* (Thomerson & Turner 1973) (Rivulidae), and the tetras *Schultzites axelrodi* Géry 1964 and *Gymnotichthys hildae* Fernández-Yépez 1950 (Characidae).

The La Plata or Paraná-Paraguay Basin in the northern end of the southern cone of the continent represents the third most diverse freshwater basin in South America (FEOW 332, 333, 342, 343, 344, 345 and 347). It is more than twice the size of the Orinoco Basin, with 2 983 000 km^2 but discharges an average 22 000 m^3 s^{-1} (Pasqualini & Depetris, 2007), two thirds of the Orinoco discharge. The La Plata Basin drains areas of Argentina, Bolivia, Brazil, Paraguay and Uruguay, possessing the second largest wetland in the continent, the Brazilian Pantanal at the border of Brazil and Paraguay. Despite being more than twice the Orinoco Basin in area, the La Plata Basin is located at higher latitudes, and includes representatives of 44 families, 242 genera and 924 species. Of these, 21 genera (8·7%) and 444 species (48%) are endemic. Some endemic genera are the monotypic *Aphyocheirodon hemigrammus* Eigenmann 1915, *Coptobrycon bilineatus* (Ellis 1911), *Lophiobrycon weitzmani* Castro, Ribeiro, Benine & Melo 2003 and *Mixobrycon ribeiroi* (Eigenmann 1907)

(Characidae), *Tembeassu marauna* Triques 1998 (Apteronotidae), and the catfishes *Merodoras nheco* Higuchi, Birindelli, Sousa & Britski 2007 (Doradidae), *Otothyropsis* with four species and *Rhinolekos* with three species (Loricariidae). Other emblematic fish species in this basin are the dourado *Salminus brasiliensis* (Cuvier 1816) and the large catfishes of the genus *Pseudoplatystoma*, highly appreciated by sport fishers. Of greatest commercial importance in the basin, however, especially in Argentina, is the sábalo *Prochilodus lineatus* (Valenciennes 1837), a migratory fish that occurs in large schools in the lower and middle Paraná River. One of the few mid-water dwellers of the genus *Corydoras*, *C. hastatus* Eigenmann & Eigenmann 1888 (Callichthyidae) and the South American lungfish *L. paradoxa* (Lepidosirenidae) represent highlights of the basin.

Besides the three large freshwater basins described above, two others are important as ichthyological biogeographic units and are considered separately. The first of those is the São Francisco Basin in north-eastern Brazil (FEOW 327), which is the fourth largest and most diverse basin in the continent, with 593 000 km^2 and an average water discharge of 2940 m^3 s^{-1} (Paredes *et al.*, 1983). Despite its large area, most of the São Francisco Basin drains semi-arid or xeric savannah-like regions, which accounts for its low water discharge rate. The São Francisco River is home to 25 families, 99 genera and 211 species of fishes. Of these, eight genera (8%) and 135 species (64%) are endemic to the basin. Among the most remarkable endemic fishes in the São Francisco Basin is the pirá-tamanduá *Conorhynchus conirostris* (Valenciennes 1840), a large, commercially important food fish and evolutionarily intriguing species that was recently removed from the family Pimelodidae and so far remains without a family assignment. Another curious and endemic, monotypic genus of the São Francisco Basin is the dorso-ventrally flattened pseudopimelodid locally known as pacamão *Lophiosilurus alexandri* Steindachner, 1876, which has been introduced in the Doce River basin to improve fisheries. Several species of characids and catfishes, especially loricariids, have been described from the upper course of the São Francisco tributaries in recent years, and it is expected that a large number of species still await to be discovered. Illustrative to such trend is the case of the dourado *Salminus franciscanus* Lima & Britski (2007) of the São Francisco Basin, a large, commercially important food fish known for centuries, which was originally described as recently as 2007 (Lima & Britski 2007). Additional remarkable taxa are the endemic, monotypic genera like the characid *Orthospinus franciscensis* (Eigenmann 1914) and the doradid *Franciscodoras marmoratus* (Lütken 1874). The São Francisco has also a large number of endemic annual killifishes (Rivulidae), most notably 30 species of the genus *Simpsonichthys* and 13 species of *Cynolebias*.

The Magdalena Basin in Colombia is the fifth largest in South America, with an area of 271 000 km^2 and an average water discharge of 7200 m^3 s^{-1} (Ducharne, 1975). In this particular case the Magdalena Basin complex includes the Sinu River (FEOW 302), which adds to the total area of 357 000 km^2. The Magdalena Basin has 36 families, 96 genera and 205 species, of which seven genera (7·3%) and 125 species (61%) are endemic. Although the Magdalena Basin is less than half the size (in km^2) of the São Francisco Basin, the two have similar numbers of genera and species. Some remarkable fishes in the Magdalena Basin are the commercially important and migratory prochilodontids *Prochilodus* and *Ichthyoelephas*, the latter endemic to the Magdalena and Atrato Rivers. Other endemic genera are *Carlastyanax* (Characidae), *Centrochir* (Doradidae), *Eremophilus* (Trichomycteridae), *Genycharax* (Characidae)

and *Grundulus* (Characidae). The monotypic *Dupouyichthys sapito* Schultz 1944 (Aspredinidae) is shared with the Maracaibo Lake basin and *Dasyloricaria* (Loricariidae) is shared with the Maracaibo and the Atrato and Tuyra Rivers. Ecologically relevant in the upper reaches of the Magdalena Basin are the mountain stream fishes that live in high-energy, highly oxygenated rivers, such as *Astroblepus* (Astroblepidae), *Chaetostoma* (Loricariidae) and *Trichomycterus* (Trichomycteridae). Despite new species of mainly characids and loricariids being described every year from the Magdalena Basin, this area is well explored taxonomically compared to other South American basins.

In addition to the above five main river basins of South America, eight other basin complexes encompass a series of smaller river catchments that are biogeographically significant and are here considered together. The Guyanas Basin (FEOW 310 and 311) is the most diverse of those areas with 49 families, 260 genera and 643 species, of which 12 genera (4·6%) and 248 species (38%) are endemic to the basin complex. Main rivers in the area are the Essequibo, Demerara, Berbice, Corantijn, Coppename, Saramaca, Maroni, Sinnamary, Approuague and Oyapock. The basin covers territories of Venezuela, Guyana, Suriname, French Guyana and Brazil, with an area of $522\,000\,km^2$. It has a large amount of Amazonian faunal components, including *E. electricus*, *L. paradoxa* and *A. gigas*. Nevertheless, it harbours a significant number of endemic taxa like two species of *Corymbophanes* (Loricariidae) in the upper Potaro, the main tributary to the Essequibo River, *Mazarunia* (Cichlidae), *Skiotocharax* (Crenuchidae), the recently described *Paulasquama callis* Armbruster & Taphorn 2011 (Loricariidae) and *Akawaio penak* Maldonado-Ocampo, López-Fernández, Taphorn, Bernard, Crampton & Lovejoy 2013 (Hypopomidae), and *Lithogenes villosus* Eigenmann 1909, a representative of the most basal genus of the Loricariidae. Other remarkable endemic genera of the Guyanas Basin are *Scissor* (Characidae), *Derhamia* (Lebiasinidae) and *Hartiella* (Loricariidae) with seven species.

The east Atlantic basin complex is entirely contained in Brazil and the main river basins are the Vaza-Barris, Itapicuru, Paraguaçu, Contas, Pardo, Jequitinhonha, Mucuri, São Mateus, Doce, Paraíba do Sul, Macaé and Macacu, totalling $523\,000\,km^2$ (FEOW 328, 329 and 352). In addition to these rivers, this basin complex includes the Guanabara Bay and several lagoon systems, especially in its southern portion. It has 25 families, 113 genera and 373 species, of which 18 genera (16%) and 251 species (67%) are endemic. Rivers in this basin contain a high number of species with basal traits, like the genera *Wertheimeria* and *Kalyptodoras* of the doradid catfishes (Arce *et al.*, 2013), the entire subfamily Delturinae of loricariid catfishes, with four species of *Delturus* and three of *Hemipsilichthys* (Reis *et al.*, 2006), and the entire trichomycterid subfamilies Copionodontinae, with three species of *Copionodon* and two of *Glaphyropoma*, and Trichogeninae, with two species of *Thichogenes* (de Pinna *et al.*, 2010). This basin is also home to *Lignobrycon myersi* (Miranda Ribeiro 1956) (Characidae), the living sister-taxon to the Eocene-Miocene fossil *Lignobrycon ligniticus* (Woodward 1898) (Malabarba, 1998). Other remarkable endemic fishes are *Nematocharax*, *Oligobrycon*, *Myxiops* and *Henochilus* (Characidae) and *Nematolebias* (Rivulidae). Despite being located in one of the most well explored regions of Brazil, numerous species of loricariids and characids have been described from this basin in the past few years.

The south-east Atlantic basin complex (FEOW 330, 331, 334 and 335) is included Brazil and a small portion of Uruguay, and the main river basins are the Ribeira de

Iguape, São João, Cubatão, Itapocu, Itajaí-Açu, Tubarão, Araranguá, Mampituba, Três Forquilhas, Maquiné and the coastal lagoon system of the Tramandaí River. In addition, the Laguna dos Patos system with its main tributaries Jacuí, Taquari, Caí, Sinos, Gravataí, Camaquã, Piratini, Jaguarão and Cebolatti, and the Lagoons Mirim and Mangueira, complete this basin complex, which is 239 000 km^2. It encompasses 29 families, 103 genera and 341 species, of which five genera (4·8%) and 165 species (48%) are endemic. Despite a relatively high number of endemic species, this region has only a few endemic genera, including *Campellolebias* (Rivulidae) with four species, the three species of *Epactionotus* and two of *Eurycheilichthys* (Loricariidae). Other relevant groups that share a few species with neighbour basins are *Jenynsia* (Anablepidae), *Parapimelodus* (Pimelodidae), *Listrura* (Trichomycteridae) and *Rachoviscus* (Characidae). The lagoon systems of Santa Catarina and Rio Grande do Sul states of Brazil, especially the Laguna dos Patos system, are very important nursery areas for various diadromous species such as mullets (*Mugil*), ariid catfishes (*Genidens*) and engraulids (*Lycengraulis*). Although this is probably the best-explored region taxonomically in South America, several new species, especially loricariids and characids, are known to exist and are being described by different authors.

The Maracaibo-Caribbean Basin complex encompasses territories of Colombia, Venezuela and Trinidad and Tobago, and basically includes coastal rivers north of the Orinoco Basin emptying in the Caribbean Sea, totalling 260 000 km^2 (FEOW 303 and 304). The largest water body in this area is Maracaibo Lake situated between the Perijá and the Mérida Andes, with its many tributary rivers, the Guasare, Palmar, Santa Ana, Catatumbo and Motatan, in addition to a series of wetlands locally called Cienegas, like the Cienega Juan Manuel and Los Patitos. Further east, there is a narrow area along the Caribbean coast with a series of short rivers, some high gradient streams in the Sierra Madre of Venezuela, and extensive mangroves, which extend east to Trinidad and Tobago. The main river basins east of the Maracaibo Basin are the Hueque, Tocuyo, Yaracuy, Tuy, Unare and the Valencia Lake. In this area there are 47 families, 168 genera and 317 species of fishes, of which six genera (3·6%) and 107 species (34%) are endemic. Noteworthy endemic taxa are the monotypic genera *Leiarius perruno* (Schultz 1944) (Pimelodidae) and *Doraops zuloagai* Schultz 1944 (Doradidae), in the Maracaibo Basin in addition to various endemic loricariid catfishes, such as a representative of the most basal lineage of the Loricariidae, *Lithogenes valencia* Provenzano, Schaefer, Baskin & Royero 2003 from Valencia Lake. Maracaibo Lake has become heavily polluted in the past decades and many mangrove areas have been destroyed or modified by coastal development and land conversion. In spite of that, various marine species spend part of their life cycle and spawn in these brackish areas.

The north-west Pacific basin complex encompasses territories of Colombia, Ecuador, Peru, Bolivia and Chile (FEOW 301, 336 and 339) and includes all river basins from the Atrato in the north, which empties into the Caribbean, to the many short, high gradient rivers on the Pacific slope of the Andes from Colombia to the region of Antofagasta in northern Chile, having a total of 682 000 km^2. The northern sector in the Chocó area of Colombia has a very high annual rainfall, and main basins included are the Atrato, Baudó, San Juan, Patia, Esmeraldas, Daute, Vinces, Tumbes and Piura further south to north Peru. The climate gets progressively drier and arid southward from the Piura Basin to Chile, and there are dozens of short, mostly intermittent rivers, dependent on

snow-melt, some being endorheic. The ichthyofauna is relatively poor and depauperate with a high degree of endemism, being richer in the north and progressively poorer southward. There are 35 families, 94 genera and 222 species of fishes, of which 23 genera (24%) and 157 species (71%) are endemic. Among endemic genera of the northern, wet portion of this basin complex are the genera *Pseudocurimata* (Curimatidae) with five species, several tetras, like the highly prized ornamental fish *Nematobrycon* with two species, in addition to the monotypic *Chilobrycon*, *Iotabrycon*, *Landonia*, *Phenacobrycon* (Characidae), and the catfish genera *Cruciglanis* (Pseudopimelodidae) and *Pseudocetopsis* (Cetopsidae). Also, most of the trans-Andean subfamily Rhoadsiinae is endemic to this area, with the two species of *Rhoadsia* and three of *Parastremma* (Characidae). Other noteworthy fishes in this area are the high mountain stream species of *Astroblepus* (Astroblepidae), *Chaetostoma* (Loricariidae) and *Trichomycterus* (Trichomycteridae). Towards the southern region, other remarkable species are the endemic silversides *Basilichthys archaeus* (Cope 1878) and *Basilichthys semotilus* (Cope 1874), the catfishes *Trichomycterus piurae* (Eigenmann 1922) and *Trichomycterus punctulatus* Valenciennes 1846 (Trichomycteridae), the cichlids *Andinocara rivulata* (Günther 1860) and *Cichlasoma festae* (Boulenger 1899) (Cichlidae), and the pupfishes *Orestias ascotanensis* Parenti 1984, *Orestias elegans* Garman 1895, *Orestias gloriae* Vila *et al.* 2012 and *Orestias parinacotensis* Arratia 1982 (Cyprinodontidae). Fish diversity in this basin complex is relatively well known and further new species are likely to be found in the northern, wet portion.

The last three basin complexes have smaller fish diversity, with > 200 fish species each. The north-east Atlantic basin complex is entirely contained in Brazil (FEOW 325 and 326) and comprises all coastal basins north of the São Francisco River to the Parnaíba River, including the Rivers Una, Ipojuca, Capibaribe, Paraíba, Curimataú, Potengi, Piranhas, Apodi, Jaguaribe, Acaraú and Parnaíba, with 638 000 km^2. This area drains arid and semi-arid areas in north-eastern Brazil known as Caatinga, and many of the rivers and its tributaries are temporary, only having running water during the rainy season. For this reason, fish diversity is small when compared to other basins of similar size, including representatives of 28 families, 90 genera and 158 species. Of these, there are no endemic genera, but 65 species (41%) are endemic to the basin complex. Endemic species in this basin are in the majority species of loricariid catfishes such as *Parotocinclus* and *Loricariichthys derbyi* Fowler 1915, other catfishes like *Auchenipterus menezesi* Ferraris & Vari 1999 (Auchenipteridae), *Hassar affinis* (Steindachner 1881) (Doradidae), *Pimelodella parnahybae* Fowler 1941 (Heptapteridae), and the Parnaíba River stingray *Potamotrygon signata* Garman 1913 (Potamotrygonidae). Most of the rivers in this basin complex suffer with extensive introduction of alien species including the tilapia *Coptodon rendalli* (Boulenger 1897) (Cichlidae), *Poecilia reticulata* Peters 1859 (Poeciliidae) and piranhas of the genera *Serrasalmus* and *Pygocentrus* (Characidae), which in many cases almost completely replaced the original fauna.

The Southern Cone basin complex is an enormous area of 2 255 000 km^2 and includes territories of Argentina, Chile and Bolivia, both on eastern and western sides of the southern Andes cordillera (FEOW 339, 340, 341, 348 and 349). Main river basins are the Dulce, Primero, Desaguadero, Salado, Colorado, Grande, Neuquen, Negro, Limay, Chubut, Deseado, Chico and Santa Cruz. Most of those basins are sediment-rich from the eroding forefront of the Andes, some are endorheic basins and many are intermittent in all or part of their courses. Very distinctive in this area is the occurrence

of extensive wetlands and brackish lake systems, the most remarkable being the Mar Chiquita in northern Argentina, which varies seasonally between 2000 and $6000 \, km^2$. Other remarkable systems are the altitude wetlands with many lagoons and salt flats (salares), most of which are endorheic and intermittent. On the western side of the Andes in Chile, there are many small river systems draining to the Pacific Ocean, the most important being the Biobío, and a spectacular multitude of freshwater and brackish lakes. Towards the southern end of this region, both in Chile and Argentina, there are many small, temporary rivers fed by snow-melt, glaciers and glacial lakes, a region very poor in fish diversity. Despite the large area, this basin complex only has 24 families, 55 genera and 110 species, of which 12 genera (22%) and 37 species (34%) are endemic. The entire family Diplomystidae, sister-group to all remaining catfishes worldwide is confined to this basin, with six species in Chile and Argentina. Another remarkable fish is the sole representative of the family Nematogenyidae, *Nematogenys inermis* (Guichenot 1848), sister taxon to the entire superfamily Loricarioidea. Several trichomycterid catfishes are endemic to this basin, including some basal groups such as the five species of *Silvinichthys* and the monotypic *Bullockia* and *Hatcheria*. Also endemic to this basin are the two species of *Percilia* and five species of *Percichthys* (Percichthyidae), the threatened naked tetra *Gymnocharacinus bergii* Steindachner 1903 (Characidae) in Argentina, and two species of the commercially important silversides *Basilichthys* (Atherinopsidae) in Chile. Outstandingly, the only two species of lampreys of South America, *Geotria australis* Gray 1851 and *Mordacia lapicida* (Gray 1851), are found in the Southern Cone river basins in Argentina and Chile, the former spending part of its life cycle in the ocean and also occurring in southern Australia and New Zealand. Finally, other fish groups typical of this region are the Galaxiidae, five species of *Aplochiton* and two *Galaxias. Galaxias maculatus* (Jenyns 1842) is a well-known anadromous fish which spawns along the Antarctic circle, larvae entering brackish and freshwater habitats in Australia, Argentina, Chile, Falkland Islands and New Zealand. A number of alien salmonid species have been introduced to this basin complex for aquaculture and are posing a significant threat to native species. Among the most important are the brook trout *Salvelinus fontinalis* (Mitchill 1814), the land-locked salmon *Salmo salar sebago* Girard 1853, the brown trout *Salmo trutta* L. 1758, the rainbow trout *Oncorhynchus mykiss* (Walbaum 1792) and the chinook salmon *Oncorhynchus tshawytscha* (Walbaum 1792) (Arismendi *et al.*, 2009).

Finally, the Titicaca Lake basin in the high elevation plains (Altiplano) of Bolivia, Chile and Peru is the smallest ($188\,000 \, km^2$) and least diverse major basin of South America (FEOW 337). The basin includes the endorheic Titicaca Lake itself located at 3800 m asl with over $8000 \, km^2$, the Lake Popoó, the Salar de Coipasa and the famous, over $10\,000 \, km^2$ Salar de Uyuni, along with all tributary streams. There are only three fish families represented in the basin, with three genera and 41 species. Despite none of the genera being endemic, 38 (93%) species are endemic to the Titicaca Basin. These include *Astroblepus stuebeli* (Wandolleck 1916) (Astroblepidae), two species of *Trichomycterus* (Trichomycteridae) and 34 species of *Orestias* (Cyprinodontidae). Most species of *Orestias* in the Titicaca Lake are now Critically Endangered or Extinct, especially from competition and predation from the lake trout *Salvelinus namaycush* (Walbaum 1792) (Salmonidae), introduced from North America.

A BRIEF OVERVIEW OF MAJOR MARINE HABITATS OF SOUTH AMERICA

South American marine habitats include a wide array of different ecosystems, ranging from the largest known continuous mangrove system of the world, in northern South America (Marceniuk *et al.*, 2013) to the depths of the abyssal plains at the border of the EEZs of most countries on both sides of the continent. Large biogenic reefs are lacking in most of the region, with the exception of the Caribbean portion of northern South America and a few isolated formations along the Brazilian coast, such as the Abrolhos Bank off the central Brazilian coast, and the Rocas Atoll, at 3°S;33°W. Tropical rocky-reef environments, however, are present on a substantial portion of the Atlantic coast and in the tropical portion of the Pacific coast north of Peru, including the Galapagos Islands (Cortés, 1997; Floeter *et al.*, 2008).

With >750 species, the southern Caribbean (in northern South America) is home to the most diverse assemblage of reef fishes in the Atlantic Ocean. This reef community is dominated by Perciformes, and endemism is high, almost 50% for the entire region (Kulbicki *et al.*, 2013). In contrast to what occurs in fresh waters, endemism in reef (and marine) fishes is low at small spatial scales. That is likely because most reef fishes have a highly dispersive pelagic larval stage that can last from a few days to a few months. During this stage, pelagic larvae can travel hundreds to thousands of kilometres, potentially connecting very distant populations (Rocha & Bowen, 2008).

On the shores of the eastern Pacific Ocean, the tropical coast of South America harbours >500 species of reef fishes, and similarly to the Caribbean, regional endemism is high (50%+, Kulbicki *et al.*, 2013). This fauna is closely related to the Caribbean: these two regions were separated by the Isthmus of Panama only *c.* 3 Ma. Here there are a few more local reef fish endemics in very isolated oceanic islands, but only a handful of species are endemic to each island (Robertson & Cramer, 2009).

The least diverse reef fish communities of the Americas are in Brazil. For a long time, the Brazilian reef fish assemblage was considered an impoverished outpost of the Caribbean, however, recent descriptions and revalidations raised the endemism level to above 10% and now the Brazilian province is recognized as separate from the Caribbean (Rocha, 2003). A total of 356 reef fishes (67 of which are endemics) are recorded for the Brazilian province (Kulbicki *et al.*, 2013). With few exceptions, the endemics are closely related to Caribbean species, and local endemism is low in isolated oceanic islands, which are impoverished outposts of the Brazilian province (Floeter *et al.*, 2008).

The Falklands (Malvinas) Islands, in the temperate portion of the South Atlantic, is one of the most important fishing grounds of the world, even though its fish diversity might be considered as relatively low (Brickle & Laptikhovsky, 2002). In the tropical Brazilian province, oceanic islands are the Trindade-Martin Vaz Archipelago, at *c.* 1160 km off the central Brazilian coast, and the Rocas Atoll, the Fernando de Noronha and Saint Peter and Saint Paul Archipelagos, all of them off the north-eastern coast of Brazil. Rocas Atoll is the only South Atlantic atoll (Longo *et al.*, 2015). Together, these island complexes harbour *c.* 23% of the reef fishes endemic to the Brazilian province (Floeter *et al.*, 2008; Pinheiro *et al.*, 2011). Taxonomic studies on most Atlantic oceanic islands are still in an early stage; the number of endemics in those systems is certainly higher, especially for cryptic species. As an example, six marine fishes have been reported as endemic to the Trindade-Martin Vaz Archipelago only

recently (Pinheiro *et al.*, 2009), including the blenny *Hypleurochilus brasil* Pinheiro *et al.*, 2013.

In the Pacific Ocean, the Galapagos Archipelago, which has a relatively well-known marine fish fauna, has *c.* 50 endemics in a total of > 550 species of shore fishes (Grove & Lavenberg, 1997; McCosker & Rosenblatt, 2010). The Galapagos are currently recognized as a distinct province in the tropical east Pacific region (Briggs & Bowen, 2012), in spite of a considerable influence of the colder Humboldt Current in terms of its fish fauna composition (McCosker & Rosenblatt, 2010). Other well known and biogeographically relevant Pacific oceanic islands are Easter Island and Juan Fernández and Desventuradas Islands, all in Chilean territory. Easter Island, located *c.* 3500 km west of the continental South American coast, has *c.* 170 species of marine fishes, 21% of which are endemics (Randall & Cea, 2010). A total of 52 species of marine fishes are reported for Juan Fernández and Desventuradas, 22 of which are endemic when both island complexes are considered (Dyer & Westneat, 2010). Desventuradas and Easter Islands, together with Salas y Gómez Islands (also on the Chilean coast), comprise the eastern province, which is included in the Central Pacific zoogeographic region (Dyer & Westneat, 2010; Kulbicki *et al.*, 2013). A close biogeographic proximity between those island complexes might be expected, since all of them are volcanic outcrops of the Easter hot line on the Nazca Plate and are basically subjected to the same macro-oceanographic features. Juan Fernández Islands, in turn, are volcanic outcrops of the Juan Fernández ridge, which extends from the Alejandro Selkirk Island to the O'Higgins seamount, located only *c.* 111 km (60 nautical miles) from the Chilean coast at Valparaiso (Dyer & Westneat, 2010). Briggs & Bowen (2012) recognized Juan Fernández Islands as a distinct province in the Tropical Indo-West Pacific region. The number of species shared by Juan Fernández and Desventuradas, including the relatively high number of endemics (Dyer & Westneat, 2010), however, suggests that they might also be included in the eastern province.

The deep sea, defined as waters and seafloor deeper than 200 m (Gage & Tyler, 1991), is the largest, least explored and possibly least understood biological environment on Earth. In South America, knowledge of the deep-reef and deep-slope fishes in general is scarce and fragmentary. Until recently, the deep sea around the continent was largely unexplored, but advances in sampling technologies and funding are increasing the opportunities for researchers to uncover the diversity of the deep ocean realm. A few regional surveys focused on deep-sea fishes have been recently conducted off Suriname and French Guyana (Uyeno *et al.*, 1983), Argentina (Nakamura, 1986), Peru (Nakaya *et al.*, 2009) and, most notably, in Brazil (Figueiredo *et al.*, 2002; Bernardes *et al.,* 2005; Costa *et al.*, 2007; Costa & Mincarone, 2010), but there are still many knowledge gaps in large slope and abyssal areas. Fishing surveys focused on the evaluation of biological parameters of fish stocks along the south-western Atlantic shelf and slope have led to significant improvements in the knowledge of the diversity and biology of deep-sea fishes. As result of these and similar initiatives, an impressive number of new distribution records has been provided and several new species were discovered in the past decade, covering a wide range of taxonomic groups, including Myxinidae (Mincarone, 2000; 2001), Scyliorhinidae (Soares *et al.*, 2015), Rajidae (Carvalho *et al.*, 2005), Anguilliformes (Melo, 2007; Melo *et al.*, 2009); Sternoptychidae (Lima *et al.*, 2011), Chiasmodontidae (Melo, 2008), Ophidiiformes (Franco *et al.*, 2007; Mincarone *et al.*, 2008; Nielsen, 2009; Nielsen *et al.*, 2009; Nielsen *et al.*, 2015), Stephanoberyciformes (Mincarone *et al.*, 2014), Gadiformes (Melo *et al.*, 2010), Ipnopidae (Franco

et al., 2009), Zoarcidae (Anderson & Mincarone, 2006; Mincarone & Anderson, 2008) and Bramidae (Carvalho-Filho *et al.*, 2009).

Despite recent efforts for improving the knowledge of deep-sea fishes off South America, deep-water diversity is still highly underestimated. For instance, for decades the crested bigscale *Poromitra crassiceps* (Günther 1878) has been the only stephanoberyciform reported in Brazilian waters (Menezes *et al.*, 2003). A recent study, however, revealed that the diversity of this group in the area is much higher, with 13 species reported so far (Mincarone *et al.*, 2014). Even some circumglobal pelagic sharks were only recently reported off Brazil, such as the goblin shark *Mitsukurina owstoni* Jordan 1898 (Holanda & Asano Filho, 2008), the kitefin shark *Dalatias licha* (Bonnaterre 1788) (Soto & Mincarone, 2001) and the megamouth shark *Megachasma pelagios* Taylor, Compagno & Struhsaker 1983 (Amorim *et al.*, 2000).

More recently, sampling with high technology gear, such as deep-sea submersibles, has resulted in the discovery of at least 32 new species and many new distribution records of deep-sea fishes in the Galapagos Islands, an area with a long history of scientific exploration (McCosker & Rosenblatt, 2010). This example only highlights the potential for new discoveries in the deep-sea environments of South America, and is in agreement with the Eschmeyer *et al.* (2010) guess that most of the presumably 800 deep-sea species awaiting formal description must live in poorly explored areas such as the ones in the continent.

THREATS

The conservation status of most South American freshwater fishes is substantially better than in many other parts of the world, although there are some problem areas. While the proportion of freshwater fishes threatened with extinction in Europe is around 37% (Freyhof & Brooks, 2011), 27% in North America (IUCN, 2014) and 27% in Africa (IUCN, 2014), only 10% of the freshwater fishes in Brazil were recently categorized as threatened (ICMBio, 2014). As all fish species in Brazil were assessed for extinction risk recently (ICMBio, 2014), this percentage can probably be extrapolated to other South American countries. There are three recent initiatives that assessed a large proportion of freshwater fishes using the criteria and categories of the International Union for Conservation of Nature (IUCN, 2012) in South America. The most ambitious of these initiatives was a partnership between the Brazilian Ministry of Environment and the IUCN, which assessed the extinction risk of all Brazilian vertebrates and select groups of invertebrates between 2009 and 2014, totalling 12 264 species, including 3130 freshwater and 1393 marine fishes.

Of the 3130 species of freshwater fishes assessed, 312 (roughly 10%) were listed in one of the threat categories: 101 as Critically Endangered (CR), two of which are probably extinct. Of these, 60 are annual fishes (Rivulidae), which are highly sensitive to habitat loss and degradation. Another 112 species were listed as Endangered (EN) and 99 as Vulnerable (VU). In addition to the 312 threatened species, 100 were categorized as Near Threatened (NT), 383 as Data Deficient (DD), 16 were Not Assessed (NA) because they had a highly peripheral distribution in Brazil, and 2319 species were categorized as Least Concern (LC). Interestingly, there are proportionally fewer species assessed as DD in the Amazon Basin (73 out of 1708) than in the remainder of Brazil (200 out of 1323), and even with all the threats, the Amazon still is the best preserved

part of South America when compared to the Atlantic coastal forest, the Cerrados or the Andean slopes. Some other interesting data on these fishes is that 1759 are endemic to Brazil, so that the Brazilian regional assessment corresponds to their global assessment. Of the assessed species, 1708 occur in the Amazon Basin, but only 80 species (4·7%) were listed as threatened, showing that the Amazon is the least impacted area on the continent. On the other hand, of the 986 species in the Atlantic Forest, 183 species (18·5%) were listed as threatened, indicating that this biome is one of the most endangered. The criteria used to assess the 312 species of freshwater fishes categorized as threatened reveals that only 33 species were placed in these categories based on population decline (criterion A), while 278 have restricted geographic ranges associated with population fragmentation, or decline in range, habitat quality, or number of individuals (criteria B and D). Species with restricted range have a higher probability of being threatened (Nogueira *et al.*, 2010), and a large percentage of the species still to be discovered will certainly fall in this situation.

The second initiative to assess extinction risk of freshwater fishes is that of the lower La Plata River basin in Argentina and Paraguay (Cappato & Yanosky, 2009; Baigún *et al.*, 2012), which assessed 185 candidate species and categorized 11 (6%) as threatened. While three species were assessed as EN and eight as VU, 49 (26%) were listed as DD, indicating that detailed information on distribution and population status is lacking for a large percentage of those species.

Finally, Colombia has also a history of assessing the extinction risk of its freshwater fishes (Mojica *et al*, 2002, 2012), using the IUCN criteria and categories. In the assessment published in 2012, 250 species (of 1435 total), were evaluated. Of those 53 (3·7%) were categorized as threatened: one Extinct (EX), one CR, four EN and 48 VU, in addition to 24 listed as NT. Contrary to the Brazilian assessment, most species (37, 70%) were assessed based on population decline, while only 16 (30%) were categorized as threatened based on restricted range and habitat degradation.

Based on the above figures, between 4 and 10% of all freshwater fishes in South America probably face some degree of extinction risk, and a large fraction of them are currently assessed as threatened because of habitat loss or degradation. Extensive land use change, hydroelectric damming and water diversion for irrigation seem to be the main types of habitat disruption, in addition to urbanization in localized areas.

A recent review of distributional records of species reported for the Brazilian EEZ, which includes a substantial portion of the south-western Atlantic Ocean and is largely equivalent to the Brazilian zoogeographic province, recognized 1393 marine species of fishes as occurring in the region. The conservation assessment conducted by the Brazilian Government to produce the new red lists using IUCN criteria indicates that two sharks (*c.* 0·1% of all marine fishes) are Regionally Extinct (RE), 2·5% of all those species are CR, 1·0% are EN, 3·6% are VU, 2·9% are NT, 13·5% are DD and 72·5% are categorized as LC. Therefore, *c.* 7% of all species reported for the Brazilian Province are threatened. Interestingly, the relative percentages of both the Threatened and NT categories are strikingly similar in the cases of Brazil and Europe, which recently also concluded a similar assessment of all marine fishes. In that continent, 7·5% of all marine species of fishes were included in one of the IUCN threat categories, whereas 2·6% were considered NT (Nieto *et al.*, 2015). Overfishing was identified as the main cause of population decline for several red-listed marine species in Brazil, followed by coastal development, habitat loss and degradation. Those were the same major threats identified in Europe (Nieto *et al.*, 2015), reinforcing the perception that threats to marine life

TABLE I. Summary of extinction risk categories of Brazilian marine fishes (source: ICMBio, 2014)

	RE	CR(PEX)	CR	EN	VU	NT	DD	LC	NA	Total
Hagfishes					1		3	1		5
Sharks/rays	2		28	8	19	13	59	33	1	163
Chimaeras							2	4		6
Bony fishes	0	1	6	6	30	27	124	972	53	1219
Total	2	1	34	14	50	40	188	1010	54	1393
Percentage	0·1	0·1	2·4	1·0	3·6	2·9	13·5	72·5	3·9	100·0

RE, regionally extinct; CR(PEX), critically endangered (probably extinct); CR, critically endangered; EN, endangered; VU, vulnerable; NT, near threatened; DD, data deficient; LC, least concern; NA, not applicable.

in general are common to different regions of the world, regardless of management strategies and legislation, both of which are notoriously lacking in Brazil (Elfes *et al.*, 2014; Di Dario *et al.*, 2015). In addition, marine protected areas (MPAs) account for only *c.* 1·5% of the Brazilian coast, whereas international agreements dictate that *c.* 10% of all ocean surface should be protected in order to ensure the viability of fish stocks for future generations (Mittermeier *et al.*, 2010; Vilar *et al.*, 2015).

With *c.* 25% of all species of the Chondrichthyes currently considered as threatened, the conservation status of sharks and rays is particularly of concern in all oceans (Dulvy *et al.*, 2014). Among the 34 species of marine fishes categorized as CR in Brazil, 28 (82·4%) are elasmobranchs, including 12 species of Carcharhiniformes, nine Rajiformes, three Squatiniformes, two Lamniformes, one Hexanchiformes and one Squaliformes (Table I). In the other threat categories, elasmobranchs were again highlighted, with eight species EN and 19 VU, totalling 55 endangered, which represents 32% of all Brazilian chondrichthyans and *c.* 56% of all marine fishes threatened with extinction in Brazil (Rosa & Gadig, 2014). The remaining threatened bony fishes are mostly represented by reef and coastal species, such as 10 Perciformes, six Labriformes and four Syngnathiformes.

Despite the absence of an extensive survey of the conservation status of the marine fish fauna in other South American countries, a similar scenario in terms of conservation and anthropogenic impacts might be expected elsewhere. In Colombia, 28 among 38 selected marine fishes are threatened according to the IUCN criteria, including the apparently endemic ariid *Notarius bonillai* (Miles 1945) and *Parasaccogaster melanomycter* (Cohen 1981), a Bythitidae (Ophidiiformes) known only from the holotype (Mejía & Acero, 2002). In this limited evaluation, the mutton snapper *Lutjanus analis* (Cuvier 1828) was the only Colombian marine fish currently classified as NT, whereas eight other species were considered as DD, including the economically important tunas *Thunnus alalunga* (Bonnaterre 1788) and *Thunnus obesus* (Lowe 1839) and the swordfish *Xiphias gladius* L. 1758. A new red list of marine Colombian fishes is currently being prepared, however, global evaluations list several Caribbean fishes that occur in Colombia as threatened, including the CR goliath grouper *Epinephelus itajara* (Sadovy de Mitcheson *et al.*, 2013).

IUCN red-list criteria have not been consistently applied to a substantial portion of the marine fish fauna in other coastal South American countries, despite their recent adoption in conservation strategies of several governments, such as in Chile

(Squeo *et al.*, 2010) and Venezuela (PROVITA, 2015). Global IUCN evaluations of all Caribbean fishes, however, are currently being done. In Argentina, Chebez & Athor (2009) tentatively recognized 163 species of marine fishes as threatened 'in some degree' in a non-governmental initiative. The elasmobranchs *Atlantoraja castelnaui* (Miranda Ribeiro 1907), *Pristis pectinata* Latham 1794, *Mustelus fasciatus* (Garman 1913), *Mustelus schmitti* Springer 1939, *Squatina argentina* (Marini 1930) and the dusky grouper *Epinephelus marginatus* (Lowe 1834), the southern bluefin tuna *Thunnus maccoyii* (Castelnau 1872), and the red porgy *Pagrus pagrus* (L. 1758) where considered as 'en peligro', a condition presumably equivalent to the IUCN's EN category. The Chilean Government is currently in the process of updating the national list of endangered species (Ministerio del Medio Ambiente, Chile). Even though not a single species of marine fish is officially recognized as threatened in Chilean territory, population declines of some commercially important species have been well documented in the past decades due to overfishing. Such is the case of the Chilean hake *Merluccius gayi* (Guichenot 1848), whose landings dramatically dropped from 120 000 t in 2004 to 40 000 t in 2007 (Arancibia & Neira, 2008), and the Patagonian toothfish (a.k.a. Chilean sea bass) *Dissostichus eleginoides* Smitt 1898, with landings dropping from an estimated 37 000 t in 1978 to *c.* 10 700 t in 2000 and a minimum of *c.* 6900 t in 1996 (FAO, 2015). Until recently, only 0·03% of the Chilean EEZ was protected as MPAs. In 2010, the Motu Motiro Hiva Marine Park was implemented in the region of the Salas y Gómez, increasing that percentage to *c.* 4·1% of the marine territory of the country (Jorquera-Jaramillo *et al.*, 2012). Finally, among the marine fish biodiversity of Venezuela, surprisingly not a single marine species was recognized as threatened in the most recent official edition of the country's red list, even though two sharks, *Negaprion brevirostris* (Poey 1868) and *Prionace glauca* (L. 1758), and the seahorse *Hippocampus erectus* Perry 1810 were categorized as NT (Lasso, 2008). Another seahorse reported for the region, *Hippocampus reidi* Ginsburg 1933 and several economically important species, such as *T. alalunga*, *T. obesus* and *X. gladius* were also considered as DD, as in the Colombian red list. As is also the case for Colombia, however, several species considered globally threatened by the IUCN were not included in those lists.

Another growing threat to the marine fish fauna of South America is the impact of invasive species, such as the salmonids *O. tshawytscha*, *Oncorhynchus kisutch* (Walbaum 1792), *O. mykiss*, *Salmo salar* L. 1758 and *S. trutta* in Chile, which are now a threat to the indigenous fauna particularly in the fjords of Chiloé and Aysen (Soto *et al.*, 2006). In the Atlantic Ocean, another invasive species that has been threatening the Caribbean reef fish fauna and is now present in Brazil is the lionfish *Pterois volitans* L. 1758. This ambush predator was introduced in the mid-1990s in Florida and is now present in the entire western Atlantic Ocean, extending even to Brazil (Ferreira *et al.*, 2015). *Pterois volitans* is very effective at consuming small reef fishes, and when this impact is added to other threats in the Atlantic Ocean, species with a certain combination of traits (such as small size and restricted distribution) are especially vulnerable (Rocha *et al.*, 2015).

LAND USE CHANGE

Land development for human use has resulted in widespread degradation of aquatic habitats in many regions of South America. Some of the most pressing problems arise from clear-cutting of tropical forests for cattle ranching and agriculture in the closed

TABLE II. Percentages of land cover classes by basin complex, based on moderate resolution imaging spectroradiometer (MODIS) satellite images

Basins	Natural land cover	Converted to agriculture	Urbanized
Amazon	87·8	12·2	0·1
East Atlantic	33·3	66·7	1·5
Guianas	97·9	2·1	0·1
Magdalena	38·4	61·6	1·1
Maracaibo-Caribbean	56·9	43·1	2·1
North-east Atlantic	57·6	42·4	0·4
North-west Pacific	83·8	16·2	0·8
Orinoco	87·4	12·6	0·3
Paraná-Paraguay	57·2	42·8	1·1
South-east Atlantic	63·5	36·5	2·3
Southern Cone	93·3	6·7	0·5
São Francisco	45·8	54·2	0·5
Titicaca	93·6	6·4	0·2

canopy forests of the Amazon Basin and the tropical savannahs and open woodlands (Cerrado) of the Brazilian shield. Neotropical dry and humid forests combined cover *c.* 830 million ha (*c.* 8·3 million km^2), which represents *c.* 47% of all tropical forests on Earth (FAO, 2000). Rates of deforestation estimated from satellite imagery for all of tropical Central and South America were *c.* 3·84 million ha year^{-1} (*c.* 38 400 km^2) from 1990 to 2000, and 3·91 million ha year^{-1} (*c.* 39 100 km^2) from 2001 to 2010 (Baccini *et al.*, 2012; Eva *et al.*, 2010; Harris *et al.*, 2012; Achard *et al.*, 2014).

Total land conversion by basin complex varies drastically, with the highest percentage of conversion concentrated in the coastal Atlantic, Magdalena and São Francisco basins, and the least conversion in the Guyanas, Southern Cone and Titicaca basins (Table II). In addition to the Amazon and the Cerrado, the newest agriculture frontiers are the Chaco of Paraguay and the llanos in Colombia, where massive amounts of savannah type environments are being targeted for commodities production, namely soy, corn and palm oil. These activities also impact marine fishes, especially those inhabiting reefs, as silted rivers carry much more sediments to the ocean decreasing habitat quality and potentially killing entire reef systems. Land conversion, especially for the production of commodities like corn and soybean, has the highest transformation footprint on the landscape. Estimates of recent land conversion rate by Jarvis *et al.* (2010) suggest that the pace shows no signs of reduction, with tropical forests, savannahs and temperate forest being the most affected in recent years. In addition to erosion, the intense use of fertilizers, herbicides and pesticides can have a severe impact on the ecology of freshwater systems and represent a significant threat to the persistence of fish populations in highly converted basins (Van den Brink *et al.*, 2006).

HYDROELECTRIC DAMMING

Hydroelectric dams cause three different types of adverse impacts on fish populations (Reis, 2013). The transformation of a flowing river into an impoundment reservoir can locally extirpate rheophilic species and cause population decline of other species. At the same time, the newly formed lake habitat can provide conditions for lentic

species to increase their population size, significantly affecting local community composition. At the scale of the river basin, hydropower projects change the hydrological regime downstream from the dam, disturbing seasonal reproductive and feeding cycles of some species, and disrupting the migratory routes of other species. The daily and weekly fluctuations of water level downstream from the dam caused by the retention of water during the periods of lesser demand of energy generation (nights and weekends), can severely impact many of the non-migratory fish species. These species generally leave the river bed during the high water season and enter the flooded forest and varzeas for feeding and spawning, usually in the flooded vegetation. The regulation of the river during the spawning season causes the desiccation and death of millions of eggs laid in the vegetation, or even the death of fishes that are retained in shallow areas that dry up over the weekend, when the energy generation demand is reduced. Contrary to most European and North American fish species, for which fish passages were originally conceived, neotropical potamodromous fishes migrate up rivers during the rainy season, passing dams through different types of fish passages, and spawning in the turbulent waters above the impoundment. Eggs are immediately carried down the river by the well-oxygenated torrent and hatch during the trip downriver. In a free-running river, larvae reach the flooded and productive floodplains where they will complete development. If a dam is placed between the spawning grounds and the floodplains, most eggs will be quickly eaten or will sink to anoxic depths as they reach the still waters of the reservoir (Godinho & Kynard, 2009; Pompeu *et al.*, 2011; Reis, 2013).

In addition to mega hydropower projects in large rivers across several countries in South America, small capacity dams have proliferated across the continent damaging small to medium sized rivers, with more than 2000 projects in the process of being licenced and constructed. Brazil alone has already built close to 500 of these small dams and has another 1650 in project stage pending licensing (ANNEL, 2015). The additional consequence of this proliferation is a widespread longitudinal connectivity fragmentation across most of the basin headwaters, having potentially severe impact by preventing faunal movements.

The extensive damming of several river systems has caused a profound change in ecosystem function, altering the sediment budget and thermal regime. Rivers like the Paraná and São Francisco (the two most dammed rivers in South America) carried significant amounts of sediments that produced rich in-channel habitats and extensive floodplain development. Both rivers now have clear waters, are sediment starved and no longer carry material to form channels or reshape their floodplains, reducing the availability and quality of in-channel habitats (Lima *et al.*, 2001, 2005; Medeiros *et al.*, 2011). In conclusion, even though hydroelectric power might be classified as low-carbon emission, it is far from being green.

URBANIZATION

Urban sprawl is intensifying in South America with eight metropolitan areas above five million inhabitants and 51 already surpassing one million inhabitants (Global Urban mapping, SEDAC University of Columbia), and an equal number of emergent cities with populations between 500 000 and 750 000 inhabitants have had an accelerated demographic growth in the past 20 years. The pressure that these urban areas impose on freshwater systems is increasing, by their insatiable need to supply

water for people, food production and industry, emissions of untreated effluents and storm water runoff, and by the indirect effect of the surrounding infrastructure. Several large metropolitan areas are located in the headwaters of their respective catchments, most notably Belo Horizonte, São Paulo, Bogotá, La Paz and Quito, and have had profound impact on the rivers that cross the metropolitan zone due to the inefficiency of sewage treatment. Both the Bogotá and Tietê Rivers are currently so contaminated by raw sewage and other effluents that they are virtually dead after passing through the urban areas. Because of the chronic deficit of sanitation infrastructure across the entire continent, the problem of river contamination is likely to grow and become an important threat to the fish fauna. Additionally, all along the coastal areas more and more land is being reclaimed for urban development, greatly affecting very sensitive habitats that harbour a large proportion of endemic fishes and decreasing the quality of several habitats, marine and freshwater alike. Just like other land use change, urbanization shows distinct patterns on the continent, where the Amazon, Guyanas and Titicaca basins show the lowest percentages of land converted to urban areas, whereas the south-east Atlantic, Maracaibo-Caribbean and east Atlantic basins have the highest degree of urbanization (Table II).

CONCLUSIONS

Despite the complex array of factors threatening South American fishes and habitats, the situation in the continental portion of South America is still significantly better than in other parts of the world. The Caribbean, in turn, seems to be the most impacted reef system on the planet. Conservation of other major marine coastal ecosystems, such as mangroves, is also critical. MPAs are notoriously lacking in the whole region, and most countries simply lack consistent fishery management strategies and effective regulations. Priorities for immediate action include completing extinction risk assessments at a continental or global level, since this step is necessary for the development of conservation action plans. The health of aquatic habitats is closely linked to what happens in nearby coastal areas, therefore both terrestrial and aquatic management plans should ideally be integrated in landscape conservation. In addition, to be effective, biodiversity data have to be integrated with on the ground conservation strategies that include all linked habitats (Abell *et al.*, 2011; Rocha *et al.*, 2014).

Also instrumental for the future of fish conservation in South America will be increasing the PhD level expertise in fish taxonomy and systematics, especially outside Brazil, improving museum facilities and inventory initiatives to uncover the undescribed fish diversity, and fostering new initiatives for on the ground conservation.

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