

Effects of long and short flooding years on the feeding ecology of piscivorous fish in floodplain river systems

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Abstract Floodplain river systems are extremely dynamic environments, where alternating dry and flooded periods affect the availability of food resources for fish. For piscivores, during drought years, a decreased availability of prey is expected, resulting in diets dominated by fewer items, narrower trophic niches with high dietary overlap. During floods, habitats become more similar, and, combined with increased connectivity, provide a wider diversity of prey to piscivores, decreasing dietary overlap and presenting wider trophic niches. This study aimed to evaluate the potential impacts of long periods of flooding on the trophic ecology of nine piscivorous fish in the upper Paraná River basin. In drought years, diets were dominated by small characids, presenting narrower niches with higher dietary overlap. The opposite situation was observed during wet years, with different species responses, likely due to species-specific feeding strategies. High niche overlap was observed between native and non-native species, suggesting competition. The inclusion of non-native species in the native piscivorous diet is a concerning

fact, as its causes and possible impacts are still unknown. In conclusion, long flooding pulses affect the diets of piscivorous fish in different ways by either increasing or decreasing niche breadth and overlap according to species-specific characteristics.

Keywords Trophic ecology · Feeding · Piscivores · Paraná River

Introduction

Floodplain rivers are extremely dynamic environments, as the connection of nearby regions to the main channel is altered depending on the water level (Power et al., 1995a, b; Arthington et al., 2005). In this sense, flood pulses are of great importance, as they alter limnological characteristics and biological processes (Thomaz et al., 2004), affecting the structure of the aquatic community (Junk, 1980) and the availability of feeding resources, particularly for fish (Junk, 1980; Wissmar et al., 1981; Adriana et al., 2002). There is increased connectivity during flooding periods, resulting in increased similarity among habitats (Thomaz et al., 2007), and prey that is not usually available to predators subsequently becomes available for consumption. On the other hand, flooding periods decrease fish prey density and availability for piscivorous fish due to the increased area and available shelters (Luz-Agostinho et al., 2008). During dry periods, the aquatic

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environment contracts, resulting in several isolated environments with increased fish densities. While over the short term, this increased fish density provides an abundant source of food for piscivores (Luz-Agostinho et al., 2008), over longer periods, and this isolation can lead to the limited availability of feeding resources for piscivorous species, due, for example, to consumption (Medeiros & Arthington, 2014).

The dynamics of floodplain rivers are influenced by several factors, such as rain fluctuation, which is able to temporarily expand the aquatic environment area (Cunico et al., 2002), resulting in changes in the river hydrology and promoting distinct patterns of dry and flooding periods among years. In addition, extreme climatic events, such as the *El Niño*-Southern Oscillation (ENSO), are able to create great hydrologic fluctuations, such as prolonged dry or flooding periods (Pinaya et al., 2016). Flow control by reservoirs is another factor that can change river hydrology, having its impacts potentiated as reservoirs are distributed in cascades (Agostinho et al., 2007a), decreasing the seasonality and variability in the river flow (Poff et al., 1997).

Piscivorous fish represent a high percentage of the total biomass of Neotropical aquatic environments. Species belonging to this guild are usually top predators and are able to sustain biodiversity and prevent strong trophic cascades (O’Gorman et al., 2008; Monteiro & Faria, 2016). For some species, piscivory is mandatory, while for others, it is an opportunistic behavior. When an alternative feeding resource is available, opportunistic piscivores can benefit from the available resource by selecting it, resulting in a better energy balance according to the optimal foraging theory (Gerking, 1994). Therefore, differences in resource use are crucial for species coexistence (De León et al., 2014).

Classical theories about competition and niche segregation predict that species coexistence is achieved through differences in species niche. When demand for a resource exceeds supply, there will be increased competition, and tolerance of niche overlap will decline (Pianka, 1974, 1981). As one possible consequence, niche differentiation will lead to a reduction in the niche overlap between possible competitors, reducing competition and allowing coexistence (MacArthur, 1958; Pianka, 1973, 1974; Schoener, 1974). These differences in niche might involve changes in some combination of strategies for habitat

use, such as feeding time, energy allocation, defense, and diet restrictions, through feeding selectivity or niche retraction (Correa & Winemiller, 2014; Winemiller et al., 2015).

As piscivorous fish play an important role in the structure of fish assemblages (Petry et al., 2010; Winnie-Jr. & Creel, 2016), it is important to understand how flooding affects the inter- and intraspecific relationships among syntopic species. Species with similar diets, such as piscivores, but different feeding strategies are expected to behave differently according to water level and resource availability (Luz-Agostinho et al., 2009). In this sense, this study aimed to evaluate piscivorous fish feeding in the upper Paraná River floodplain, comparing years of high hydrometric level with years of low hydrometric level. Specifically, it was expected that during years with a high water level, there would be greater variability in feeding resources due to high connectivity among habitats, resulting in larger trophic niches and less dietary overlap.

Materials and methods

Samples were taken in the three distinct rivers of the upper Paraná River floodplain (Baía, Ivinhema and Paraná rivers; 22°40′–22°50′S and 53°15′–53°40′W), totaling 36 sampling stations (12 in each river) in different environments, including connected and non-connected lakes, secondary channels, and the river main channel (Fig. 1). Fish species were captured quarterly from March 2005 to June 2013 (in March, June, September and December). Gill nets with different mesh sizes (2.4–16 cm between opposite knots) were used to capture fish. The nets were deployed for 24 h and checked at 8:00 A.M., 4:00 P.M., and 10:00 P.M. In wide tropical rivers, where other sampling methods are difficult or impossible to utilize, gill net sampling has been shown to be an efficient sampling method, especially for fish with high mobility (Tejerina-Garro et al., 1998; de Mérona et al., 2001; Lapointe et al., 2006; Portt et al., 2006; Oliveira et al., 2014), as is the case for piscivores. All sampled fish were identified, measured, anesthetized, euthanized, and then their stomachs were removed and preserved in 10% formalin for later analysis.

The piscivorous fish species that had more than 30 adult individuals with content in their stomachs were analyzed. These species were *Acestrorhynchus*

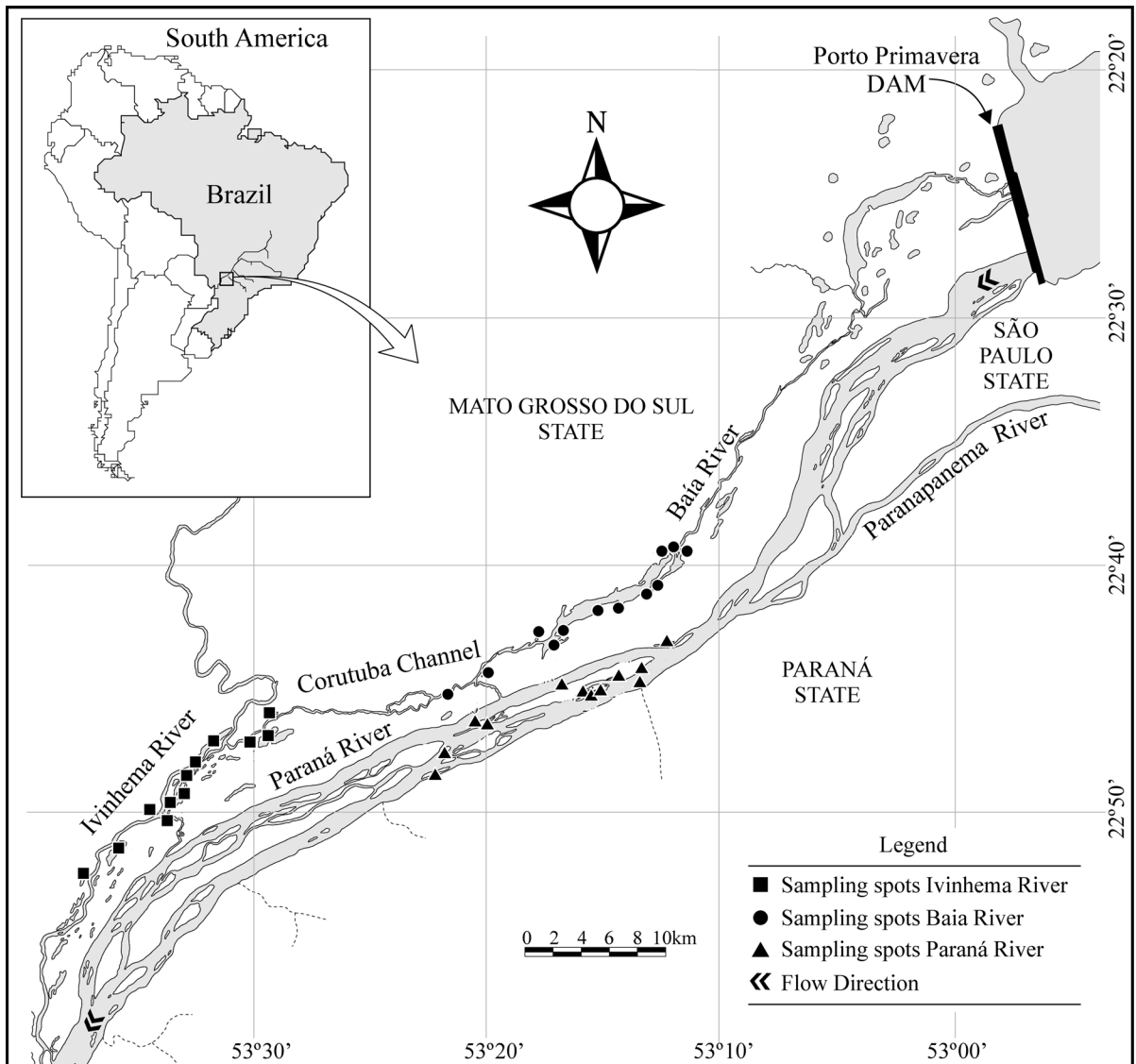


Fig. 1 Location of sampling stations in the upper Paraná River floodplain, downstream from the Porto Primavera Dam

lacustris (Lütken, 1875), *Cichla kelberi* Kullander & Ferreira, 2006, *Hoplias* spp., *Hemisorubim platyrhynchos* (Valenciennes, 1840), *Pseudoplatystoma corruscans* (Spix & Agassiz, 1829), *Plagioscion squamosissimus* (Heckel, 1840), *Rhaphiodon vulpinus* Spix & Agassiz, 1829, *Salminus brasiliensis* (Cuvier, 1816) and *Sorubim lima* (Bloch & Schneider, 1801).

From more than 12,000 piscivores captured, only 1,310 individuals had content in their stomachs. The prey species found in the stomach contents of the 961 piscivorous fish that presented identifiable content in

the stomachs were identified to the lowest feasible taxonomic level according to the identification key Graça & Pavanelli (2007). The nomenclature of the sampled fish follows Reis et al. (2003), Miranda (2010), Azpeticueta et al. (2015), De Lucena & Soares (2016), and Thomaz et al. (2015). The fish prey were counted, and the relative proportions of each prey category were determined from the volumetric water displacement (determined to the nearest 0.05 ml), as described by Winemiller (1990). Partially digested unidentified material and fish fragments of unknown

origin were excluded from the total. To facilitate the statistical analyses, arthropods (excluding shrimps) and mollusks were aggregated as invertebrates. Terrestrial vertebrates (*Trachycephalus typhonius*) were excluded from the analysis, as this prey type was only found in the stomach content of one individual.

Possible dietary differences among species were assessed through a permutational multivariate analysis of variance (PERMANOVA; Anderson et al., 2008), followed by a Wilcoxon signed-rank test to assess possible dietary differences between species pairs. A permutational analysis of multivariate dispersions (PERMDISP) was used to assess differences in niche breadth, measured as dispersion in diet space among species. This analysis measures the distance between each individual to the group multivariate median and determines any differences in distance in the spatial median between groups (Anderson, 2006). The probability values used to determine significant differences in the dispersion in diet space between species were calculated by permutation of residuals (999 permutations). Post hoc pairwise comparisons were performed using permutation tests based on a pairwise *t* test of the dispersion of different group combinations (9,999 permutations). The original data matrix containing the stomach content data was ($\log + 1$) transformed to reduce undue influence of extreme values and then transformed into a dissimilarity matrix by the Bray–Curtis method (Bray & Curtis, 1957).

The niche overlap of species pairs during drought and wet years was quantified using Pianka's niche overlap index, $O = \frac{\sum p_{ij}p_{ik}}{\sqrt{\sum p_{ik}^2 p_{ij}^2}}$, where O represents the overlap between the species pair, with possible values ranging from 0 (no overlap) to 1 (total overlap), and p_{ij} and p_{ik} representing the proportions of the i th resource (i) used by the species (j and k , respectively) (Pianka, 1973). The significance of the observed mean overlap between species was determined by comparison with a null model of expected niche overlap when resources are randomly consumed. Simulated diets were generated with a randomization algorithm in which the diet breadths were preserved, zero values were reshuffled, and all resources had the same probability of being consumed (Gotelli & Graves, 1996; Gotelli & Entsminger, 2010). A Friedman test was used to assess possible differences in diet overlap by

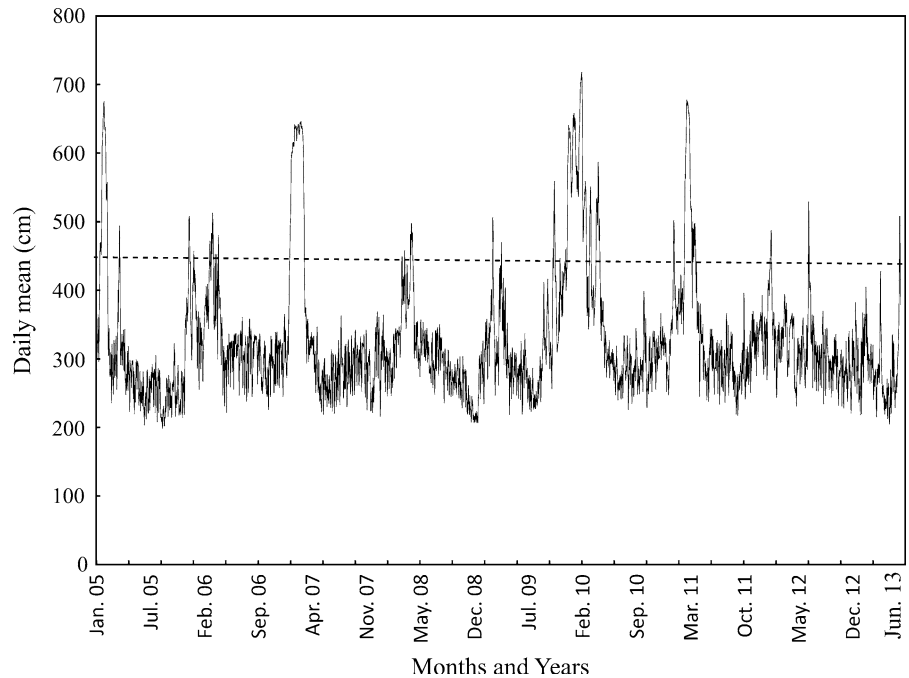
comparing the matching pairwise niche overlap across different year types.

To test if piscivores present preferences in terms of prey type, a selectivity test was performed considering drought and wet years. The selectivity coefficient W_i (Vanderploeg & Scavia, 1979) was used as a mathematical measure of feeding preference. This index is calculated as $E_i = \frac{W_i - 1/n}{W_i + 1/n}$, where n is the number of prey types available, and $W_i = \frac{r_i/p_i}{\sum r_i/p_i}$, where r_i is the percentage of prey item i in the diet of the fish and p_i is the percentage of prey item i in the environment. E_i varies from -1 to 1 . Negative values indicate avoidance of the prey, positive values indicate active selection, and null values indicate predation by chance. This index assumes that the gut samples and habitat samples accurately reflect the relative abundance of prey consumed and in the environment, respectively (Kohler & Ney, 1982). The data used to calculate the feeding selectivity were based on the relative numerical composition of prey in the stomach contents and in the environment. Prey species not found in the stomach contents during the study were omitted from the analysis, as they are deemed inaccessible to each predator (Cantanhêde et al., 2009). Environmental data were obtained in the same samples described above, in which each sampled fish was identified and counted as described in the sampling methods.

Piscivorous fish have good swimming performance and can sometimes travel great distances (Webb, 1978, 1982; Domenici & Blake, 1997; Porter & Motta, 2004; Langerhans & Reznick, 2010). Therefore, the analysis did not consider differences between distinct river systems, as it is possible that some individuals feed in one river and then are captured in another, which is mainly observed during flooding periods due to the high connectivity among habitats.

Years in which a flooding period lasted for at least 40 days were considered wet years. The 40-day threshold was determined a priori because this is the minimum period for effective fish reproduction in the floodplain, decreasing young mortality and increasing recruitment (Suzuki et al., 2009; Oliveira et al., 2015). These factors would potentially provide a high availability of feeding resources (e.g., young and small-sized fish) for piscivores. Consequently, the years 2007, 2010, and 2011, which each presented more than

Fig. 2 Daily river level variation (stream flow heights, in cm) during the period in which sampling was performed. The horizontal dashed line shows the corresponding threshold for the beginning of floods (450 cm) in the Paraná River



40 days of flooding, were pooled as “wet years,” while 2005, 2006, 2008, 2009, 2012, and 2013, in which the annual flooding period was fewer than 40 days, were pooled as “drought years” (Fig. 2).

The statistical analyses, including PERMANOVA, the Wilcoxon signed-rank test, PERMDISP, and the Friedman test, were performed using R software version 3.3.1 (R Core Team, 2015). The PERMANOVA and PERMDISP analyses were conducted using the vegan package (Oksanen et al., 2015). Pianka’s niche overlap index and Monte Carlo simulations were performed using EcoSim version 7.72 (Gotelli & Entsminger, 2010).

Results

A total of 45 food resources, including fish, invertebrates, and plants, were found to have been consumed by the nine piscivorous fish species. *Astyanax lacustris* (Lütken, 1875) and *Moenkhausia* spp. were consumed by all species, with the exception of *S. lima*. In general, the piscivores presented a more diverse diet during the wet years than during the drought years. The species that presented the most diverse diet was *Hoplias* spp., which consumed 28 different food resources in drought years and 37 during wet years. On the other

hand, the diet of *S. lima* was composed mainly of invertebrates, dominated by *Macrobrachium amazonicum* in the wet years. *Prochilodus lineatus* was only consumed by *P. corruscans*, making up a large proportion of the diet during the wet years, while *Gymnotus* spp. were consumed in at least 1 year type for all species (by *Acestrorhynchus lacustris*, *C. kelberi*, *H. platyrhynchus*, *P. squamosissimus*, and *S. brasiliensis* only during wet years, by *R. vulpinus* only during drought years, and by *Hoplias* spp. and *P. corruscans* during both wet and drought years). Shrimp (*M. amazonicum*) was consumed by the nine species, being particularly fundamental in the diets of *P. squamosissimus* and *S. lima*. However, while *P. squamosissimus* consumed shrimp during either wet or dry years, *S. lima* only consumed shrimp in drought years. Intraguild predation was common in several species, especially during wet years, in which *Acestrorhynchus lacustris*, *Hoplias* spp., *C. kelberi*, *P. squamosissimus*, and *Serrasalmus marginatus* were consumed by at least one of the analyzed species. Consumption of conspecifics was observed for *Acestrorhynchus lacustris* in wet years and for *C. kelberi* and *P. squamosissimus* in both drought and wet years. The consumption of *Hoplias* spp. by other *Hoplias* spp. was observed in both wet and dry years, with higher consumption during the wet years (Table 1).

Significant differences were observed in the species diets between wet and drought years (PERMANOVA, $F_{p(8,942)} = 1.90$, $P < 0.001$). Most of the species pairs showed significant differences between the wet and dry years, with higher intraspecific differences observed in the wet years. The Wilcoxon signed-rank tests detected intraspecific variation for most species in the wet and dry years (Table 2), while the interspecific variation among species pairs had a greater number of differences in the wet years. When the differences between year categories were considered, only *R. vulpinus* and *S. brasiliensis* did not significantly differ in their diets (Wilcoxon signed-rank test: *R. vulpinus*, $W = 33,803$, $P = 0.50$; *S. brasiliensis*, $W = 8,594.5$, $P = 0.34$; Table 2).

Differences in diet breadth between wet and drought years were observed (PERMDISP, $F_{m(17,942)} = 9.62$, $P < 0.001$, where the subscript m refers to spatial medians), with most of the variability observed during wet years. There were significant differences between drought and wet years for *Acestrorhynchus lacustris*, *C. kelberi*, *Hoplias* spp., *H. platyrhynchus* and *S. lima*. It was a general tendency of the species to present larger diet breadth during wet years when compared to drought years. Of all nine species, *Cichla kelberi* presented the widest niche breadth and *H. platyrhynchus* presented the smallest niche breadth during wet and drought years, respectively (Fig. 3).

The average dietary overlap between species was greater than expected for both drought and wet years under a null model ($P > 0.05$). However, the general degree of dietary overlap between drought and wet years did not differ (Friedman $\chi^2 = 1.12$, $df = 1$, $P = 0.28$). *Cichla kelberi* presented high dietary overlap with *P. squamosissimus* during drought years and with *Acestrorhynchus lacustris* during wet years. Low dietary overlap was observed between species that usually inhabit the main river channel (*H. platyrhynchus*, *P. corruscans*, *R. vulpinus*, *S. brasiliensis*, and *S. lima*) in both drought and wet years, with the exception of *P. corruscans* with *R. vulpinus* (Pianka's index = 0.8) and with *S. brasiliensis* (Pianka's index = 0.43) (Table 3).

Piscivores presented different patterns in prey selectivity (Fig. 4). *Acestrorhynchus lacustris* presented negative selection for most of the consumed prey during the drought years, while during the wet years, this species presented positive selection for all

consumed prey. An opposite pattern was observed for *Hoplias* spp., which presented positive selection for most of the consumed prey during the drought years, while negative selection was observed for several prey species during the wet years. In general, positive selection for *C. kelberi* (prey) was observed during the drought years, with this species being consumed by most of the piscivores during these years. The prey *Serrasalmus marginatus*, consumed by several piscivores, was negatively selected by most of them, with the exception of *S. brasiliensis*, which presented positive selection for this prey species during drought years. *Plagioscion squamosissimus* presented slightly negative selection for conspecifics, while *C. kelberi* positively selected conspecifics during drought years, with negative selection for conspecifics during the wet years. Cheirodontinae was negatively selected by all species that consumed this prey item in at least 1 year type.

Discussion

This is the first study to evaluate differences in years with long or short flooding periods, at least for the studied region. This is because most, if not all, studies directly focus on flooding and dry periods and their effects on the ichthyofauna. However, the environmental effects of flooding events (e.g., fish recruitment, invertebrate availability) differ from 1 year to another, and some patterns do not appear in isolated periods, making the analysis by years with long and short flooding periods ideal for observing patterns in species diet influenced by water level fluctuations.

Changes in water level are the main determinant of resource availability for fish in floodplains (Luz-Agostinho et al., 2008). When the water level is low, the prey become more concentrated and are therefore more available for piscivorous predation. Additionally, as the water level falls, predators can aggregate near lake connections with the river main channel and benefit from the increased young fish density passively carried by the water, a phenomenon known as "lufada" (Agostinho et al., 2007a). On the other hand, during prolonged droughts, with short floods or no floods at all, the availability of food resources and their diversity becomes limited, mainly due to consumption, low recruitment, and decreased connectivity (de Almeida et al., 1997; Hahn et al., 2004; Balcombe

Table 1 General dietary composition (vol%) of the nine piscivorous fish species of the upper Paraná River floodplain in drought and wet years, including the number of individuals with empty stomachs, stomachs with unidentified material, and stomachs used in the analysis

Number of stomachs	A		B		C		D		E		F		G		H		I	
	1,094	2,869	267	770	816	2,455	115	281	154	545	309	228	220	134	160	205	43	221
Empty	13	104	10	7	29	59	4	17	8	21	7	17	6	20	11	9	0	7
Non identified material	46	187	22	59	108	137	23	42	24	58	76	63	19	29	12	23	3	30
Identified content	D	W	D	W	D	W	D	W	D	W	D	W	D	W	D	W	D	W
Year category																		
Fish prey																		
Callichthyidae					1.35	0.14	10.83	0.76	17.87			3.48		5.08		5.48		
Characidae	10.72	2.66	0.86	8.53	0.34	0.24	8.51	0.95	0.01	0.36	0.44	0.59		42.68		0.97		<0.001
Cheironominae	4.95	8.84	5.76	6.75	0.86	0.95	2.62	5.47	0.02	0.23	0.86	0.17	0.5	0.38				0.03
Cichlidae		0.41	1.44	3.24		1.8									0.08	4.04		
<i>Astyanax lacustris</i>	30.46	12.92		27.63	1.78	1.51	9.98	11.6	0.52	1.83	16.09	3.2	5.11	21.52	4.2			<0.001
<i>Aphyocharax dentatus</i>		0.14			0.02	0.04							1.44					
<i>Acestrorhynchus lacustris</i>		8.45			5.04	7.21					15.67							
<i>Auchenipterus osteomystax</i>									2.6			0.31				5.11		
<i>Bryconamericus stramineus</i>	6.09	1.93			0.29	0.12		0.38				0.35				0.61		
<i>Cichla kelberi</i>	2.67	0.14	1.73	1.08	9.58	5.67	2.95	0.19	0.21		1.07		1.11			15.09		
<i>Cichlasoma paranaense</i>					4.32	0.16			2.08						21.02	2.43		
<i>Crenicichla</i> spp.		2.7						0.1								3.16		
<i>Eigenmannia irilineata</i>	9.37			9.12	0.92	0.45		4.28		0.13	9.66	10.1	3.06	3.17		7.3		0.03
<i>Geophagus cf. proximus</i>					3.84	1.24						0.87				15.82		
<i>Gymnotus</i> spp.		1.45		6.8	1.15	5.07		1.9	3.38	30.42		4.18	15			20.54		0.01
<i>Hyphessobrycon eques</i>	1.9	0.17			0.14	0.04												<0.001
<i>Hemiodus ornatus</i>						1.15												
<i>Hoplerethrinus unitaeniatus</i>		3.38				0.6								1.27				
<i>Hoplias</i> spp.				0.32	18.77	26.17	1.31	0.95	41.14	12.69		3.48	61.1	6.35		5.48		
<i>Hypostomus</i> spp.						0.7					5.9							
<i>Laetacara araguaiae</i>			1.73		0.04				0.1	0.1								
<i>Leporinus</i> spp.		5.77		7.56	10.76	6.41		26.15		8.36		4.53		2.22				0.01
<i>Loricariichthys</i> spp.			14.41	1.35	3.71	1.2						0.38			17.23	4.87		
<i>Moenkhausia</i> spp.	31.98	12.61	8.65	0.49	2.17	0.27	5.56		0.29	0.17	4.29	3.17	1.94	2.54	6.22	0.34		<0.001
<i>Ossancora eigenmanni</i>						1.45												
<i>Porotergus ellisi</i>						0.14												

Table 1 continued

Number of stomachs	A		B		C		D		E		F		G		H		I	
	1,094	2,869	267	770	816	2,455	115	281	154	545	309	228	220	134	160	205	43	221
<i>Parauchenipterus galeatus</i>					7.97						0.43							
<i>Psellogrammus kenedy</i>	0.99	5.76	6.8		0.52	0.44	0.82	6.42	0.08		0.21					0.24		<0.001
<i>Prochilodus lineatus</i>						12.1			19.74	31.88								
<i>Plagioscion squamosissimus</i>	0.38		0.11		5.52		3.44				0.21	0.42				5.84		
<i>Pamphorichthys</i> sp.			2.31															
<i>Pimelodella</i> spp.					4.04	0.51	0.12	8.18		0.36		6.79						0.01
<i>Pimelodus</i> spp.									8.31							0.73		
<i>Roeboides descabradensis</i>	5.99	7.34			1.85	1.27	19.64	8.89	2.6	1.27	2.26					1.7		
<i>Rhamphichthys hahni</i>	0.02					1.89				8.01	8.05							
<i>Schizodon borellii</i>	4.59				2.11	1.71	2.38			1.2	1.74		8.25					0.01
<i>Serrasalminus marginatus</i>	8.65	3.78			11.86	1.52	2.45	7.13	0.42		7.8			42.03				
<i>Satanoperca pappaterra</i>	3.43					1.29			0.1	0.6	7.51							
<i>Steindachnerina</i> spp.	2.67	8.19			4.32		30.76	18.73				4.88	5.08	7.57				
<i>Trachydoras paraguayensis</i>										0.65	0.63							
Invertebrates	1.14				0.14	0.03	0.02	0.01			1.88	0.19	0.01	0.01	1.64			99.9
<i>Macrobrachium amazonicum</i>	3.62	0.57	57.35	2.91	1.43	0.45	3.76	3.47	0.45	1.66	43.61	24.59	10.72	1.4	0.24	100	0.02	
Others																		
<i>Trachycephalus typhonius</i>											1.37							
Plants	0.05		0.54	0.67	1.67	<0.001	0.26	0.08	0.08	0.08								

The species codes used are A *Acestrorhynchus lacustris*, B *Cichla kelberi*, C *Hoplias* spp., D *Hemisorubim platythyngchos*, E *Pseudoplatystoma corruscans*, F *Plagioscion squamosissimus*, G *Rhaphiodon vulpinus*, H *Salminus brasiliensis*, and I *Sorubim lima*. The year categories were the drought (D) and wet (W) years

Table 2 Wilcoxon signed-rank test results for the species pair comparisons in the diets of nine piscivorous fish species during drought and wet years in the upper Paraná River floodplain

Species	<i>C. kelberi</i>		<i>H. platyrhynchos</i>		<i>Hoplias</i> spp.		<i>P. corruscans</i>	
	W	P	W	P	W	P	W	P
Dry years								
<i>A. lacustris</i>	122,890	0.01	2,863,900	<0.001	137,570	0.113	1,884,600	<0.001
<i>C. kelberi</i>			24,013	<0.0001	560,850	<0.001	26,938	0.003
<i>H. platyrhynchos</i>					745,370	0.311	35,801	<0.001
<i>Hoplias</i> spp.							802,010	<0.001
<i>P. corruscans</i>								<0.001
<i>P. squamosissimus</i>								0.035
<i>R. vulpinus</i>								0.001
<i>S. brasiliensis</i>								<0.001
Wet years								
<i>A. lacustris</i>	14,953,000	0.5052	7,823,400	<0.001	76,644,000	<0.001	15,356,000	<0.001
<i>C. kelberi</i>			766,830	0.002	7,492,900	<0.001	1,505,200	<0.001
<i>H. platyrhynchos</i>					3,609,500	<0.001	728,540	0.103
<i>Hoplias</i> spp.							8,421,700	<0.001
<i>P. corruscans</i>								0.58
<i>P. squamosissimus</i>								<0.001
<i>R. vulpinus</i>								0.011
<i>S. brasiliensis</i>								<0.001
Species	<i>P. squamosissimus</i>		<i>R. vulpinus</i>		<i>S. brasiliensis</i>		<i>S. lima</i>	
	W	P	W	P	W	P	W	P
Dry years								
<i>A. lacustris</i>	1,884,600	<0.001	95,414	0.009	31,918	0.137	2,904	<0.001
<i>C. kelberi</i>	381,860	<0.001	19,000	0.386	6,258.5	0.002	614	0.003
<i>H. platyrhynchos</i>	484,660	<0.001	24,722	<0.001	8,305	0.891	737.5	<0.001
<i>Hoplias</i> spp.	10,922,000	<0.001	555,240	<0.001	185,920	0.509	16,756	<0.001
<i>P. corruscans</i>	519,580	<0.001	26,408	0.001	8,837.5	0.477	801.5	<0.001
<i>P. squamosissimus</i>			194,690	<0.001	61,768	<0.001	6,973.5	0.035
<i>R. vulpinus</i>					4,835.5	0.011	468.5	0.001
<i>S. brasiliensis</i>							191.5	<0.001
Wet years								
<i>A. lacustris</i>	20,002,000	<0.001	4,048,800	<0.001	2,088,700	0.0,068	4,084,800	<0.001
<i>C. kelberi</i>	1,965,200	<0.001	397,800	<0.001	204,110	0.0,043	400,500	<0.001
<i>H. platyrhynchos</i>	953,520	<0.001	193,290	<0.001	98,228	<0.001	193,840	0.103
<i>Hoplias</i> spp.	10,963,000	<0.001	2,215,800	<0.001	1,149,000	0.477	2,241,200	<0.001
<i>P. corruscans</i>	1,791,200	<0.001	363,160	<0.001	183,740	<0.001	363,590	0.58
<i>P. squamosissimus</i>			388,410	0.414	188,740	<0.001	382,440	<0.001
<i>R. vulpinus</i>					41,021	<0.001	81,888	0.011
<i>S. brasiliensis</i>							62,420	<0.001

Species pairs that had statistically significant ($P < 0.05$) differences in their diets are presented in bold. Note that the comparison between drought and wet years is not shown, as there were no significant differences (Friedman $\chi^2 = 1.12$, $df = 1$, $P = 0.28$)

Table 3 Pianka's overlap index between the nine piscivorous fish species from the upper Paraná River floodplain in drought and wet years

Species	<i>C. kelberi</i>		<i>H. platyrhynchos</i>		<i>Hoplias</i> spp.		<i>P. corruscans</i>		<i>P. squamosissimus</i>		<i>R. vulpinus</i>		<i>S. brasiliensis</i>		<i>S. lima</i>	
	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet
<i>A. lacustris</i>	0.18	0.69	0.36	0.63	0.11	0.19	0.011	0.09	0.35	0.49	0.08	0.38	0.14	0.13	0.07	0
<i>C. kelberi</i>			0.12	0.64	0.09	0.17	0.009	0.2	0.85	0.33	0.16	0.59	0.09	0.23	0.94	0
<i>H. platyrhynchos</i>					0.14	0.24	0.05	0.18	0.17	0.36	0.071	0.26	0.19	0.08	0.09	0
<i>Hoplias</i> spp.							0.55	0.59	0.08	0.29	0.62	0.18	0.43	0.38	0.04	0
<i>P. corruscans</i>									0.01	0.16	0.8	0.07	0.02	0.43	0.008	0
<i>P. squamosissimus</i>											0.18	0.15	0.03	0.19	0.88	0.005
<i>R. vulpinus</i>													0.01	0.07	0.16	0
<i>S. brasiliensis</i>															0	0

et al., 2005; Luz-Agostinho et al., 2008, 2009). This in turn decreases prey availability, and fewer prey items are therefore found in diets. This was observed for *Acestrorhynchus lacustris*, *C. kelberi*, *S. brasiliensis* and *S. lima*; in drought years, their diets were mainly composed of small-sized characids and shrimp.

After prolonged flooding, a higher recruitment of migratory species is expected, as they depend of these flooding periods for relevant reproduction (Suzuki et al., 2009; Oliveira et al., 2015); thus, such species will present high juvenile abundance in the floodplain, including predator feeding areas. During 1992–1993, a study in the same region showed that the migratory species *Prochilodus lineatus* made up a high proportion of the piscivorous fish diet, mainly during flooding periods (Luz-Agostinho et al., 2008). The low proportion of migratory species in the piscivore diet observed in the present study might be indicative of a reduction in migratory species in the floodplain. This reduction would likely be caused as a consequence of the large number of dams, mainly in the Paraná River, that block migratory fish routes and control the water level (Agostinho et al., 2003, 2004, 2007b). This would result in failures in reproduction and recruitment due to the absence of floods that promote final gonadal maturation, the flooding of nursery areas (Vazzoler, 1996; Suzuki et al., 2009) and the incorporation of terrestrial items in the aquatic environment (Hahn & Fugi, 2007). Decreases in the abundance of migratory species have already been detected in the floodplain region (Suzuki et al., 2009; Oliveira et al., 2015), highlighting the fact that this observation merits further investigation in order to determine if this decrease is real and the possible causes of such a reduction. If this hypothesis proves to be true, urgent conservation projects should be proposed.

The different responses in trophic niche expansion and feeding selectivity observed among species strongly suggest interspecific differences in foraging behavior. *Hoplias* spp. are ambush opportunistic predators that inhabit macrophyte covered areas, mainly in lagoons, where they benefit from this feeding strategy (Petry et al., 2007; Luz-Agostinho et al., 2008). As a consequence of their ambush strategy, the feeding of *Hoplias* spp. is usually limited to species that search for shelter in more structured habitats, mainly in macrophytes (Jacobsen & Berg, 1998; Pelicice et al., 2008), and their diets rarely

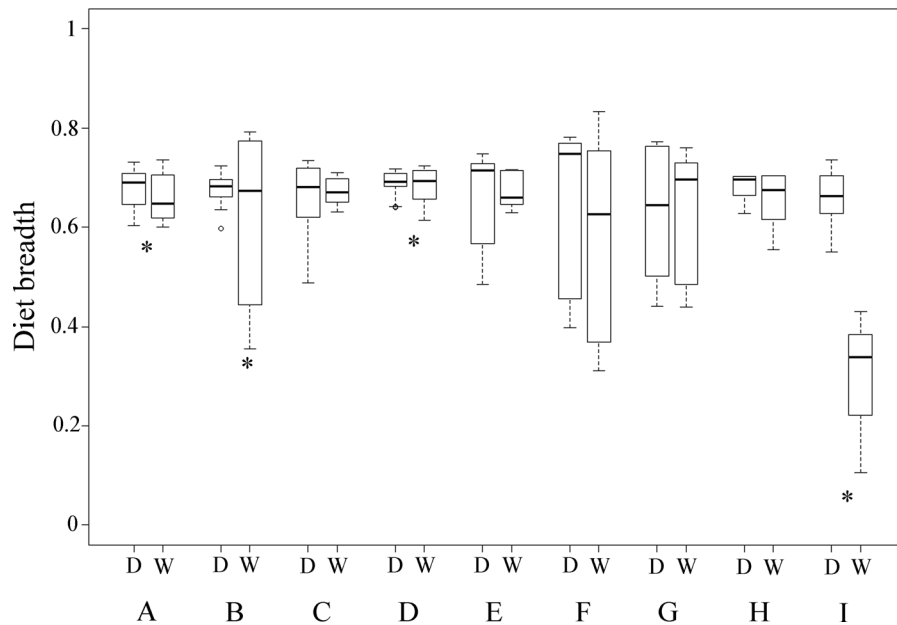


Fig. 3 Variation in dietary breadth among nine piscivorous fish species based on 45 prey items consumed during dry and wet years. Diet breadth was assessed as the species dispersion in diet space using permutational analysis of multivariate dispersions (PERMDISP) (e.g., a greater distance to the spatial median indicates a larger dispersion and therefore a broader trophic niche). The upper and lower hinges correspond to the 25th and 75th quartiles, respectively. The *horizontal bars* represent the

median dietary breadth, and outliers are represented by *open ovals*. The species codes used are *A* *Acestrorhynchus lacustris*, *B* *Cichla kelberi*, *C* *Hoplias* spp., *D* *Hemisorubim platyrhynchos*, *E* *Pseudoplatystoma corruscans*, *F* *Plagioscion squamosissimus*, *G* *Rhaphiodon vulpinus*, *H* *Salminus brasiliensis*, and *I* *Sorubim lima*. The year categories were the drought (D) and wet (W) years. *Statistically significant differences ($P < 0.05$) between the drought and wet years for each species

include prey that only occasionally or never visit these macrophytes. This is one of the reasons why the diet of this species was unaffected by prolonged flooding periods and explains the extremely narrow trophic niche and positive prey selectivity observed in drought years. For other species that capture prey using a pursuit strategy, their response to dry periods would differ according to their preferential habitat. Species such as *H. platyrhynchos* and *P. corruscans*, which feed mainly in the river channel, would present larger trophic niches during dry periods when prey are more vulnerable (Luz-Agostinho et al., 2008). Thus, the low diet overlap between these species would reflect the high heterogeneity of habitats that these species are able to reach; this fact is highlighted by the consumption of and selectivity for different prey types. Alternatively, species that inhabit more closed habitats (e.g., lagoons) that are sometimes disconnected from the main channel, such as *C. kelberi* and *P. squamosissimus*, would have larger trophic niches during flood periods due to increased access to a higher

diversity of prey from the rise in water level (Junk et al., 1989). In contrast, during drought years, such species would be subjected to few prey types, as their diets are restricted to the prey inhabiting these closed habitats, or to low prey abundance, explaining the narrower niche breadth, high incidence of cannibalism and intraguild predation observed for these pairs of species.

Despite piscivores being considered as a specialist guild, there seems to exist some plasticity in their behavior, which is highlighted by the inclusion of invertebrates in the diets of several species. According to optimal foraging theory, fish should feed on the resources that provide the maximum energy gain with the least energy expenditure (Gerking, 1994); thus, the consumption of invertebrates would be higher when fish consumption is likely to be highly expensive in terms of energy, through searching for, pursuing or capturing prey. It also must be highlighted that the species will be restricted to the food resources that are present in their usual habitat, mainly during drought

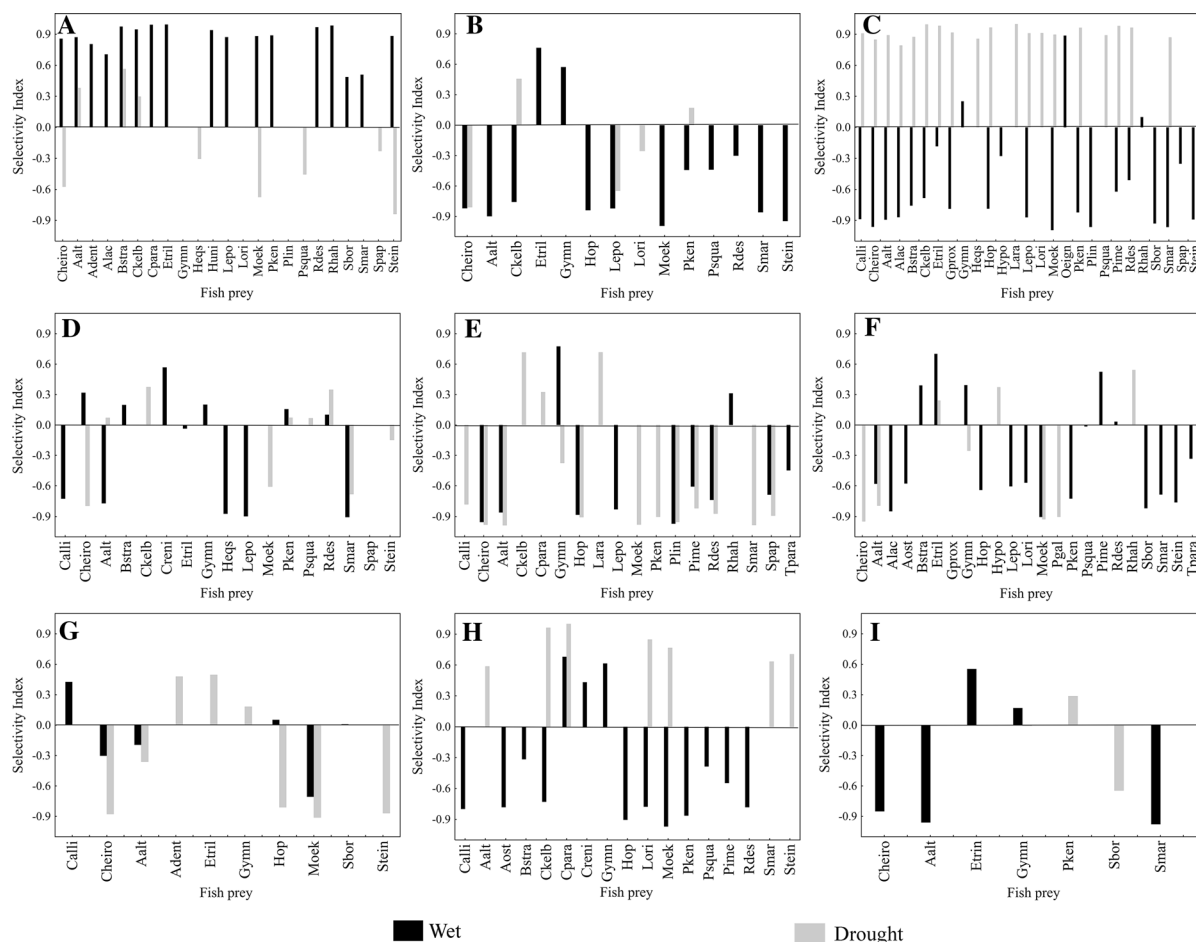


Fig. 4 Feeding selectivity (E_i) for the nine piscivorous fish species from the upper Paraná River floodplain, considering drought (gray bars) and wet years (black bars). E_i varies from -1 to 1 . Negative values indicate avoidance of the prey, positive values indicate active selection, and null values indicate predation by chance. Codes for predators are: **A** *Acestrorhynchus lacustris*, **B** *Cichla kelberi*, **C** *Hoplias* spp., **D** *Hemisorubim platyrhynchos*, **E** *Pseudoplatystoma corruscans*, **F** *Plagioscion squamosissimus*, **G** *Rhaphiodon vulpinus*, **H** *Salminus brasiliensis*, and **I** *Sorubim lima*. Codes for prey are *Calli*, Callichthyidae; *Cheiro*, Cheirodontinae; *Aalt*, *Astyanax lacustris*; *Adent*, *Aphyocharax dentatus*; *Alac*, *Acestrorhynchus lacustris*; *Aost*, *Auchenipterus osteomystax*; *Bstra*, *Bryconamericus stramineus*; *Ckelb*, *Cichla kelberi*; *Cpara*, *Cichlasoma*

paranaense; *Creni*, *Crenicichla* spp.; *Etril*, *Eigenmannia trilineata*; *Gprox*, *Geophagus* cf. *proximus*; *Gymn*, *Gymnotus* spp.; *Heqs*, *Hyphessobrycon eques*; *Huni*, *Hoplerthrinus unitaeniatus*; *Hop*, *Hoplias* spp.; *Hypo*, *Hypostomus* spp.; *Lara*, *Laetacara araguaiaae*; *Lepo*, *Leporinus* spp.; *Lori*, *Loricariichthys* spp.; *Moek*, *Moenkhausia* spp.; *Oeign*, *Ossancora eigenmanni*; *Pelli*, *Porotergus ellisi*; *Pgal*, *Parauchenipterus galeatus*; *Pken*, *Psellogrammus kennedyi*; *Plin*, *Prochilodus lineatus*; *Psqua*, *Plagioscion squamosissimus*; *Pime*, *Pimelodus* spp.; *Rdes*, *Roeboides descavadensis*; *Rhah*, *Rhamphichthys hahni*; *Sbor*, *Schizodon borellii*; *Smar*, *Serrasalmus marginatus*; *Spap*, *Satanoperca pappaterra*; *Stein*, *Steindachnerina* spp.; *Tpara*, *Trachydoras paraguayensis*

years, in which low connectivity does not allow fish to access all habitats in the floodplain. In this case, the avoidance of several prey types during the wet years observed for the predators that inhabit more closed habitats indicates that these species are in contact with a higher diversity of prey types but possesses some preference over other prey items, while during the

drought years, this avoidance seems to be reduced, as predators are subject to a reduced variety of prey. It is important to note that the great number of empty stomachs found in this study is not an abnormal finding, as piscivores are usually found with empty stomachs (Arrington et al., 2002); however, the number of stomachs with content should be

representative of the species diets in nature. Nevertheless, it must be highlighted that for some species, such as *S. lima* and *S. brasiliensis*, there was an extremely limited number of stomachs with identifiable content (3 and 11 stomachs, respectively), and therefore, the diet in such a situation might be slightly different from what is reported here. In addition, the number of stomachs with unidentifiable content represents a small proportion of the total and should not have influenced the analyses.

A concerning finding of this study includes the results for the dourado, *S. brasiliensis*, a voracious fish predator, which is highly ecologically valuable (Carvalho et al., 2008) and has even been suggested to be a possible umbrella species in the floodplain region (Agostinho et al., 2005). With the exception of *P. corruscans*, the diet of the dourado only showed high values of dietary overlap with the non-native species *C. kelberi* and *P. squamosissimus*, both of which originated in the Amazon basin (Kullander & Ferreira, 2006; Neves et al., 2015), and with *Hoplias* spp., which includes *Hoplias mbigua*, a species that was introduced after the construction of the Sete Quedas dam (Júlio-Jr et al., 2009). This high dietary overlap can indicate competition between native and non-native species, which is particularly important when resources are limited. The observation that *S. brasiliensis* fed on *C. kelberi* suggests that these species occupy similar habitats and could therefore compete for resources. However, this also indicates that *S. brasiliensis* could potentially drive biotic resistance against *C. kelberi* if this species was able to regain its abundance (Pereira et al., 2014). Nevertheless, as competition is only present when the demand for resources exceeds supply (Pianka, 1974, 1981) and there is no available information about the common environmental resources used by *S. brasiliensis* and *C. kelberi*, this hypothesis is based on speculation and must be confirmed by more accurate observation of foraging behavior and environmental resource availability.

Non-native species, including *Auchenipterus osteomystax*, *Geophagus* cf. *proximus* and *Hemiodus ortonops* (Langeani et al., 2007; Júlio-Jr et al., 2009), were found to compose a large proportion of the piscivorous diet. In particular, the shrimp *M. amazonicum*, also native to the Amazon basin, which was introduced to the Paraná River basin as a feeding strategy for fish in repopulation programs, was also a

major component. This shrimp has adapted well to the new habitat and has spread throughout the upper Paraná River floodplain (Bialetzki et al., 1997). It was found to be consumed by all nine piscivorous species, with a high percentage observed in the diet. It is still unknown whether piscivores are feeding on non-native species due to their high availability or if there is a low availability of alternative prey. In addition, the long-term impact on fish nutrition and community structure and dynamics are also unknown.

Intraguild predation was common for several species, and the specific results and possible implications in the floodplain have been previously published (Pereira et al., 2014). A high cannibalism rate during the wet years has also been observed by Neves et al. (2015) for *P. squamosissimus* due to the increased availability of juveniles. The opposite has also been previously reported, where predators shifted to cannibalistic behavior during periods of long drought, in which the long dry period and the intense consumption of prey items resulted in reduced food availability (Luz-Agostinho et al., 2008). This highlights that predators are extremely plastic, responding according to environmental variability that, when summed to morphological and behavioral traits, will lead to different kinds of responses. It is important to note that the cannibalism of *Hoplias* spp. was not evaluated in this study. As *Hoplias* consists of a complex of species (Dergam & Bertollo, 1990; Vicari et al., 2005; Blanco et al., 2010), with at least three recognized morphotypes with different cytotypes in the upper Paraná River floodplain region (Pazza & Júlio-Jr, 2003; Graça & Pavanelli, 2007), the predation of *Hoplias* spp. by other *Hoplias* spp. can also account for congeneric predation and not only cannibalism.

Fish species are well adapted to exploit a variety of feeding resources in order to maintain a positive energy balance, which is required for growth and reproduction (Abelha et al., 2001; Arrington et al., 2002). Furthermore, dietary differences can even be found within the same guild (Luz-Agostinho et al., 2008), as feeding strategies and preferential habitats vary among species. Tracking and evaluating changes in the dietary patterns of fish are effective ways to assess environmental changes caused either by natural or human impacts. Due to the upstream dam, the flow of water can be controlled, which has downstream impacts that may be greater than previously considered (Luz-Agostinho et al., 2008). Therefore,

understanding and predicting how extreme events, such as prolonged droughts or floods, can affect fish assemblages is of great importance in order to create management programs to control and reduce their impacts. It must be considered that fish species are extremely plastic, responding to environmental variability in different ways, such that the available theory may not always conform to the real dynamics.

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