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Determinants of changes in fish diversity and composition in floodplain lakes in two basins in the Pantanal wetlands, Brazil

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Abstract The aim of this study was to investigate the effects of physical characteristics on fish assemblages. To this end, we studied 42 lakes distributed in two river basins of the Brazilian Pantanal: the Negro River basins in the South Pantanal and the Cuiabá River basins in the North Pantanal. We hypothesized that fish diversity and composition change significantly between these basins in response to physical differences and landscape structure (the geographical position of the basins). The alternative hypothesis was that local assemblages are distributed randomly between the two basins because of a regional homogenizing factor in the system. Our analysis suggests that the physical characteristics (lake area, depth and distance from the river margin) and the effect of geographical position of the basin were the main factors determining the organization of fish assemblages in these basins. This would indicate that regional fish diversity is not uniform over large areas of these Pantanal floodplains, but that communities close to each other are more similar than those that are further apart. Although there was a small variation between the lakes, this was not sufficient to affect the communities of both basins, either in composition or in diversity. Our study also supports the hypothesis that fish assemblages in the littoral zone of the Cuiabá River are richer and more diverse than assemblages in the corresponding area of the Negro River and that these differences

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are related to landscape characteristics. Hence, our results strongly suggest that area lake, depth, position of the basin, and smaller contribution of distance from the river margin are the key factor determining fish assemblage structure in floodplain lakes in the Cuiabá River and Negro River basins.

Keywords Species richness · Alpha diversity · Neutral theory · Neotropical ichthyofauna

Introduction

Tropical lowland rivers are more diverse than subtropical and temperate ones. South American rivers in particular host the richest freshwater fish fauna in the world and contain from 3,000 to 8,000 species (Schaefer 1998). Around 2,100 species have already been described for the Amazon basin and about 1,200 for the La Plata basin (Reis et al. 2003; Buckup et al. 2007; Langeani et al. 2009). The flood pulse and river continuum concepts have been combined to explain this high diversity using productivity gradients, landscape heterogeneity, high structural habitat complexity and seasonal hydrologic variability as determinant factors (Vannote et al. 1980; Junk et al. 1989). Floodplain rivers are indeed very dynamic, as seasonal flooding connects water bodies that are isolated during dry seasons (e. g., Florentino and Penha 2011; Freitas et al. 2013a), affecting local dynamics by increasing the ability of species to spread and re-colonize several types of water bodies (Arrington and Winemiller 2006; Dembkowski and Miranda 2013; Fernandes et al. 2014).

Lakes are very common in floodplains and increase habitat heterogeneity and dynamics in floodplain rivers. Lake morphometry (e. g., area and depth) can be expected to affect the probability of extinction of many species, since susceptibility to extinction is associated with habitat availability (Rodríguez and Lewis 1997; Miranda 2011). Furthermore, differences in water quality between lakes (e.g., dissolved oxygen, pH, temperature and turbidity) influence the distribution and habitat selection of fish species (Jackson et al. 2001; Miranda 2011; Lourenço et al. 2012). In the dry season, isolation increases differences in water quality and produces a patch mosaic of species abundance, which becomes more homogeneous during the flood period (Baginski et al. 2007; Thomaz et al. 2007; Freitas et al. 2010). Also, climatic phenomena such as heavy rains and storms may intensify flooding, while prolonged droughts increase the period when water bodies have reduced water volumes or dry up, dynamically affecting fish metacommunities (Freitas et al. 2013a; Fernandes et al. 2014).

Recently, studies have been conducted to gain an understanding of large-scale diversity patterns in freshwater fish. Many of these have shown that the high beta diversity observed is a result of multiple habitat types and that landscape heterogeneity influences the regional species pool (Arrington and Winemiller 2004; Súarez et al. 2004; Arrington et al. 2005). Fish assemblages in floodplains are nested-organized systems where effects on a large scale may influence beta diversity patterns on smaller scales (Florentino and Penha 2011; Freitas et al. 2013b). Therefore, basin-level processes could affect lake diversity. For example, Freitas et al. (2013b) showed that high beta diversity among lakes in the Solimões-Amazon-River floodplain system depends on connectivity between the lakes and the main channel. Once adjacent water bodies are connected to the main channel, there is higher probability of successful fish dispersal (Súarez et al. 2001, 2004; Fernandes et al. 2010).

Several studies on alpha diversity or the structural factors determining fish assemblages in floodplain lakes have been carried out (Rodríguez and Lewis 1997; Tejerina-Garro et al. 1998; Hoeinghaus et al. 2003; Súarez et al. 2004; Arrington and Winemiller 2006; Lourenço et al. 2012), but few have investigated the processes influencing the maintenance of fish diversity on a regional scale. The Pantanal comprises the floodplains of the Upper Paraguay River in Central South America and is one of the largest freshwater wetlands in the world, hosting 269 species of fish (Britiski et al. 2007). Its fauna is highly diverse and is adapted to a complex and dynamic aquatic system composed of rivers, seasonal streams, different types of floodplain lakes and swamps. The annual floods are the main driving force affecting fish assemblages, since water turnover in the floodplains determines the availability of habitat and food (Súarez et al. 2001; Baginski et al. 2007; Fernandes et al. 2010; Ximenes et al. 2011). This study aims to understand the structure of fish assemblages in littoral zones in two floodplain lake systems in river basins in the Pantanal with distinct geomorphologies. The Negro River basin contains lakes in depressions, while lakes in the Cuiabá River basin are mainly of the oxbow type. We hypothesized that there is a major difference in fish diversity and composition between these basins as a result of the physical differences and landscape structure, both of which are related to the geographical position of the basins. An alternative hypothesis is that the fish assemblages are randomly distributed in these two basins as a result of the flood pulse.

Materials and methods

Study area and fish collection

The study was carried out in 16 lakes in the Cuiabá River floodplain (16° 30′ to 16° 44′ S and 56° 20′ to 56° 30′ W) and 26 in the Negro River floodplain (16° 30′ to 16° 44′ S and 56° 20′ to 56° 30′ W) (Fig. 1). Most of the lakes in the former are of the oxbow type and were formed when meanders (regionally known as *corixos*) were cut off from the main river channel. In general, these lakes are within 1 to 5 km of the main river channel. Lakes in the Negro River floodplain were formed in natural depressions and are between 1 and 15 km from the river channel.

Fish were collected in March and June 2005 and September and December 2006. To ensure that the fish caught reflected the diversity of fish in the lakes, we used two different types of fishing gear: (a) where macrophytes were sparse, a 1 m^3 cube-type "throw trap" open at the top and bottom was used (Baber et al. 2002; Fernandes et al. 2010); and (b) where plant stands were dense—typically areas covered predominantly with the floating macrophytes *Eichhornia azurea*, *Eichhornia crassipes* and *Salvinia* spp—we used a 1 m^2 screen made of 1.5 mm nylon mesh with an aluminum rim. The sampling procedure involved placing the screen at the chosen point under the floating aquatic macrophytes, waiting for at least 1 min and then rapidly lifting it up (Florentino and Penha 2011). Each lake was sampled at nine points at least 5 m apart. In lakes in the Negro River floodplain, each point was sampled once using type (a) gear, but type (b) gear was also used once at sampling points with dense vegetation cover that were more than one meter deep. In lakes in the Cuiabá River floodplain, each point was sampled only once using type (b) gear.

The fish were preserved in 10 % formalin in the field and kept in this solution for at least 48 h before being transferred to a 70 % ethanol solution. All individuals were taken to the Laboratório de Ecologia e Manejo de Recursos Pesqueiros (LEMaRPE) at the Universidade Federal do Mato Grosso (UFMT), and the Laboratório de Ecologia (CInAM) at the Universidade Estadual de Mato Grosso do Sul (UEMS), and later identified using taxonomic keys (mainly Britiski et al. 2007) or by specialists. Identifications were confirmed by experts from the Zoological Museum at the Universidade de São Paulo (MZUSP) using nomenclature proposed by Reis et al. (2003). Specimens were deposited in the LEMaRPE, MZUSP, CInAM and UFMT fish collections.

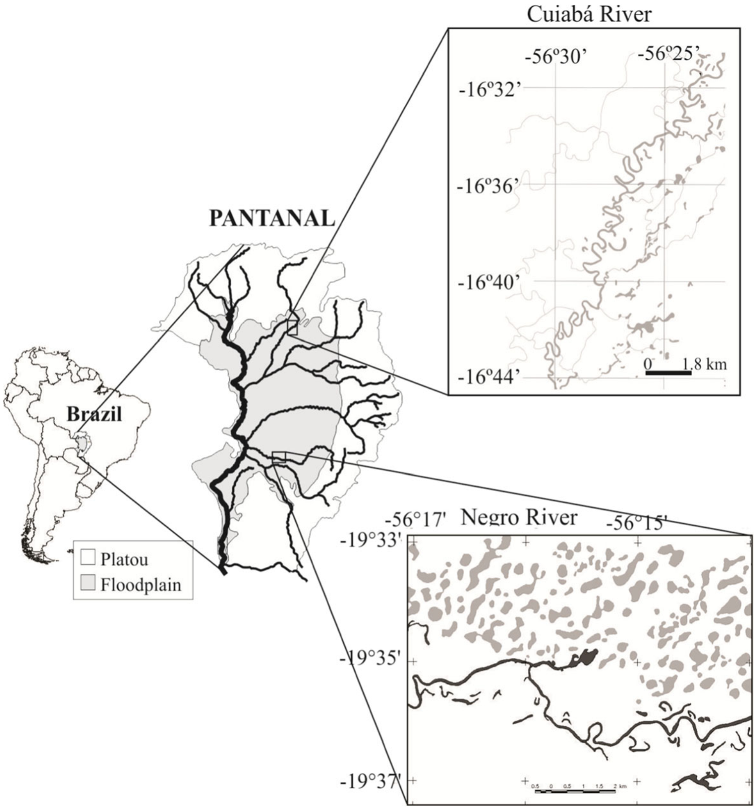
Data analysis

The Chao index was used to measure richness. Simpson's diversity index and Fisher's alpha index were used to estimate diversity. The former is suitable for a log-normal species distribution, which best fitted our dataset (Appendix: Fig. S1), while the latter assumes that the species abundance follows a log-series distribution. However, Fisher's alpha index is widely recommended (Hayek and Buzas 1997) and is robust for deviations from a log-series distribution. We used Student's t -test to check for differences in richness and diversity between basins. When the assumptions of normality and homogeneity of variances were violated even after a ($\ln x+1$) transformation, the Mann–Whitney test was used (Sokal and Rohlf 1995).

To test for differences in composition between basins we used a Permutational Multivariate Analysis of Variance (PERMANOVA) with 9999 permutations based on the Bray-Curtis dissimilarity matrix. We also applied a permutation test for homogeneity of multivariate dispersions (Anderson et al. 2006) among the lakes to test for differences in composition between fish assemblages in lakes in both basins. The test was based on the distances from each lake to the group centroid in the full-dimensional space calculated in a principal coordinates analysis (PCoA). The Bray-Curtis dissimilarity matrix was also used to perform this test on 9999 permutations. As the use of non-metric dissimilarity coefficients produced principal coordinate axes with negative eigenvalues, we computed the square root of distances prior to the analyses (Legendre and Legendre 1998).

PERMANOVA models were used to test for the effect of basin and lake physical characteristics on fish composition, richness and diversity. Bray-Curtis dissimilarity matrices were calculated using quantitative (abundance) and qualitative (presence/absence) species data. Also, a Bray-Curtis matrix was calculated using data of richness (Chao index) and diversity (Fisher's alpha). These

Fig. 1 Study area in the Cuiabá River (**a**) and Negro River (**b**) in the Brazilian Pantanal



dissimilarity matrices were used in the PERMANOVA models as response variables, while basin was included as a predictor factor and the physical characteristics of the lakes (area, distance from the river margin and depth) as covariables. As lakes are nested into basins, we constrained the permutations for each basin, allowing this factor to account for some within-group variability, which makes hypothesis testing about lake physical characteristics more powerful. All the analyses were carried out with the software environment R Core Team (2013) using the ape (Paradis et al. 2004), car (Fox and Weisberg 2011) and vegan (Oksanen et al. 2012) packages.

Results

Fish assemblage composition

A total of 14,050 individuals belonging to eight orders, 25 families and 99 species were caught in lakes in the Cuiabá River and Negro River floodplains (Appendix). Although they had lower abundance (5,581 versus 8,469 specimens caught in the Negro River floodplain), lakes in the Cuiabá River floodplain had higher total richness (80 versus 55 species). Characiformes and Perciformes were the richest orders in both basins (Cuiabá River basin: 42 and 13 species, respectively; Negro River basin: 35 and 12, respectively). Siluriformes species were only found in representative numbers in the Cuiabá River basin (14 species). With regard to abundance, Characiformes and Perciformes predominated in both basins (Cuiabá River basin: Characiformes 59.3 %, Perciformes 78.9 %; Negro River basin: Characiformes 17.5 %, Perciformes 13.1 %). Species distribution was not uniform between the basins: 45 and 19 species were unique to the Cuiabá River and Negro River basins, respectively, and 35 species occurred in both (Appendix: Fig. S2).

Species richness and diversity were significantly ($P < 0.05$) higher in the Cuiabá River basin than in the Negro River basin. There was no statistically significant difference in average abundance between the basins ($P > 0.05$), but a PERMANOVA (not using lake physical characteristics as covariates) revealed significant differences in species composition for quantitative ($F_{1,40} = 6.97$, $P = 0.001$) and qualitative ($F_{1,40} = 18.85$,

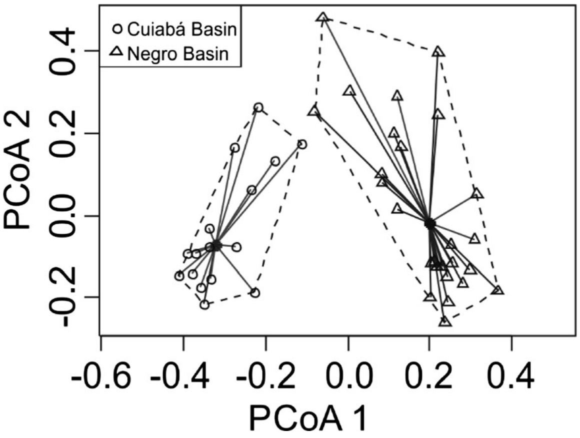


Fig. 2 Principal Coordinates Analysis (PCoA) run on a Bray-Curtis dissimilarity matrix of fish sampled in floodplain lakes in two basins in the Pantanal wetlands. The differences in dispersion relative to the group centroid (*solid circles*) for lakes in each basin can be interpreted as differences in community structure between the basins. Polygons represent maximum dispersion. *Open circles* indicate PCoA scores for lakes in the Cuiabá Basin, and *open triangles* are scores for lakes in the Negro Basin

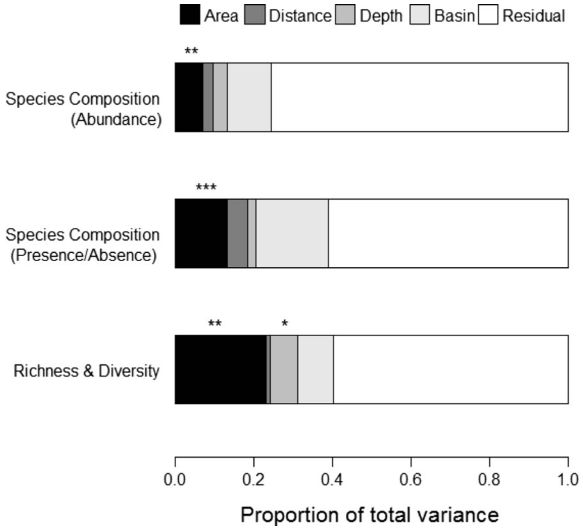


Fig. 3 Partitioning of matrix total variance of fish assemblage composition (abundance and presence/absence), richness (Chao Index) and diversity (Fisher's Alpha) into lake physical characteristics (area, distance and depth), river basin and residual components extracted from Permutational Multivariate Analysis of Variance (PERMANOVA).*: $P<0.05$, **: $P<0.01$, ***: $P<0.001$

$P=0.001$) data, indicating that the fish assemblages in each basin are distinct and that there is a high beta diversity between them (Fig. 2).

Effect of basin and lake physical characteristics on fish assemblage properties

Fish assemblage composition, richness and diversity were affected differently by basin and covariates (lake area, distance from the river margin and lake depth) in the PERMANOVAs (Fig. 3). The predictor variables together explained 24 and 39 % of the variation in the matrix of species composition (abundance and presence/absence, respectively) and 40 % of the variation in the richness and diversity matrix (Fig. 3).

Although not significant in the PERMANOVA models, basin explained most of variation in quantitative (11 %, $F_{1,37}=5.38$, $P=0.07$) and qualitative (19 %, $F_{1,37}=11.23$, $P=0.5$) composition (Fig. 3). This can be explained by the large proportion of unique species in each basin (Cuiabá River: 45 %; Negro River: 18 %) (Fig. 3). Although less variation was accounted for by area, this covariate explained almost twice the variation in qualitative composition (13 %, $F_{1,37}=7.97$, $P=0.001$) compared with quantitative composition (7 %, $F_{1,37}=3.43$, $P=0.009$), indicating that new rare species added per unit lake area play a more critical role in beta diversity within basin than changes in common species abundance. Twenty-nine species were found only in lakes larger than the average size (1319.33 m^2) (Appendix: Fig. S2), partially explaining the compositional changes for qualitative data associated with lake area. Distance from the river margin and depth explained a small quantity of variation (≤5 %, $F_{1,37}<3.5$, $P>0.05$) in quantitative as well as in qualitative composition.

In contrast to composition, most variation in richness and diversity matrix was explained by area (23 %, $F_{1,37}=14.37$, $P=0.007$) rather than by depth (7 %, $F_{1,37}=4.25$, $P=0.048$), basin (9 %, $F_{1,37}=5.74$, $P=0.9$) or distance from the river margin (1 %, $F_{1,37}=0.63$, $P=0.9$) (Fig. 3). Approximately 40 % of the species uniquely found in each basin (18 out of 45 to Cuiabá Basin and 7 out of 19 to Negro Basin) only appeared in lakes larger than the average size (Appendix: Fig. S2), highlighting the marked influence of lake area on fish richness and diversity.

Discussion

Our results corroborate the hypothesis that local fish assemblages are randomly distributed between these two basins. PCoA and PERMANOVA showed that regional fish diversity is not uniform over large areas of the Brazilian Pantanal. The results showed also that the differences in the organization of fish assemblages are a result of the heterogeneity of the landscape, which in turn is due to geomorphological processes that have created distinct types of lakes. In the Negro River basin the lakes are depression lakes while in the Cuiabá River basin they are oxbow lakes.

Estimates of Fisher's alpha, Shannon and Simpson diversity indexes were statistically higher in the Cuiabá River basin than in the Negro River basin. The simplest explanation for this is that lakes in the former basin are closer to the river margin, allowing a higher rate of colonization. More elaborate explanations could involve systems connectivity (Petry et al. 2003); lake morphometry and area (Rodríguez and Lewis 1997; Súarez et al. 2001; Arrington and Winemiller 2004, 2006; Miranda 2011); habitat selection (McMahon and Matter 2006); the probability of the species becoming extinct (MacArthur and Wilson 1967; Loreau 2000); and the type of landscape (Súarez et al. 2001; Dembkowski and Miranda 2012).

Our results strongly suggest that lake dimension is a key factor in the structuring of fish assemblages in the basins of Pantanal. Numerical abundance in lakes in the Negro River floodplain (8,469 fish, making up 54 species out of a total of 100) accounted for about 60 % of the total number of individuals (14,040). The fact that lakes in the Cuiabá River floodplain have significantly higher values for diversity and richness descriptors suggests that the Cuiabá River acts as a source of species for the complex system of floodplain lakes. Indeed, the influence of the river as a source of species for adjacent areas has been described in several studies (Súarez et al. 2001; Fernandes et al. 2009). In addition, the lakes in the Negro River floodplain investigated in this study are both large and shallow. This may result in significant variations in daily water temperature, which, associated with other factors, may limit or reduce fish diversity in what constitutes a stressful habitat. Similar findings were reported by Súarez et al. (2004), who found, in a study of fish communities in the Pantanal, that very large, shallow floodplain lakes isolated from the main river are not good species richness predictors.

The differences in the diversity patterns of the fish assemblages in the two basins, particularly in terms of species composition, may indicate that distinct processes predominate in each basin. Some species in the assemblages appear to have abundances below the minimum level needed for survival (Magurran 2005) and would therefore, at least in theory, appear to be more vulnerable to extinction (Gaggiotti and Hanski 2004; Falke et al. 2012). Nevertheless, although local extinctions may occur, regional extinctions are less likely. In small floodplain lakes, local extinctions may occur as a result of the intensification of biological interactions (Arrington et al. 2005). A relatively large proportion of fish species have this pattern of low local abundance, which may be indicative of an evolutionary pattern, according to which they use a small fraction of a niche or exhibit plasticity in the use of resources. On the other hand, low densities may help fish to elude predators and may be the end product of a long evolutionary interaction between predators and their prey (Winemiller 1989; Rodríguez and Lewis 1994; Pompeu and Godinho 2001). The pattern of rarity of the species in this study was strongly captured in the geomorphological model (lake area, depth, distance and basin position), reflecting the high diversity of the fishes distributed in the flooded areas.

Magurran and Henderson (2003), analyzing the frequency of rare species in a community, suggest that species with low abundance are usually those that occupy habitats only temporarily while migrating between their preferred habitats. However, the large differences in composition in the present study are probably a result of the connectivity of the lakes in each basin. The Negro River basin has a higher beta diversity (between lakes) because the lakes are more isolated from the river, while the Cuiabá River basin has a smaller diversity as the lakes are less isolated. Hence, species are distributed more evenly in the landscape. This was in fact corroborated by the PERMANOVA models, in which the factor lake area explained most of the variance. Another hypothesis is that lakes in the Negro River basin, being circular and far from the river, have a more homogeneous littoral region. This makes species distribution more uniform while, in the Cuiabá River basin, the format of the lakes and their proximity to the river result in an environmental gradient that leads to differences between local communities, increasing the importance of beta diversity.

We examined the hypothesis that fish assemblages in the two systems analyzed are different because the two lake complexes have distinct geomorphologies (lakes in depressions in the floodplain versus oxbow lakes). These characteristics would generate different biotic and abiotic conditions, resulting in unequal assemblages in terms of the number of individuals, relative species abundance and species composition, as not all species possess adaptations for all habitats. Our findings support this hypothesis, as fish assemblages in the littoral zone of the Cuiabá River are richer and more diverse than those of the Negro River.

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Appendix

Table 1 Abundance of fish species sampled in 16 and 26 floodplain lakes in the Cuiabá River and Negro River basins (respectively) in the Pantanal wetlands

Taxonomic position	Negro	Cuiabá	Total
Order Beloniformes			
Family Belonidae			
Potamorrhaphis eigenmanni Miranda Ribeiro, 1915	1	—	1
O. Characiformes			
F. Curimatidae			
Curimatella dorsalis (Eigenmann & Eigenmann, 1889)	2	4	6
Curimatopsis myersi Vari, 1982	50	3	53
Cyphocharax gillii (Eigenmann & Kennedy, 1903)	7	6	13
Potamorhina squamoralevis (Braga & Azpelicueta, 1983)	2	8	10
F. Anostomidae			
Abramites hypselonotus (Günther, 1868)	—	3	3
Leporinus friderici (Bloch, 1794)	—	2	2
Leporinus striatus Kner, 1858	—	108	108
Schizodon borellii (Boulenger, 1900)	—	18	18
Leporinus elongatus Valenciennes, 1850	—	1	1
F. Crenuchidae			
Characidium borellii (Boulenger, 1895)	208	—	208
Characidium laterale (Boulenger, 1895)	—	431	431
F. Gasteropelicidae			
Thoracocharax stellatus (Kner,1858)	—	7	7
F. Characidae			
Aphyocharax anisitsi Eigenmann & Kennedy, 1903	90	6	96
Aphyocharax paraguayensis Eigenmann, 1915	21	11	32
Aphyocharax rathbuni Eigenmann, 1907	198	9	207
Astyanax assuncionensis Géry, 1972	—	2	2
Bryconamericus exodon (Eigenmann, 1977)	3	—	3
Catoprion mento (Cuvier, 1819)	2	—	2
Gymnocorymbus ternetzi (Boulenger, 1815)	5	40	45
Hemigrammus marginatus (Ellis, 1911)	82	—	82
Hemigrammusulreyi (Boulenger, 1895)	1	16	17
Hyphessobrycon eques (Steindachner, 1882)	219	72	291
Metynnismola eigenmann & Kennedy, 1903	34	—	34
Moenkausia sanctaefilomenae (Steindaner, 1907)	3	284	287
Moenkausia dichroura (Kner, 1858)	1166	223	1389
Serrapinnus calliura (Boulenger, 1900)	1744	749	2493
Serrapinnus kriegi (Schindler, 1937)	1962	—	1962
Serrapinnus microdon (Eigenmann, 1915)	394	84	478
Charax leticiae (Lucena, 1987)	1	15	16
Roeboides paranensis Steindachner, 1879	51	95	146
Roeboides prognathus Boulenger, 1895	5	—	5
Serrasalmus marginatus Valenciennes, 1837	10	—	10
Serrasalmus spilopleura Kner, 1858	14	2	16
Tetragonopterus argenteus Cuvier, 1816	5	23	28
Psellogrammus kennedyi (Eigenmann, 1903)	76	78	154
Triportheus nematurus (Kner, 1858)	1	—	1
Brycon hilarii (Valenciennes, 1850)	1	—	1
Aphyocharax dentatus Eigenmann & Kennedy, 1903	—	7	7
Astyanax abramis (Jenyns, 1842)	—	2	2
Hemigrammus lunatus Durbin, 1918	—	55	55
Hemigrammus cf. ocellifer (Steindachner, 1882)	—	11	11
Hyphessobrycon elachys Weitzman, 1984	—	92	92
Markiana nigripinnis (Perugia, 1891)	—	4	4
Odontostilbe paraguayensis Eigenmann & Kennedy, 1903	—	8	8
Odontostilbe pequira (Steindachner, 1882)	—	151	151

Table 1 (continued)

Taxonomic position	Negro	Cuiabá	Total
Piabucus melanostoma (Holmberg, 1891	—	1	1
Poptella paraguayensis (Eigenmann, 1907)	—	35	35
Prionobrama paraguayensis (Eigenmann, 1914)	—	44	44
Xenurobrycon macropus Myers & Miranda Ribeiro, 1945	—	2	2
Triportheus paranensis (Günther, 1874)	—	1	1
F. Acestrorhynchidae			
Acestrorhynchus pantaneiro Menezes, 1992	2	—	2
F. Erythrinidae			
Erythrinus erythrinus (Bloch & Schneider, 1801)	1	4	5
Hoplerythrinus unitaeniatus (Agassiz, 1829)	1	—	1
Hoplias malabaricus (Bloch, 1794)	16	52	68
F. Lebiasinidae			
Pyrrhulina australis Eigenmann & Kennedy, 1903	308	426	734
O. Cyprinodontiformes			
F. Poeciliidae			
Pamphorichthys hasemani (Henn, 1916)	473	—	473
F. Rivulidae			
Rivulus punctatus Boulenger, 1895	89	—	89
Pterolebias longipinnis Garman, 1895	–	4	4
Rivulus sp.	—	21	21
O. Gymnotiformes			
F. Apteronotidae			
Apteronotus albifrons (Linnaeus, 1766)	—	1	1
F. Gymnotidae			
Gymnotus carapo Linnaeus, 1758	—	30	30
F. Hypopomidae			
Brachyhypopomus sp.	28	187	215
F. Rhamphichthyidae			
Rhamphichthys hahni (Meinken, 1937)	—	22	22
F. Sternopygidae			
Eigenmannia trilineata López & Castelo, 1966	10	452	462
Sternopygus macrurus (Bloch & Schneider, 1801)	—	76	76
O. Lepidosirniformes			
F. Lepidosirenidae			
Lepidosiren paradoxa Fitzinger, 1837	—	1	1
O. Perciformes			
F. Cichlidae			
Aequidens plagiozonatus Kullander, 1984	89	81	170
Apistogramma trifasciata (Eigenmann & Kennedy, 1903)	309	266	575
Apistogramma borellii (Regan, 1906)	426	313	739
Astronotus crassipinis Heckel, 1840	6	—	6
Bujurquina vittata (Heckel, 1840)	43	3	46
Crenicichla lepidota Heckel, 1840	7	138	145
Crenicichla vittata (Heckel, 1840)	13	4	17
Gymnogeophagus balzanii (Perugia, 1891)	10	2	12
Laetacara dorsigera (Heckel, 1840)	208	9	217
Mesonauta festivus (Heckel, 1840)	2	6	8
Satanoperca pappaterra (Heckel, 1840)	2	—	2
Apistogramma commbrae (Regan, 1906)	—	158	158
Chaetobranchopsis australis Eigenmann & Ward, 1907	—	1	1
Crenicichla semifasciata (Heckel, 1840)	—	3	3
O. Siluriformes			
F. Auchenipteridae			
Entomocorus benjamini Eigenmann, 1917	—	41	41
Parauchenipterus galeatus (Linnaeu, 1766)	—	56	56
Parauchenipterus striatulus (Steindachner, 1876)	—	24	24
F. Callichthyidae			
Callichthys callichthys (Linnaeus, 1758)	4	—	4
Corydoras aeneus (Gill, 1858)		15	15
*Corydoras hastatus*Eigenmann&Eigenmann, 1888	28	51	79
Hoplosternum pectorale (Boulenger, 1895)	—	39	39
F. Doradidae			
Anadoras weddellii (Castelnau, 1855)	—	6	6
Doras eigenmanni (Boulenger, 1895)	—	1	1
F Loricariidae			
Hypoptopoma inexspectatum (Holmberg, 1893)	—	91	91
Liposarcus anisitsi (Eigenmann& Kennedy, 1903)	—	19	19
Hypostomus spA	—	26	26
Hypostomus spB	28	—	28
Rinoloricaria parva (Boulenger, 1895)	—	67	67
F. Pimelodidae			
*Pimelodus maculatus*Lapépède, 1803	—	4	4
Pimelodella gracilis (Valenciennes, 1840)	—	5	5

Table 1 (continued)

Taxonomic position	Negro	Cuiabá	Total
Rhamdia quelen (Bleeker, 1858)	—	1	1
F. Trichomycteridae			
Ituglanis amazonicus (Steindachner, 1882)	—	2	2
O. Synbranchiformes			
F. Synbranchidae			
Synbranchus marmoratus Bloch, 1795	8	160	168
Total	8,469	5,581	14,050

Order (O) and family (F) are in bold while genus and species are italicized

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