

Effects of the interannual variations in the flood pulse mediated by hypoxia tolerance: the case of the fish assemblages in the upper Paraná River floodplain

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The effects of the duration of the floods on abiotic variables and attributes of species tolerant and intolerant to hypoxia (STH and SIH respectively) were evaluated in rivers and lakes of the upper Paraná River. Fish were sampled once a year, in six sampling stations, during the high water period from 2000 to 2003. There were overall reductions in dissolved oxygen levels and increases in transparency of water in lakes in years of moderate floods. The duration of floods influenced species differentially based on their tolerance to hypoxia: in moderate floods, richness of STH increased and numerical abundance and biomass of SIH reduced significantly. Opposite relationships were detected between dissolved oxygen and the attributes of STH and SIH. Dissolved oxygen was the best predictor of variability of STH and SIH in years of moderate floods, whereas water transparency predicted significant amounts of STH in years of short floods. Being positively affected by dissolved oxygen reductions, STH seem to take advantages in persisting in seasonally harsh lentic habitats. The incorporation of abiotic data as well the differential tolerance of species to hypoxia would improve further investigations of the effects of interannual variations in the flood pulse on tropical fish assemblages.

Os efeitos da duração da cheia sobre algumas variáveis abióticas e atributos das assembleias de peixes (espécies tolerantes e intolerantes à hipóxia, STH e SIH, respectivamente) foram avaliados em rios e lagoas do alto rio Paraná. Os peixes foram amostrados uma vez ao ano, em seis localidades, durante o período de águas altas entre 2000 e 2003. Houve reduções generalizadas nos níveis de oxigênio dissolvido e aumentos na transparência da água em lagos em anos de cheias moderadas. A duração das cheias influenciou as espécies diferencialmente em função de sua tolerância à hipóxia: em anos de cheias moderadas, a riqueza das STH aumentou e a abundância numérica e de biomassa das SIH reduziram significativamente. Relações opostas foram detectadas entre o oxigênio dissolvido e os atributos das STH e SIH. O oxigênio dissolvido foi o melhor preditor da variabilidade de STH e SIH em anos de cheias moderadas, enquanto a transparência da água explicou uma significativa proporção das STH em anos de cheias curtas. Por serem positivamente afetadas pelas reduções no oxigênio dissolvido, as STH parecem ter vantagens em persistir em ambientes lênticos sazonalmente inóspitos. A incorporação de dados abióticos bem como da tolerância diferencial das espécies à hipóxia deve aprimorar as investigações dos efeitos das variações interanuais no pulso de inundação nas assembleias de peixes tropicais.

Key words: Dissolved oxygen, Duration of floods, Lakes and rivers, Neotropical, Water transparency.

Introduction

It is widely recognized that seasonal oscillations in the hydrometric level are important for the maintenance of the biotic integrity of floodplains (Thomaz *et al.*, 2007; Agostinho *et al.*, 2009). The annual flood pulse promotes predictable alterations in limnological variables of large rivers. By increasing the hydrological connectivity among habitats, the flood pulse

exchanges matter and organisms, reduces the influence of local factors such as water supply, degree of wind exposure and area of aquatic environments (Rocha *et al.*, 2009). Therefore, the annual reduction in the spatial heterogeneity of the aquatic habitats of floodplains is a consequence of the homogenizing effect of the flood pulse (Lewis Jr. *et al.*, 2000; Thomaz *et al.*, 2007).

In tropical floodplains, the concentration of dissolved oxygen and water transparency are among those limnological

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variables that present pronounced natural variations, attributed mostly to the hydrological cycle (Lewis Jr. *et al.*, 2000; Rocha *et al.*, 2009). In periods of decreasing water levels, factors such as low depth, increased temperature, microbial respiration and vertical mixture alter the substrate, producing turbid waters depleted in oxygen in swamps, pools and lakes. The conditions of hypoxia, when oxygen concentrations attain less than 2-3 milligrams per liter of water, and anoxia, when water becomes devoid of dissolved oxygen, strongly influence composition and abundance of aquatic organisms (Rosenberger & Chapman, 1999; Nilsson & Östlund-Nilsson, 2008; Mormul *et al.*, 2012). For most fish species, a critical threshold is reached when dissolved oxygen falls below 2 mg.L⁻¹ (Okada *et al.*, 2003; Suárez *et al.*, 2003; Epaphras *et al.*, 2007). Therefore, massive mortality may occur due to fish intolerance to these conditions, if escape of these lentic habitats is not possible (Calheiros & Hamilton, 1998; Crampton, 1998). For some species, however, surviving under conditions of hypoxia or anoxia is possible through physiological, morphological and behavioral adaptations (Winemiller, 1989; Martínez *et al.*, 2009; Rosenberger & Chapman, 1999; Scarabotti *et al.*, 2011).

Decreases in transparency and oxygen content in the water may also occur in the entire floodplain in periods of high water levels, even in river channels and permanently connected lakes (Rocha *et al.*, 2009; Anjos *et al.*, 2008; Agostinho *et al.*, 2009). Although apparently conflicting, these findings of reductions in transparency and dissolved oxygen in both low and high water periods of the hydrological cycle are not mutually exclusive, but related to different processes: as the low water period progresses, the decreasing of depth increases insolation, temperature and wind-induced turbidity; whereas with the onset of the floods, the inundation of previously dry floodplain areas increases the heterotrophic metabolism under elevated temperatures, the runoff of particulate matter and the mixing of deoxygenated waters up to the water column (Lewis Jr. *et al.*, 2000; Rocha *et al.*, 2009). Despite floods may reduce the concentration of dissolved oxygen and water transparency, by enhancing hydrological connectivity they allow the displacement to more suitable habitats for those species able to detect these environmental variations (Winemiller, 1995; Crampton, 1998). In fact, reproduction and recruitment of species are differentially affected by attributes of the flood pulse, being the duration of the floods (*i.e.*, the number of days in which the river level remains above the flood stage) one of the most important (Gomes & Agostinho, 1997; Agostinho *et al.*, 2004; Bailly *et al.*, 2008). Although there is strong evidence that these responses to flood regime may vary according to the life-history traits of the species (Bailly *et al.*, 2008; Tedesco *et al.*, 2008), the relative influence of their tolerance to hypoxia is still less investigated.

In the upper Paraná River, the annual flood pulse varies in duration as a consequence of interannual differences of summer precipitation and upstream regulation by dams (Agostinho *et al.*, 2009). However, it still plays a major role in maintaining high levels of biodiversity over a stretch of 230 km between Porto Primavera Dam and Itaipu Reservoir. There, an extensive

floodplain encompasses main and secondary channels and lakes of the rivers Paraná, Baía and Ivinhema. In this study, we consider that the longer the flood, the longer the time the plain is inundated and more adverse may be environmental conditions in stagnant waters of small lakes or river backwaters. Therefore, our aim was to evaluate how the duration of the floods between the years 2000 and 2003 affects the abiotic and biotic components of the upper Paraná River floodplain, and the association between them. Dissolved oxygen, water transparency and attributes of the fish assemblage structure were selected as response variables. Sampling sites were selected in order to represent the main habitats of this plain, namely shallow lakes and river channels. We intended to answer the following questions: (i) Do selected abiotic variables and fish assemblage attributes differ between years with distinct flood duration (short or moderate floods)? (ii) Is there a relationship between selected abiotic variables and the attributes of fish assemblages? We analyzed the entire fish assemblage and the subsets of species tolerant and intolerant to hypoxia, since it is expected that the former will take advantages in persisting in the initial harsh conditions prompted by the floods. According to our expectations, oxygen content and transparency of the water, species richness, occurrence and abundance of fish species should vary according to the duration of the floods. In addition, taking into account differential tolerance to hypoxia, it should be expected differences on the relationships between the attributes of assemblage and the selected abiotic variables.

Material and Methods

Study area and the hydrological regime

The upper Paraná River floodplain (22°20' - 22°80'S; 53°10' - 53°40'W) is formed by an anastomosed network of shallow lakes, secondary and main river channels of the Paraná River and its main tributaries on the right bank, the rivers Baía and Ivinhema. The Paraná River regulates the outflow of both tributaries (Fig. 1).

Aside from interannual variations in the annual maximum level and duration of the floods, the hydrologic cycle of the upper Paraná River is historically characterized by a period of low waters from June to October and of high waters from November to May. Long lasting annual floods (up to 160 days), whose amplitudes reached up to 7.5 m were common in this system until the 1990's (Fig. 2a) (see Agostinho *et al.*, 2009 for more details). Since 1990's, when the large reservoirs were constructed just above the study area, mean water levels during high water period decreased almost 40% and therefore is quite common the occurrence of two or three flood pulses of short to moderate duration (up to 50 days) during the high water period, between January and March (Fig. 2a). Therefore, our four year analysis was limited to these months that historically record the highest hydrometric levels in the upper Paraná River (Fig. 2b). The low rainfall in the watershed and the filling of the Porto Primavera reservoir in 1998 resulted in reductions in the duration of the floods in the following years (Petry *et al.*, 2003a; Agostinho *et al.*, 2009).

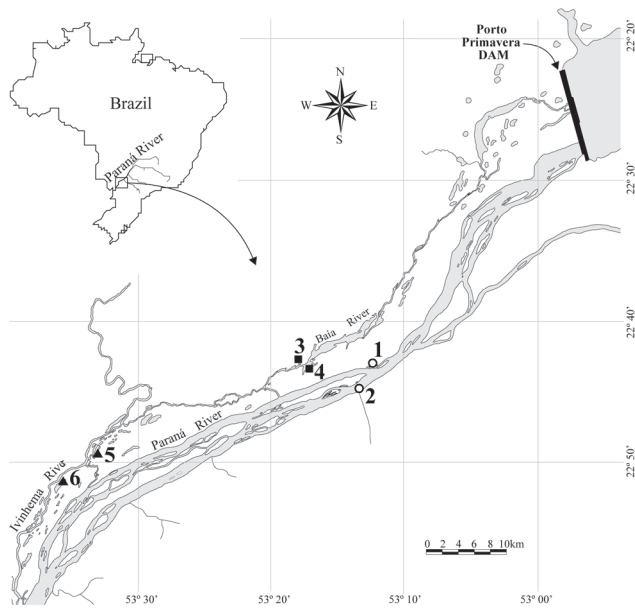


Fig. 1. Study area with location of the sampling stations in the main habitats (1 - Garças Lake, 2 - Paraná River channel, 3 - Guaraná Lake, 4 - Baía River channel, 5 - Patos Lake, and 6 - Ivinhema River channel) of the upper Paraná River floodplain.

Samplings

Fish samplings were carried out once a year (February or March), from 2000 to 2003, in the lakes Garças, Guaraná, and Patos and in the channels of the rivers Paraná, Baía and Ivinhema (Fig. 1). In these 24 samplings (four years x six sampling stations), fish were captured with gill nets with mesh sizes of 2.4, 3, 4, 5, 6, 7, 8, 10, 12, 14, and 16 cm between opposite knots. Gill nets were set from the shoreline to open water for 24 h and checked at 08:00 h, 16:00 h and 22:00 h. After identification, individuals were weighed (total weight: g). Catch per unit effort (CPUE) was used to express data on numerical abundance (number of individuals per 1,000 m² of net in 24 h; CPUE_n) and biomass (kg for 1,000 m² of net in 24 h; CPUE_b). Voucher specimens were deposited in the Ichthyological Collection of the Núcleo de Pesquisas em Limnologia, Ictiologia e Aquicultura (NUP), Universidade Estadual de Maringá, Maringá, Brazil. The abiotic variables dissolved oxygen (YSI Yellow Springs, 52CE, mg.L⁻¹) and water transparency (Secchi depth, cm) were recorded during fish samplings.

Data analysis

Variations in abiotic variables. Duration of floods was inferred based on the number of days in which the level of the upper Paraná River surpassed 350 cm (Agostinho *et al.*, 2004), increasing water into the plain throughout groundwater elevation and overflow into the nearby shallow lakes. River level varying between 351 and 507 cm were recorded up to 16 days in the year 2000, and between 350 and 414 cm up to 11

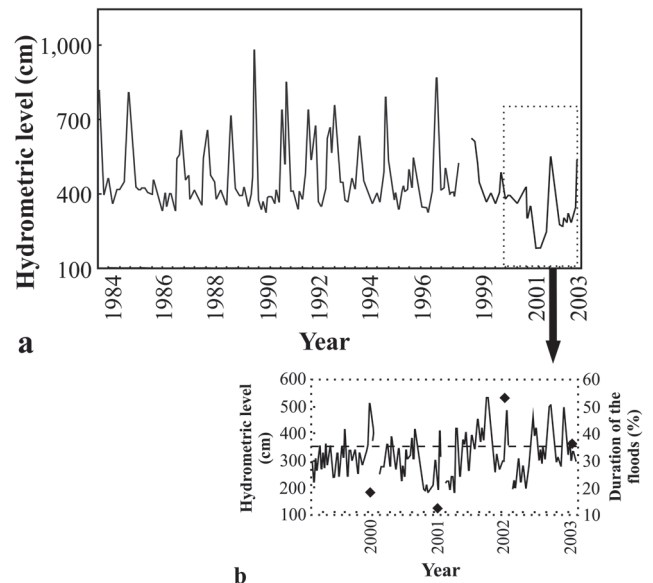


Fig. 2. Monthly (a) and daily level (b, between January and March) of the upper Paraná River recorded in Porto São José municipality. In b (right axis), the number of days between January and March, when the upper Paraná River surpassed the threshold of 350 cm (horizontal dashed line). The years 2000 and 2001 were considered as years of short floods and 2002 and 2003 as years of moderate floods. Source: National Department of Waters and Electric Energy.

days in 2001 (herein named years of short floods). The level of the upper Paraná River varied between 354 and 530 cm up to 48 days in 2002, and between 350 and 502 cm up to 32 days in 2003 (herein named years of moderate floods) (Fig. 2b).

Interannual variations in the selected abiotic variables were described and tested by two-way analyses of variance (ANOVA). Main factor were the a priori determined duration of the floods (short floods and moderate floods) and habitat (lake and river channel) and their interaction. Log₁₀ transformations were applied to response variables whenever assumptions of normality (Shapiro Wilk test) and homoscedasticity (Levene test) were not met. The post-hoc Tukey test was applied whenever significant differences were detected within the interaction term of the ANOVA (duration of the floods and habitat). The ANOVA was performed using Statistica™ (Statsoft Inc., 2007).

Variations in fish assemblage attributes. The ordination of samples based on composition and abundance of the fish assemblages was evaluated through a detrended correspondence analysis (DCA) performed with the square rooted (sqrt) CPUE_n data using PC-Ord 4.10 (McCune & Mefford, 1999). Only the first axis (DCA 1) presented eigenvalue ≥ 0.20 and therefore it was retained for interpretation (Matthews, 1998). The most important species

in the ordination were those with the highest correlations between the scores of DCA1 with the main CPUE_n matrix ($|r| > 0.4$; Correlation with main matrix).

Species richness, numerical abundance and biomass were the attributes chosen to describe the structure of the fish assemblage. As the ordination was influenced by species tolerant to hypoxia, these three assemblage attributes were either calculated for the entire fish assemblage, for this subset of species (herein named STH) and for all the other species excepting the STH, which were considered species intolerant to hypoxia (herein named SIH). STH were identified on the basis of reports in the literature (Junk *et al.*, 1983; Graham, 1997; Silva *et al.*, 1997; Almeida-Val *et al.*, 1999; Fernandes *et al.*, 1999; Graham, 1999; Val & Almeida-Val, 1999; Soares *et al.*, 2006; Casatti *et al.*, 2009; Lima Filho *et al.*, 2012), excluding those that may present reversible morphological adaptations for the uptake of atmospheric air (Scarabotti *et al.*, 2011). We adopted these criteria because we were not able to detect any morphological differentiation that could be related to aquatic surface respiration in our samples, such as development of dermal lip protuberances (*e.g.*, Winemiller, 1989; Scarabotti *et al.*, 2011).

The interannual variation of the floods (short floods and moderate floods) and habitat (lake and river channel) were considered the main sources of variation in the attributes of the structure of the entire fish assemblage (STH + SIH) and of the subsets of STH and SIH. The effect of these main sources of variation as well as their interaction on the response variables were tested through two-way ANOVA. Square-root and log₁₀ transformations were applied to response variables whenever assumptions of normality (Shapiro Wilk test) and homoscedasticity (Levene test) were not met.

Association between abiotic variables and assemblage attributes. The degree of association between abiotic variables and the attributes of the fish assemblage and of the subsets of STH and SIH was explored through Pearson correlations. Since significant correlations were detected for most attributes of the subsets, including numerical abundance, we employed the distance-based linear modeling with forward selection of predictor variables (DISTLM *forward*) to assess the relative contributions of the abiotic variables in structuring fish assemblages across lakes and river channels, during short and moderate floods (Anderson, 2003). According to Anderson (2003), DISTLM *forward* allows for significance testing of explanatory variables X for a multivariate response variable Y in the form of a resemblance matrix. The multivariate data matrices based on numerical abundance (sqrt CPUE_n) data were constructed for STH (13 species) and SIH (60 species) and the Chi-square distance was chosen as the measure of distance. The amount of variation of the subsets of STH and SIH explained by the abiotic variables was tested by fitting dissolved oxygen and water transparency sequentially with DISTLM *forward*. The low correlation between these variables ($|r| < 0.7$) suggests the absence multicollinearity in the regression analyses. Pseudo-F values in DISTLM *forward* were computed via 9,999 permutations of

the residuals under reduced models and only explanatory variables whose $p < 0.05$ were retained for interpretation. Pearson's correlations were performed using Statistica™ (Statsoft Inc., 2007) and the permutational linear modeling using DISTLM *forward* (Anderson, 2003) softwares. The level of significance assumed in all of the tests was $\alpha = 0.05$.

Results

Variations in abiotic variables

Dissolved oxygen and water transparency presented interannual variation across habitats, and in general they varied inversely over time. There was an overall temporal reduction on the levels of dissolved oxygen, more pronounced within lakes than within river channels (Figs. 3a-b). Guaraná and Patos lakes presented the lowest levels of dissolved oxygen over the study period, and the Paraná River channel, the highest. In this river, dissolved oxygen never dropped below 6.10 mg.L⁻¹. In years of moderate floods, Guaraná and Patos lakes and the Baía River channel experienced values near anoxia (0.62 mg.L⁻¹) (Fig. 3a). For water transparency, increases over the study period were observed mainly in lakes. The high amplitude of Secchi depth values within sampling stations diminished in 2003. Water transparency of the Paraná River, for example, reduced 3.68-folds (Figs. 3c-d).

The ANOVA detected a significant effect of the duration of the floods over the abiotic variables. Independently of the habitat, sampling stations presented significantly lower levels of dissolved oxygen in years of moderate floods compared to those of short floods. For water transparency however, the significance of the interaction term revealed that the effect of the duration of floods depended on the habitat. Lakes presented Secchi depth values significantly lower in years of short floods than those registered in years of moderate floods (Table 1).

Variations in fish assemblage attributes

A total of 73 fish species was recorded, with a high spatial and interannual variability in their occurrence and abundance, as shown by the ordination of samples (Fig. 4) along the first two DCA axes. The differential fish assemblage composition in lakes and Baía River at moderate floods was the main pattern evidenced by the first DCA axis. DCA1 (eigenvalue = 0.43) discriminated positively the lakes Guaraná and Patos and the Baía River in years of moderate floods, based on the occurrence of few species, but whose CPUE_n comprised almost 10% of the overall numerical abundance. All these species were tolerant to hypoxia and positively correlated ($r > 0.4$) with DCA1 (Appendix). Excepting *Pterygoplichthys ambrossetii* (Holmerg, 1893), their numerical abundance increased from two to six-folds in years of moderate floods. Species negatively correlated ($r < -0.4$) with DCA1 presented lower interannual variations in occurrence and abundance and were frequent in river channels and Garças Lake (Appendix).

Species richness varied locally from 8 to 33. River channels presented in general more species than lakes and interannual

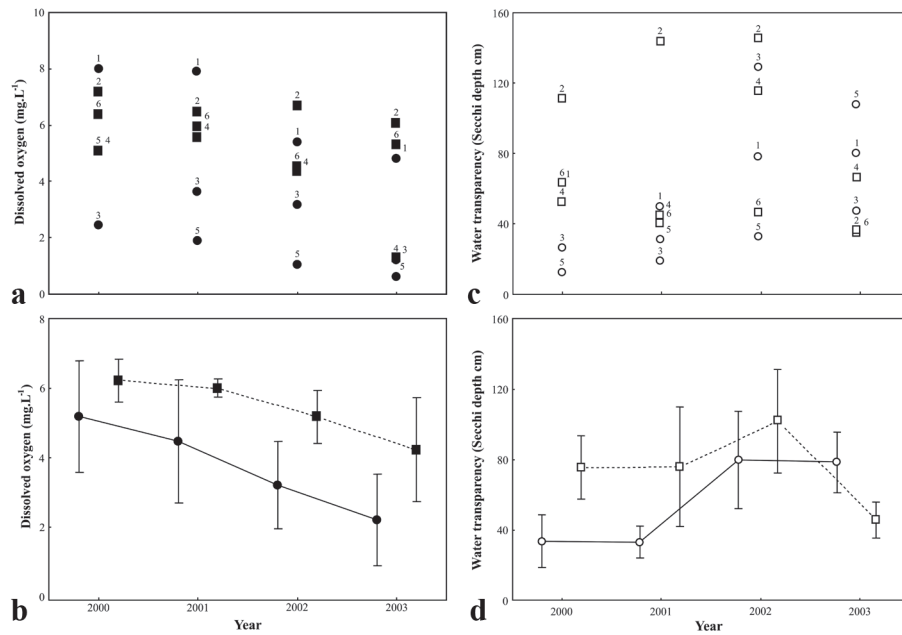


Fig. 3. Interannual variation of the absolute and mean \pm s.e. values of dissolved oxygen (a, c) and water transparency (b, d) in lakes (circle) and river channels (square) of the upper Paraná River floodplain, in years of short (2000 and 2001) and moderate (2002 and 2003) floods. Numbers 1-6 are codes of the sampling stations (see Fig. 1).

variations in species richness were higher in lakes connected to the tributaries of Paraná River, where richness dropped below 50% of their initial values. In river channels, on the other hand, an increase in species richness occurred in Paraná and Ivinhema and a decrease in Baía (Fig. 5a). Numerical abundance and biomass in general followed these tendencies (Fig. 5b-c).

A two-fold increase of the numerical abundance occurred in Garças Lake in 2001 due to the high catch of *Moenkhausia intermedia* Eigenmann, 1908 and *Steindachnerina insculpta*

(Fernández-Yépez, 1948), whereas Baía River channel experienced pronounced reductions in abundance and biomass over time (Fig. 5b-c). A slight increase in numerical abundance and biomass occurred in Ivinhema River channel during years of moderate floods. In the Paraná River channel, numerical abundance remained relatively constant and biomass

Table 1. Results of the ANOVAs that examined the main effects (duration of the floods and habitat) on the selected abiotic variables (dissolved oxygen and water transparency) in the upper Paraná River floodplain, between 2000 and 2003. d.f. = degrees of freedom; SS = sum of squares; MS = mean square; F = ratio of variance between and within groups; p = probability of Type I error.

Response variable	d.f.	SS	MS	F	p
Dissolved oxygen (mg.L ⁻¹)					
Duration of the floods (Df)	1	18.612	18.612	4.796	0.041
Habitat (H)	1	16.327	16.327	4.207	0.054
Df x H	1	0.749	0.749	0.193	0.665
Error	20	77.622	3.881		
Water transparency (log ₁₀ Secchi depth cm)					
Duration of the floods (Df)	1	0.198	0.198	3.360	0.082
Habitat (H)	1	0.148	0.148	2.509	0.129
Df x H	1	0.265	0.265	4.484	0.047
Error	20	1.180	0.059		

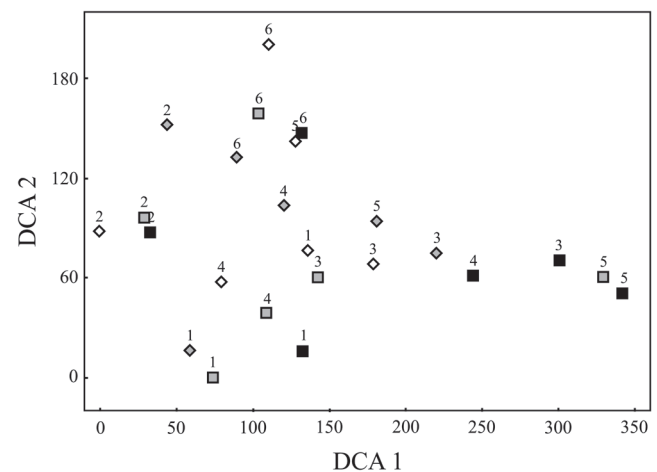


Fig. 4. Ordination of the samples of the upper Paraná River floodplain, through the detrended correspondence analysis (DCA), in years of short (diamond: 2000 white, 2001 gray) and moderate floods (square: 2002 gray, 2003 black). Numbers 1-6 are codes of the sampling stations (see Fig. 1).

diminished in years of moderate flood (Fig. 5b-c). According to the ANOVA, species richness and numerical abundance did not differ with the duration of the floods or with the habitat. Biomass, however, was significantly lower in years of moderate floods, independently of the habitat (Table 2).

Reversed patterns in species richness and numerical abundance for STH and SIH canceled each other out, resulting in these non-significant effects of the duration of floods and habitat over of these attributes for the entire fish assemblage. When species were split by the tolerance to hypoxia, the small subset of STH attained greater proportional importance in species richness over time in both habitats (Fig. 5). In years of minor floods, STH comprised almost 22 and 19% of the species richness in lakes and rivers, respectively. In years of moderate floods, however, these frequencies increased to 51% and 32% of the species richness in these habitats (Fig. 5a). The ANOVA detected a significant effect of the interannual variation of the floods over the number of STH, but not for their numerical abundance and biomass. STH were numerically more abundant and presented greater biomass in lakes than in rivers,

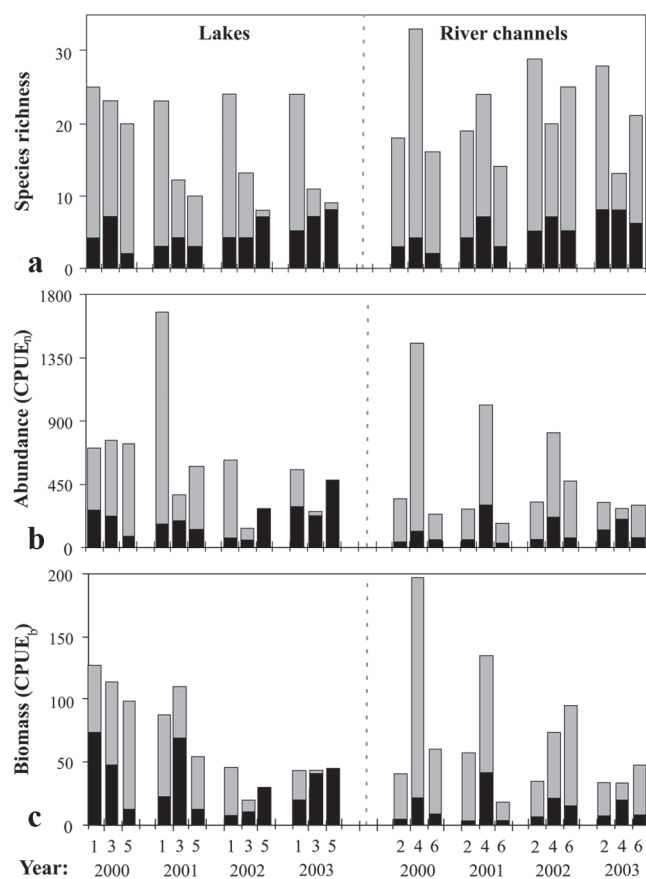


Fig. 5. Fish assemblage attributes in the main habitats of the upper Paraná River floodplain in years of short (2000 and 2001) and moderate (2002 and 2003) floods. The black area of the bars represents the proportion of STH. Numbers 1-6 on the abscissa are codes of the sampling stations (see Fig. 1).

independently of the duration of the floods. On the other hand, numerical abundance and biomass of SIH were negatively affected by duration of floods. For biomass, however, significant decreases were restricted to lakes (Fig. 5b-c; Table 2).

Association between abiotic variables and assemblage attributes

Dissolved oxygen was significantly correlated to species richness of the entire fish assemblage (Fig. 6a). Numerical abundance and biomass, however, were not significantly correlated to dissolved oxygen (Fig. 6b-c), but these results were influenced by differential responses based on tolerance to hypoxia. STH and SIH presented opposite relationships with dissolved oxygen. Sampling stations presenting low levels of dissolved oxygen attained in general the greater values of these three attributes for STH (Fig. 6d-f) and the lower for SIH (Fig. 6g-i). Water transparency, however, were not significantly correlated neither with attributes of the entire fish assemblages nor with attributes of the subsets of STH and SIH ($p \geq 0.110$).

The distance-based linear modeling revealed that dissolved oxygen explained more variation across fish assemblages than water transparency, but their effects depended on the duration of floods and habitat (Table 3). In years of moderate floods, dissolved oxygen was a better predictor of STH in lakes and of SIH in river channels, explaining high amounts of their variations in species composition and abundance (59.4 and 38.1%, respectively). In years of short floods, however, water transparency was the significant predictor of STH, explaining 39.4% of their variation in river channels.

Discussion

Duration of floods explained a great amount of variation in abiotic variables and the attributes of fish assemblages across the upper Paraná River floodplain. According to the initial expectations, the interannual variations in the flood pulse affected differentially species based on their tolerance to hypoxia. The representativeness of the species able to cope with the limitations imposed by the low dissolved oxygen levels increased in years of moderate floods, especially in lakes, whereas SIH decreased in number, numerical abundance and biomass. Rather than massive fish mortality due to the low oxygen contents reported elsewhere (Calheiros & Hamilton, 1998; Vaquer-Sunyer & Duarte, 2008), dispersal of organisms by lateral migrations between lakes and river channels and their redistribution according to their differentiated tolerance to hypoxia may account for the absence of significant effects of durations of floods on the entire assemblage level (Fernandes, 1997; Petry *et al.*, 2003b; Arrington & Winemiller, 2006; Fernandes *et al.*, 2009).

Some fish species in floodplains exhibit abilities related to the perception of changes in the environmental conditions. When low concentrations of dissolved oxygen are detected, active species such as the reophilic Characiformes and large-

Table 2. Results of the ANOVAs that examined the main effects (duration of the floods and habitat) on the fish assemblage attributes [species richness, numerical abundance and biomass of the fish assemblage (SIH+STH) and of the subsets of STH and SIH] in the upper Paraná River floodplain, between 2000 and 2003. d.f. = degrees of freedom; SS = sum of squares; MS = mean square; F = ratio of variance between and within groups; p = probability of Type 1 error.

Response variable	d.f.	SS	MS	F	p
Fish assemblage (SIH+STH)					
Species richness					
Duration of the floods (Df)	1	6.000	6.000	0.136	0.716
Habitat (H)	1	140.17	140.17	3.177	0.090
Df x H	1	54.000	54.000	1.224	0.282
Error	20	882.333	44.117		
Numerical abundance (CPUE _N)					
Duration of the floods (Df)	1	529,616	529,616	3.804	0.065
Habitat (H)	1	56,361	56,361	0.405	0.532
Df x H	1	96,487	96,487	0.693	0.415
Error	20	2,784,804	139,24		
Biomass (log ₁₀ CPUE _b)					
Duration of the floods (Df)	1	0.428	0.428	7.739	0.012
Habitat (H)	1	0.004	0.004	0.068	0.797
Df x H	1	0.142	0.142	2.577	0.124
Error	20	1.106	0.055		
Subset of STH					
Species Richness					
Duration of the floods (Df)	1	32.667	32.667	12.099	0.002
Habitat (H)	1	0.667	0.667	0.247	0.625
Df x H	1	0.667	0.667	0.247	0.625
Error	20	54.000	2.700		
Numerical abundance (log ₁₀ CPUE _N)					
Duration of the floods (Df)	1	8,996.7	8,996.7	0.811	0.379
Habitat (H)	1	53,501.4	53,501.4	4.821	0.040
Df x H	1	1,639.6	1,639.6	0.148	0.705
Error	20	221,941.2	11,097.1		
Biomass (log ₁₀ CPUE _b)					
Duration of the floods (Df)	1	0.001	0.001	0.002	0.965
Habitat (H)	1	1.298	1.298	8.685	0.008
Df x H	1	0.184	0.184	1.232	0.280
Error	20	2.988	0.149		
Subset of SIH					
Species Richness					
Duration of the floods (Df)	1	66.667	66.667	1.358	0.258
Habitat (H)	1	121.500	121.500	2.476	0.131
Df x H	1	42.667	42.667	0.869	0.362
Error	20	981.667	49.083		
Numerical abundance (CPUE _N)					
Duration of the floods (Df)	1	676,668	676,668	5.300	0.032
Habitat (H)	1	37	37	0.001	0.987
Df x H	1	123,282	123,282	0.966	0.338
Error	20	2,553,620	127,681		
Biomass (log ₁₀ CPUE _b)					
Duration of the floods (Df)	1	2.599	2.599	9.018	0.007
Habitat (H)	1	1.230	1.230	4.270	0.052
Df x H	1	1.359	1.359	4.717	0.042
Error	20	5.764	0.288		

sized Siluriformes tend to occupy more oxygenated areas, resulting in local changes in the structure of the assemblages (Crampton, 1998; Petry *et al.*, 2003b; Soares *et al.*, 2006). Therefore, dissolved oxygen often plays an important role in limiting the distribution of organisms (Breitburg, 1992; Rosenberger & Chapman, 1999; Petry *et al.*, 2003b). In the present work, STH did not show pronounced temporal changes in absolute numerical abundance and biomass, even when the levels of dissolved oxygen dropped below 4 mg.L⁻¹ in lakes. The higher similarity within fish composition and abundance even in years of moderate floods suggests that

these species preferentially occupy the floodplain lakes. At a first glance, it seems counterintuitive that species richness, numerical abundance and biomass of STH were negatively related to dissolved oxygen levels, but life-history traits may account for possible advantages in persisting in these temporary harsh environments.

Most of the 13 STH caught in our samplings (i) inhabit the well structured littoral areas of lentic environments, which are enlarged under floods, (ii) produce large adhesive eggs and/or develop parental care during an extended reproductive activity, (iii) are detritivorous or piscivorous territorialists

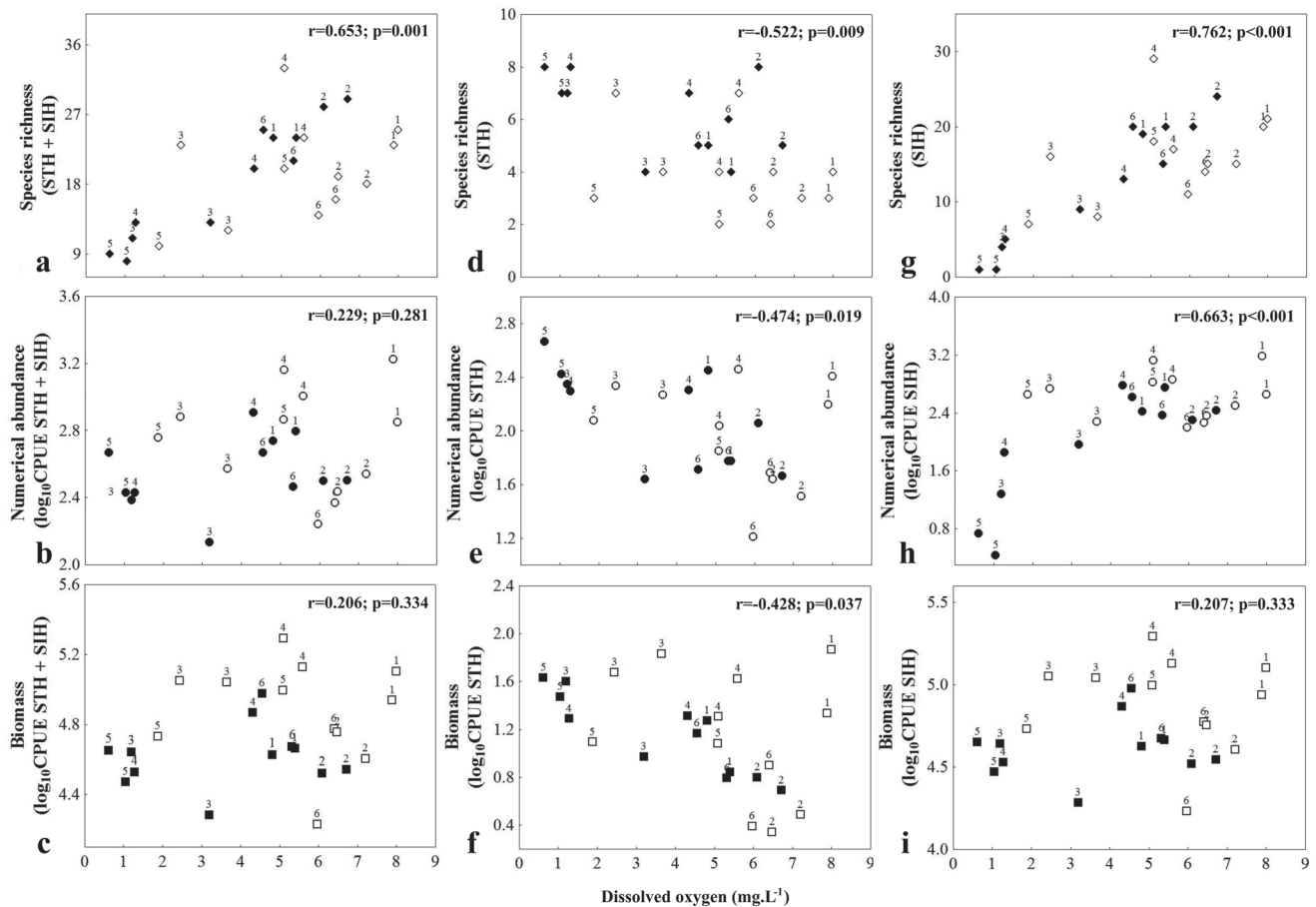


Fig. 6. Relationships between each assemblage attribute and dissolved oxygen, in years of short (white) and moderate floods (black). Attributes were either calculated for the entire fish assemblage (STH+SIH) (a-c) and for the subsets of STH (d-f) and SIH (g-i). Numbers 1-6 are codes of the sampling stations (see Fig. 1).

(Petry *et al.*, 2003a-b; Lima Filho *et al.*, 2012). Reduced mobility to escape from sub-lethal hypoxia has been related to the nest-guarding behavior of fish, determining that not all members of the population escape the low oxygen disturbances (Breitburg, 1992). By evasion of most individuals of the SIH species, pressures of competition for food and for nesting areas or predation may be relaxed for the remainder STH during moderate floods in lakes. These aspects should be considered in further studies aiming to identify the processes related to how and when some species successfully attain potential growth and reproductive rates in environmental changing systems as tropical floodplains.

In tropical lowland rivers, the annual flood pulse is considered the major driving force for the functioning of the ecological processes evolving biotic and abiotic components (Junk *et al.*, 1989; Neiff, 1990; Agostinho *et al.*, 2009). The upper Paraná River floodplain is still subjected annually to predictable hydrometric variations, in spite of the considerable control over the flood regime exerted by the chain of reservoirs upstream (Agostinho *et al.*, 2009). In

this study, we relate the changes on the biotic and abiotic components of this system due to the interannual variability in the flood pulse.

Despite the low spatial replication of the sampling design (three river channels and lakes), this study covers a large and simultaneously sampled area, on the first years after the closure and filling of Porto Primavera Reservoir, located 30 km upstream. Since the summer of 1999, the upper Paraná River floodplain has experienced an increased effect of flow regulation, which possibly exacerbates the interannual variations of floods. Therefore, the short floods of the upper Paraná River in 2000 and 2001 were partially a consequence of the water retention by others upstream reservoirs associated to a strong regional drought (for more details see Petry *et al.*, 2003a; Agostinho *et al.*, 2009).

In general, the sampling stations presented more oxygenated waters in these years of short floods and lower values of dissolved oxygen in years of moderate floods, independently of the habitat. Decreases in oxygen content are expected elsewhere in the floodplain during high waters

Table 3. Results of the multivariate regression models that fitted sequentially the explanatory variables dissolved oxygen and water transparency (DO and WT, respectively) in order to explain the composition of the subsets of STH and SIH in the upper Paraná River floodplain, between 2000 and 2003. SS = sum of squares; Pseudo-F = ratio associated to the variance between and within groups on the basis of the Chi-square measure of distance; p = probability of error obtained by permutation procedure; Prop. Explained = proportion of variance explained.

	Lakes				River channels			
	SS	Pseudo-F	p	Prop. Explained	SS	Pseudo-F	p	Prop. Explained
	Subset of STH							
Short floods								
DO	0.894	1.740	0.150	0.303	1.018	1.374	0.284	0.191
WT	0.258	0.431	0.431	0.088	2.103	2.596	0.011	0.394
Moderate floods								
DO	1.739	5.843	0.010	0.594	1.122	1.311	0.239	0.247
WT	0.212	0.648	0.706	0.072	1.137	1.492	0.194	0.250
	Subset of SIH							
Short floods								
DO	2.036	1.625	0.064	0.289	1.237	0.733	0.737	0.144
WT	0.936	0.689	0.791	0.133	2.275	1.445	0.155	0.265
Moderate floods								
DO	8.710	0.938	0.507	0.507	4.171	2.463	0.017	0.381
WT	153.211	1.676	0.135	0.135	1.747	1.042	0.160	0.541

as a consequence of the heterotrophic processes related to the flooding of surrounding terrestrial areas, incorporation of plant biomass and nutrients accumulated during the low waters (Lewis Jr. *et al.*, 2000; Petry *et al.*, 2003a; Rocha *et al.*, 2009). The effect of duration of the floods on water transparency, however, was restricted to lakes. During moderate floods, transparency increased significantly on this habitat, attaining values similar to those on river channels. Possibly, physical processes taking place upstream, such as the retention of matter in suspension by the reservoirs (Pagioro & Thomaz, 2002; Agostinho *et al.*, 2007; Souza Filho *et al.*, 2004) might have contributed to higher and less variable values of Secchi depth on river channels, between years of short and moderate floods. Results suggest the occurrence of a diluting effect of moderate floods (*sensu* Thomaz *et al.*, 2007), when the unusually clearer waters of river channel enhance water transparency of lakes.

The ability in evaluating the effects of the interannual variations in the flood pulse on fish assemblages across the floodplain was improved by adding data of abiotic variables and splitting fish assemblages in the subsets of STH and SIH. During short floods in river channels, water transparency predicted a considerable amount (39.4%) of the variation in composition and abundance of STH, being basically composed by few species of Loricariids. During moderate floods, however, dissolved oxygen was a better predictor of the variation of the assemblages, explaining 59.4% of STH in lakes and 38.1% of SIH in river channels. According to these results, fish assemblages of the upper Paraná River floodplain seem to follow a non-random composition in years of moderate floods primarily determined by dissolved oxygen concentrations. But in some neotropical floodplains, water transparency is recognized as determinant in fish assembling, being visually oriented species predominant in clearer waters

and species with sensory adaptations in turbid waters as predicted by the piscivory-transparency-model (PTM) (Rodríguez & Lewis Jr., 1997; Tejerina-Garro *et al.*, 1998). It is important to note that these studies were carried out at the beginning and at the end of the dry season (*i.e.*, low waters) and in our survey, water transparency was a strong predictor of species composition and abundance in river channels only in years of short floods. Therefore, maybe the relative strength of dissolved oxygen and water transparency in shaping fish communities of floodplains depends on the occurrence, duration, timing and intensity of the flood pulse (Súarez *et al.*, 2003; Bailly *et al.*, 2008). In this sense, we would predict that a sequence of years with short floods in the upper Paraná floodplain by increasing differences in water transparency would lead to patterns of species co-occurrence similar of those described for fish communities of the lakes of the Orinoco (Rodríguez & Lewis Jr., 1997) and Araguaia (Tejerina-Garro *et al.*, 1998) rivers.

Fish species highly specialized in surviving in hypoxic and turbid environments are encountered in several phylogenetic lineages. Approximately 370 species, which is slightly more than 1% of the total number of fish species in marine and freshwater ecosystems, exhibit some kind of adaptation for survival in conditions of hypoxia or anoxia (Graham, 1997; Nelson, 2006). Beyond morphological adaptations for the uptake of atmospheric air (Scarabotti *et al.*, 2011), survival in environments that are temporarily deoxygenated, which can vary from hours to months (during the night or during hydrological/climatic seasonality) may involve physiological (*e.g.*, higher concentration of erythrocytes, anaerobic ATP production) and behavioral strategies (*e.g.*, hypometabolic or aestivation state, branchial ventilation at the air-water interface) (Saint-Paul & Soares, 1987; Juccá-Chagas & Boccardo, 2006; Nilsson & Östlund-Nilsson, 2008; Martínez *et al.*, 2009; Lima

Filho *et al.*, 2012). The identification of adaptive or behavioral strategies for hypoxia still requires empirical confirmation for most species and continuous or facultative air breathing are being described for some species of Characiformes, Siluriformes, Cyprinodontiformes, and Synbranchiformes (Graham, 1997; Scarabotti *et al.*, 2011).

As species richness, numerical abundance and biomass of STH were negatively related to dissolved oxygen concentrations, these species may play an important role in their habitats at the periodic resetting which is provided by the long lasting annual floods, when an initial heterotrophic metabolism prevails. Studies developed in the upper Paraná River floodplain and other tropical floodplains support the idea that flood pulses prevent species dominance and therefore control the strength of biotic interactions within communities (Rosenberger & Chapman, 1999; Fernandes *et al.*, 2009). According to several authors, STH presented smaller probabilities of extinction following abrupt reductions in dissolved oxygen and may benefit from low-oxygen refuge against predators (Rosenberger & Chapman, 1999; Petry *et al.*, 2003b; Pompeu & Godinho, 2006; Anjos *et al.*, 2008). Therefore, the general overwhelming negative impacts of oxygen depletions described elsewhere (Breitburg, 1992; Lewis Jr. *et al.*, 2000; Danylchuk & Tonn, 2003; Altieri & Witman, 2006) may be lessened in tropical lowland floodplains by its diverse fish fauna, which responds differentially to the environmental conditions imposed by the interannual variations in the flood pulse.

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Appendix: Fish species recorded in the upper Paraná River floodplain, between 2000 and 2003. Species are listed according to the correlation of their CPUE_n values with the scores of the first axis of the DCA. Species tolerant to hypoxia STH are identified by X. Numerical abundance (individuals per 1,000 m². 24 h⁻¹; CPUE_n) in years of short (2000 and 2001) and moderate (2002 and 2003) floods is presented for the main habitats (lakes and river channels).

	Vouchers (NUP)	STH	DCA 1	Short floods		Moderate floods	
				Lakes	River channels	Lakes	River channels
<i>Hoplosternum littorale</i> (Hancoc, 1828)	161	X	0.90	114	5	533	73
<i>Hoplerythrinus unitaeniatus</i> (Spix, 1829)	3437	X	0.84	11	0	84	11
<i>Gymnotus</i> spp.	10716	X	0.67	0	0	101	8
<i>Erythrinus erythrinus</i> (Schneider, 1801)	4158	X	0.58	0	0	19	0
<i>Callichthys callichthys</i> (Linnaeus, 1758)	1722	X	0.57	0	0	5	8
<i>Pterygoplichthys ambrosettii</i> (Holmberg, 1893)	1529	X	0.42	190	65	65	19
<i>Eigenmannia trilineata</i> López & Castello, 1966	12241		0.23	16	0	0	5
<i>Loricariichthys platytopon</i> Isbrücker & Nijssen, 1979	2121	X	0.18	516	283	473	332
<i>Rhamphichthys hahni</i> (Meiken, 1937)	1734		0.11	27	0	0	0
<i>Pseudoplatystoma corruscans</i> (Agassiz, 1829)	523		0.10	22	16	5	5
<i>Cichlasoma paranaense</i> Kullander, 1983	6293		0.09	5	0	0	0
<i>Serrasalmus maculatus</i> Kner, 1858	396		0.06	49	22	19	0
<i>Hoplias</i> aff. <i>malabaricus</i> (Bloch, 1794)	3457	X	0.03	163	82	54	103
<i>Pimelodus microstoma</i> Steindachner, 1877	7007		0.01	0	0	3	0
<i>Pimelodus misteriosus</i> Azpelicueta, 1998	12108		-0.01	0	0	5	0
<i>Ageneiosus militaris</i> Valenciennes, 1836	537		-0.03	5	0	0	0
<i>Astronotus crassipinnis</i> (Heckel, 1840)	3449		-0.03	11	11	3	0
<i>Cyphocharax modestus</i> (Fernández-Yépez, 1948)	3290		-0.03	11	0	3	3
<i>Ossancora eigenmanni</i> (Boulenger, 1895)	11028		-0.03	5	0	0	3
<i>Schizodon altoparanae</i> Garavello & Britski, 1990	13410		-0.03	22	0	0	3
<i>Rhinodoras dorbignyi</i> (Kröyer, 1855)	1723		-0.08	0	0	0	3
<i>Parauchenipterus galeatus</i> (Linnaeus, 1766)	3302		-0.08	679	250	95	71
<i>Cyphocharax nagelii</i> (Steindachner, 1881)	431		-0.10	0	0	8	0
<i>Serrasalmus marginatus</i> Valenciennes, 1847	439		-0.10	880	495	65	440
<i>Sternopygus macrurus</i> (Schneider, 1801)	2096		-0.10	0	5	0	3
<i>Metynnis lippincottianus</i> (Cope, 1870)	443		-0.11	22	5	14	8
<i>Hemisorubim platyrhynchos</i> (Valenciennes, 1840)	2506		-0.11	11	38	0	0
<i>Leporinus lacustris</i> Campos, 1945	3308		-0.13	43	60	0	5
<i>Pimelodus ornatus</i> Kner, 1857	2492		-0.13	0	11	0	0
<i>Loricariichthys rostratus</i> Reis & Pereira, 2000	4730	X	-0.15	5	0	3	14
<i>Schizodon borellii</i> (Boulenger, 1900)	1925		-0.16	228	98	24	24
<i>Pterodoras granulosus</i> (Valenciennes, 1833)	4423		-0.16	5	22	0	38
<i>Iheringichthys labrosus</i> (Kröyer, 1874)	671		-0.17	33	163	0	3
<i>Hypostomus ancistroides</i> Ihering, 1911	332	X	-0.18	5	11	0	5
<i>Pinirampus pirinampu</i> (Spix, 1829)	666		-0.18	0	16	0	0
<i>Steindachnerina brevipinna</i> (Eigenmann & Eigenmann, 1889)	2372		-0.21	0	0	87	11
<i>Leporellus vittatus</i> (Valenciennes, 1849)	1902		-0.22	0	5	0	0
<i>Pimelodus maculatus</i> Lacépède, 1803	420		-0.22	38	27	24	3
<i>Salminus brasiliensis</i> (Cuvier, 1816)	1865		-0.22	0	0	0	8
<i>Trachydoras paraguayensis</i> (Eigenmann & Ward, 1907)	1724		-0.22	54	92	19	68
<i>Cichla kelberi</i> Kullander & Ferreira, 2006	1746		-0.23	0	0	3	14
<i>Crenicichla britskii</i> Kullander, 1982	6276		-0.23	5	27	0	8
<i>Salminus hilarii</i> Valenciennes, 1829	1893		-0.23	0	5	0	3
<i>Eigenmannia virescens</i> (Valenciennes, 1847)	10766		-0.24	0	0	0	3
<i>Leporinus octofasciatus</i> Steindachner, 1917	281		-0.24	0	0	0	3
<i>Loricaria</i> sp.	2567	X	-0.25	0	33	0	27
<i>Astyanax fasciatus</i> (Cuvier, 1819)	32		-0.25	0	0	0	22
<i>Astyanax schubarti</i> Britski, 1964	397		-0.25	0	0	0	11
<i>Bryconamericus stramineus</i> Eigenmann, 1908	3298		-0.25	0	0	0	5
<i>Myloplus tiete</i> (Eigenmann & Norris, 1900)	2484		-0.25	0	0	0	3
<i>Acestrorhynchus lacustris</i> (Reinhardt, 1874)	7579		-0.27	147	27	19	3
<i>Hypophthalmus edentatus</i> Spix, 1829	1749		-0.27	5	5	5	0
<i>Hypostomus</i> spp.	11840; 11841	X	-0.29	0	11	0	33
<i>Satanoperca pappaterra</i> (Heckel, 1840)	339		-0.28	109	0	19	27
<i>Moenkhausia intermedia</i> (Eigenmann, 1908)	2389		-0.30	609	560	182	310
<i>Leporinus obtusidens</i> (Valenciennes, 1847)	274		-0.33	5	33	0	19
<i>Sorubim</i> cf. <i>lima</i> (Schneider, 1801)	2494		-0.34	5	22	0	0
<i>Pimelodella gracilis</i> (Valenciennes, 1835)	1778		-0.36	0	22	0	3
<i>Leporinus piavussu</i> Britski, Birindelli & Garavello, 2012	13775		-0.37	16	49	14	22
<i>Prochilodus lineatus</i> (Valenciennes, 1836)	13776		-0.38	54	65	27	30
<i>Cichla piquiti</i> Kullander & Ferreira, 2006	3379		-0.40	5	5	24	8
<i>Galeocharax knerii</i> (Steindachner, 1879)	263		-0.41	0	11	0	3
<i>Steindachnerina insculpta</i> (Fernández-Yépez, 1948)	1424		-0.41	283	103	8	19
<i>Roeboides descalvadensis</i> Fowler, 1932	3286		-0.44	43	76	106	11
<i>Crenicichla jaguarensis</i> Haseman, 1911	58		-0.45	0	5	0	19
<i>Auchenipterus osteomystax</i> (Ribeiro, 1918)	2627		-0.48	125	82	95	63
<i>Schizodon nasutus</i> Kner, 1859	2495		-0.49	0	5	0	8
<i>Hypostomus regani</i> (Ihering, 1905)	2286	X	-0.53	0	49	0	38
<i>Apareiodon affinis</i> (Steindachner, 1879)	12676		-0.54	0	158	0	63
<i>Plagioscion squamosissimus</i> (Heckel, 1840)	1924		-0.54	16	3	60	73
<i>Astyanax altiparanae</i> Garutti & Britski, 2000	8630		-0.59	87	38	22	35
<i>Leporinus friderici</i> (Bloch, 1794)	1180		-0.60	5	71	33	171
<i>Rhaphiodon vulpinus</i> Agassiz, 1829	1513		-0.64	130	179	11	130