PRIMARY RESEARCH PAPER

Influence of flood pulses on diet composition and trophic relationships among piscivorous fish in the upper Paraná River floodplain

Karla D. G. Luz-Agostinho · Angelo A. Agostinho · Luiz C. Gomes · Horácio F. Júlio Jr.

Abstract The aim of this article is to evaluate whether alterations in flood pulses differentially affect diet composition, feeding niche breadth, and diet overlap of piscivorous fish. Species examined were *Acestrorhynchus lacustris*, *Hoplias* aff *malabaricus*, *Plagioscion squamosissimus*, *Rhaphiodon vulpinus*, and *Salminus brasiliensis*. These species were collected with gillnets (different mesh sizes) in the upper Paraná River floodplain, during four distinct flood events (four periods; A = 1992/1993; B = 2000; C = 2001; and D = 2002). The volumetric method was chosen to express diet results. Feeding niche breadth was calculated using Levins measure, and diet overlap was evaluated by the Pianka's Index. Flooding was more intense and lasted longer in the first period (1992/1993—A). Diet composition of the studied species was broad (47 total items consumed). For period A, *Prochilodus lineatus* was the main item taken by four out of five species. In the other periods, there were relevant alterations in diet, since *P. lineatus* was not recorded in any stomach of the five species; rather, it was replaced by the shrimp, *Macrobrachium amazonicum*. Diet overlap was low in all periods. The greatest overlap was obtained in period C for *P. squamosissimus* and *R. vulpinus*, due to high consumption of shrimps. There were no significant differences in niche breadth among species. However, the species presented distinct variation patterns in niche breadth. For example, *H.* aff. *malabaricus* showed a tendency toward increasing niche over the period, but the other species presented larger niches only during period A. Therefore, it can be concluded that the intensity and duration of the flood pulse influences: (i) the diet composition of piscivores; (ii) the breadth of their niches; and (iii) feeding overlap among species.

Keywords Feeding · Piscivores · Floodplain · Paraná River

Handling editor: J. Cambray

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Introduction

One of the main characteristics of "river-floodplain" systems in tropical and subtropical regions is high species diversity, particularly of fish (Horne & Goldman, 1994). An important factor affecting diversity is the high heterogeneity of habitats found in these systems. This heterogeneity is a result of

flooding seasonality and different degrees of connectivity between the distinct biotopes that comprise a floodplain (Lowe-McConnell, 1999). Connectivity between biotopes, provided by flood pulses, plays an essential role in structuring and maintaining ecological processes in floodplain remnant water bodies, as demonstrated by several authors (Miranda & Raborn, 2000; Petry et al., 2003; Súarez et al., 2003; Thomaz et al., 2007).

Water level oscillations directly influence water velocity, depth of aquatic environments, and floodplain surface area exposed to flooding. This fact should be reflected in the food supply for fish. According to Agostinho et al. (2004a), river water overflowing onto a floodplain should increase habitat area, availability of shelter and allochthonous food sources, and should provide water enrichment with nutrients carried from adjacent areas or present in flooded organic or inorganic material.

On the other hand, floods dilute the aquatic biota by increasing water depth, reducing the availability of food resources, especially mobile ones. As a result, the hydrological cycle should affect interspecific relations, particularly predation and competition. The flooding regime seems to favor piscivores, since floods are associated with the reproductive success of many of their prey species. However, due to their diluting effect, floods also reduce the density of prey species. In addition, increased shelter may also reduce prey availability.

In the upper Paraná River floodplain, piscivorous species constitute the most diverse group, contributing about 30% of the total species recorded for the area, and representing substantial number and biomass proportions (Hahn et al., 2004). Of these species, some are typical of lentic environments, developing their entire life cycle in them (ex. *Hoplias* aff. *malabaricus*, *Acestrorhynchus lacustris*, and *Serrasalmus* spp.), while others present great seasonal fluctuations in abundance, and occur either in a constant or transient manner (e.g., migrators such as *Rhaphiodon vulpinus* and *Salminus brasiliensis*). Agostinho et al. (2004b) suggest that the high proportion of piscivorous fish in the ichthyofauna of this region is expected, since the area constitutes an important natural nursery with a high density of juvenile forms. In addition, floodplains present high food and shelter availability for small fish (forage species) of other trophic groups.

The dams constructed upstream the upper Paraná River floodplain, especially the Porto Primavera (closed in 1998), have redistributed discharges throughout the year, changing the flood pulses, which are the main functioning force that regulates floodplains (Agostinho et al., 2004a; Junk & Wantzen, 2004). Due to the importance of piscivores in structuring biotic communities, the effect of these alterations on dietary aspects of five species of this trophic group was analyzed in this work. The species, selected based on their initial abundance and life history diversity, were *A. lacustris* (Reinhardt, 1874), *H. malabaricus* (Bloch, 1794), *R. vulpinus* Agassiz, 1829, *Plagioscion squamosissimus* (Heckel, 1840), and *S. brasiliensis* (Cuvier, 1816).

Considering four periods in which the water level of the upper Paraná River floodplain was submitted to different regulation levels by impoundments, the present study attempted to address the following questions: (i) does the absence of flood pulses alter the diet and niche breadth of piscivores? (ii) does the absence of pulses alter the feeding overlap of these species?

Materials and methods

Samplings were performed in the upper Paraná River floodplain, in different sampling stations, located in lagoon, channel, and river environments, distributed among the Paraná, Baía, and Ivinheima river subsystems (Fig. 1). The hydrological cycle data for the Ivinheima and Paraná rivers were supplied by Itaipu Binacional's Hydrology Department, and were obtained at the Porto Sumeca and Porto São José hydrological stations, respectively.

Fish were captured monthly from March 1992 to February 1993 (period A) and quarterly in the years 2000 (period B), 2001 (period C), and 2002 (period D). Gill nets of different mesh sizes were used to capture fish; the nets were set for a 24-h period, and were checked at 08:00, 16:00, and 22:00 h. After harvesting, individuals were identified, measured, and eviscerated, and their stomachs were removed and preserved in 10% formalin for later analysis.

In the diet analysis, fish stomach contents were examined under stereoscopic microscope, and items were identified to the lowest possible taxonomic level. Identification of prey fish was performed based

Fig. 1 Location of sampling stations in the upper Paraná River floodplain: ■ Ivinheima Subsystem, ● Baía Subsystem, and ▲ Paraná Subsystem
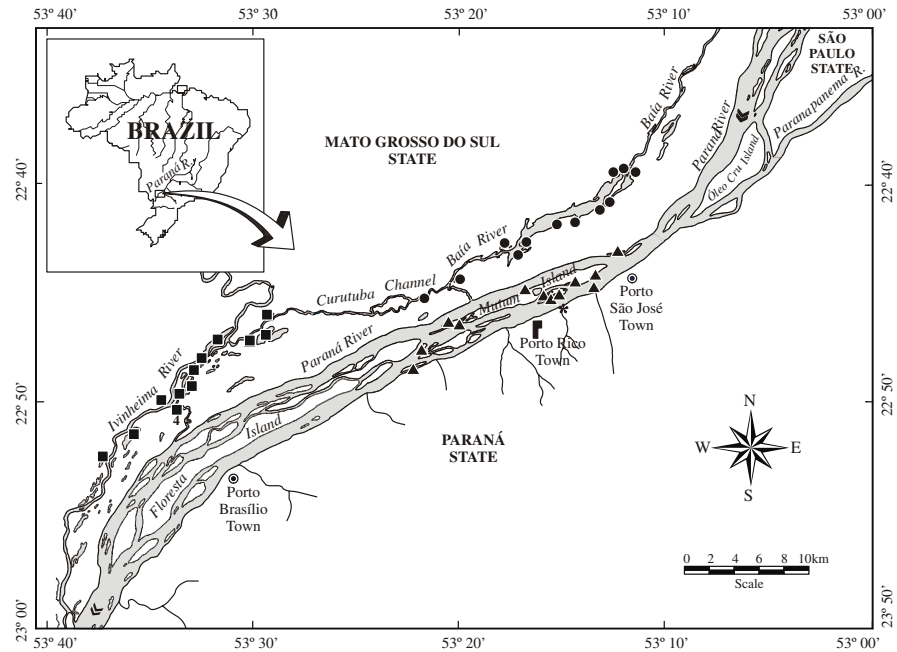
on Britski et al. (1999). To express diet results, we used the volumetric method (Hyslop, 1980), in which prey volume is obtained by water column displacement, using a set of graduated cylinders.

The importance of each item in the diet of the different species was established by the volume percentage values for the resources, estimated by species and sampling period. Diet data for period A (1992–1993) were obtained from Almeida et al. (1997). The species studied (*A. lacustris*, *H.* aff. *malabaricus*, *P. squamosissimus*, *R. vulpinus*, and *S. brasiliensis*) are the same during that period as in the other periods, and were selected based on abundance.

The feeding similarity patterns among species and periods were synthesized by detrended (to remove the arch effect) correspondence analysis (DCA; Hill & Gauch, 1980; Gauch, 1994) applied to volume percentage values as recommended by Sheldon & Meffe (1993) and Luz-Agostinho et al. (2006). Analyses were conducted using PC-ORD (McCune & Mefford, 1997), with low frequency items given less weight, because they usually influence ordinations (Palmer, 1993). Scores were generated for axes 1 and 2 and their means tested, by period, via analysis of variance (one-way ANOVA). If ANOVA was significant, the Tukey test (Zar, 1996) was applied a posteriori to identify the period that presented a different mean score.

Niche breadth was calculated by species and period, using Levins measure (Krebs, 1999), given by the formula below. It measures the uniformity of distribution of items among the various food resources.

$$B = 1 / \left(\sum_{i=1}^{n} p_i^2 \right)$$

where B = niche breadth, p_i = the proportion of food item i; n = number of food items.

As this formula yields the reciprocal value of Simpson's diversity index, and therefore, reflects the dominance effect (D), D was also presented $(D = 1/B)$.

Feeding overlap among the species for each sampling period was evaluated by Pianka's Index (Pianka, 1973), described as:

$$O_{jk} = \frac{\sum_{i}^{n} p_{ij} p_{ik}}{\sqrt{\sum_{i=1}^{n} p_{ij}^2 \sum_{i}^{n} p_{ik}^2}}$$

where O_{jk} = Pianka's niche overlap Index, between species j and species k, P_{ij} = amount represented by the proportion of resource "i" used by species "j", P_{ik} = amount represented by the proportion of resource "i" used by species "k", n = total number of resources established, i = resource, ranging from 1 to "i".

To evaluate whether the estimated feeding overlap values were higher than expected at random, we used the niche overlap module in the EcoSim 7.00 software program (Gotelli & Entsminger, 2000). The data matrices were submitted to 5,000 iterations.

Results

Hydrological regime

The daily water level variations for the Ivinheima and Paraná rivers in the periods from October 1991 to February 1993 and from October 1999 to September 2002 (Fig. 2) reveal that floods were more intense and lasted longer in the first period (A) in both rivers. In the Ivinheima River, less intense but relevant
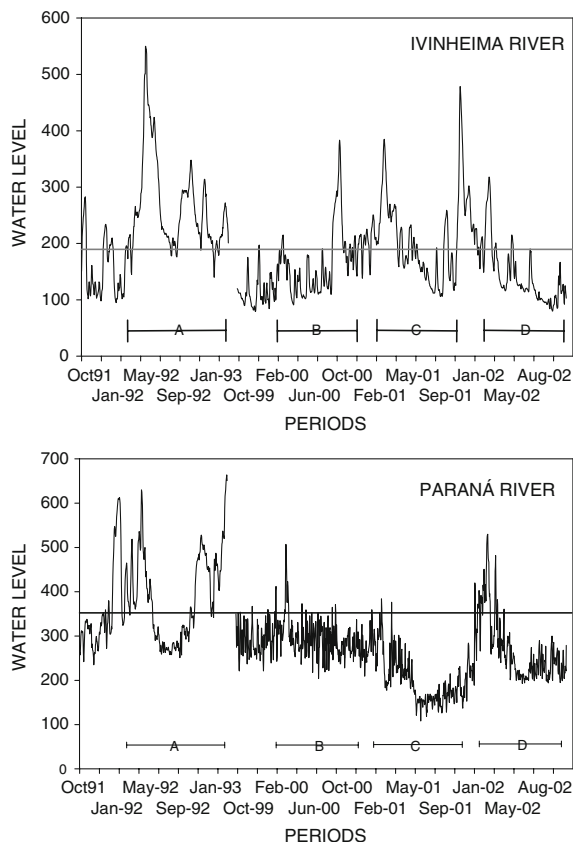

Fig. 2 Daily river level variations (streamflow heights, in cm) during the hydrological cycles in which period samplings were performed (solid line represents the mean values for the period, lines bounded by bars show the periods sampled, where A = 1992–1993, B = 2000, C = 2001, and D = 2002)

floods were observed in the subsequent periods. In the Paraná River, however, floods did not occur or were irrelevant in the three subsequent years, showing high weekly level fluctuations. Although there was little rain in the region in 2000 and 2001 (dry years), the Porto Primavera Dam construction, about 40 km upstream from the floodplain, also contributed to the reductions in water levels, as well as to the high frequency pulses (daily and weekly) during these periods. The Baía River water level data were omitted, as their variations are similar to those of the Paraná River, whose course runs parallel and close, establishing surface connection during floods.

Variation in diet composition

The study revealed that the selected species show a wide feeding spectrum, consuming a total of 47 items, of which 38 were recorded in period A (1992–1993), 22 in B (2000), 23 in C (2001), and 26 in period D (2002). As congeneric species should play similar roles in the assemblage, prey belonging to the same genus were grouped for analysis (Piana et al., 2006). The importance of each item in the diet for each species per sampling period and the number of stomachs analyzed are presented in Table 1.

In period A, the main resource consumed by the various species was *Prochilodus lineatus*, which dominated the diets of four species. Only *A. lacustris* did not exploit this resource, and consumed *Steindachnerina* spp., *Leporinus* spp., *Moenkhausia* spp., and *Astyanax* spp. as main items. Other important resources in this period were *Schizodon* spp. and *Loricariichthys platymetopon* for *S. brasiliensis*; *Leporinus* spp. for *H.* aff. *malabaricus*, which also consumed conspecifics; *Astyanax* spp. and *Gymnotus* spp. for *R. vulpinus*, and *Pimelodella* spp. for *P. squamosissimus* (Table 1).

The diet analysis for the other periods (B, C, and D) revealed important changes, especially the absence of *P. lineatus* in the diet of any of the species and the high importance of the shrimp *Macrobrachium amazonicum*. Marked modifications were also recorded for other items, including *Roeboides paranensis* and *Hemigrammus marginatus* for *P. squamosissimus; Gymnotus* spp. for *R. vulpinus* and *H.* aff. *malabaricus*; *Eigenmannia* spp. for *R. vulpinus* and *P. squamosissimus*, and *Laetacara* sp. for *S. brasiliensis*, although only a small number of stomachs of the latter were analyzed.

Table 1 Volumetric percentage of food items found in the stomachs of: 1 = *A. lacustris*, 2 = *H.* aff. *malabaricus*, 3 = *P. squamosissimus*, 4 = *R. vulpinus*, 5 = *S. brasiliensis* (A = 1992–1993, B = 2000, C = 2001, and D = 2002)

Items	Period A					Period B					Period C				Period D				
	1	2	3	4	5	1	2	3	4	5	1	2	3	4	1	2	3	4	5
Insects	0.01	0.19	0.06	0.11	0.02		0.67	0.62				1.42	0.66			0.98	0.03		1.29
Plants	0.03	0.76	0.3	0.08	0.33		0.23		0.07			6.00		4.00		0.33	0.01		
Macrobrachium amazonicum		0.21	3.32	2.27		0.82	2.08	13.28	25.33		1.98	15.22	65.83	31.92		1.34	59.02	3.53	
Apareiodon affinis									1.42						10.50				
Acestrorhynchus lacustris		3.37		1.13															
Astyanax spp.	18.6	2.63	1.2	26.25	1.08	26.97	3.10		1.24		15.19	5.80	12.91	44.79	23.11	1.60	26.25	16.72	4.96
Aphyocharax spp.	0.27						0.10					1.15							
Apteronotus spp.				2.62															
Bryconamericus stramineus	0.42		7.05	4.64	0.4								9.61					13.40	
Callichthydae		0.88		2.75															
Characidae	2.01	2.14		0.84	2.34		0.61		12.43			5.68		12.68	23.11	0.89	1.48	26.01	34.70
Corydoras sp.		0.29																	
Crenicichla spp.				0.64															
Cyphocharax modestus	3.04						15.07					1.70							
Cichla spp.		0.34										2.84		1.10	6.19	28.01	9.44	2.39	
Characidium zebra	0.20		0.23	0.10															
Eigenmannia spp.	4.03	1.37									5.61	3.18	10.99			4.84	0.82	14.20	
Geophagus brasiliensis												0.48						1.06	
Gymnotus spp.		0.29	0.29	12.32		4.91	0.88		22.74		16.18	7.17		5.51		1.43	1.59		
Hoplosternum littorale																10.64			
Hyphessobrycon spp.	2.54	0.04		0.12			0.77												
Hypostomus spp.		0.30			0.73														
Hoplias aff. *malabaricus*		43.16		2.47	9.33		21.99				9.90	20.94				10.34	10.22	14.44	
Hemigrammus marginatus								26.80				2.71					3.78		
Hopleryhrinus unitaeniatus																9.99			
Laetacara sp.												2.79					1.00		
Leporinus spp.	14.23	20.02		2.69	3.83		20.85					1.75					0.80		
Loricariichthys platymetopon		0.39			10.2							0.96							
Metynnis cf. *maculatus*							2.97									3.11			
Moenkhausia spp.	9.84	3.23	2.13	3.54	6.63	4.09	5.13	35.86	12.79			6.29			6.73	0.30	4.44		
Odontostilbe sp.	0.63	0.02	0.44	0.16					9.95										

Table 1 continued

Items	Period A					Period B				Period C				Period D				
	1	2	3	4	5	1	2	3	4	1	2	3	4	1	2	3	4	5
Parauchenipterus galeatus			10.11	0.59			1.83								2.33			
Pimelodella spp.		0.22	11.14		0.63													
Pterodoras granulosus		0.23																
Prochilodus lineatus	0.59	18.42	46.01	21.1	21.56					21.79								
Plagioscion squamosissimus	2.15			5.15	11.11										0.49			
Roeboides paranensis	5.69	0.81	2.52	2.31	3.93		2.02	20.96	1.77		1.43			4.58				
Rhamphichthys spp.				0.41											1.11			
Rhaphiodon vulpinus				0.39														
Serrapinus spp.	0.8	0.43	1.44	0.28	0.41	5.97		2.48	12.26									
Pimelodidae			0.29	0.24	0.34		1.22				5.32				2.84	2.95	0.86	
Steindachnerina spp.	28.09	2.08	7.18	0.43	6.66	57.24	19.32				7.17			25.59	19.43			
Schizodon spp.	6.51	0.21		0.96	20.24													
Serrasalmus marginatus	0.32	0.42	3.37	1.59	0.23													
Synbranchus marmoratus		0.24																
Satanoperca pappaterra							1.16											
Trachydoras paraguayensis		0.33	0.19	3.82														
Stomachs analyzed	181	61	48	109	33	7	55	8	14	22	77	23	22	15	47	49	32	5

To provide a general evaluation of alterations in diet observed among the distinct periods, the feeding similarity patterns were summarized by DCA axes 1 and 2, which showed eigenvalues of 0.554 and 0.373, respectively. The analysis of variance (assumptions of normality and homogeneity of variance were met) revealed significant differences between mean scores on axis 1 per period (ANOVA; df = 3, 14; $F = 7.402$; $P = 0.003$), with the greatest differences observed between the first (A) and the last two periods (C and D) (Tukey; $P < 0.05$; Fig. 3A). No differences, however, were observed on axis 2, which separated the species (ANOVA; df = 3, 14; $F = 2.585$; $P = 0.095$; Fig. 3B). The items that most influenced the ordination were *Trachydoras paraguayensis*, *Parauchenipterus galeatus*, *P. lineatus*, *Hypostomus* spp., *Serrasalmus marginatus*, *Characidium zebra*, and *Schizodon* spp. Diet variability, evaluated based on standard error and
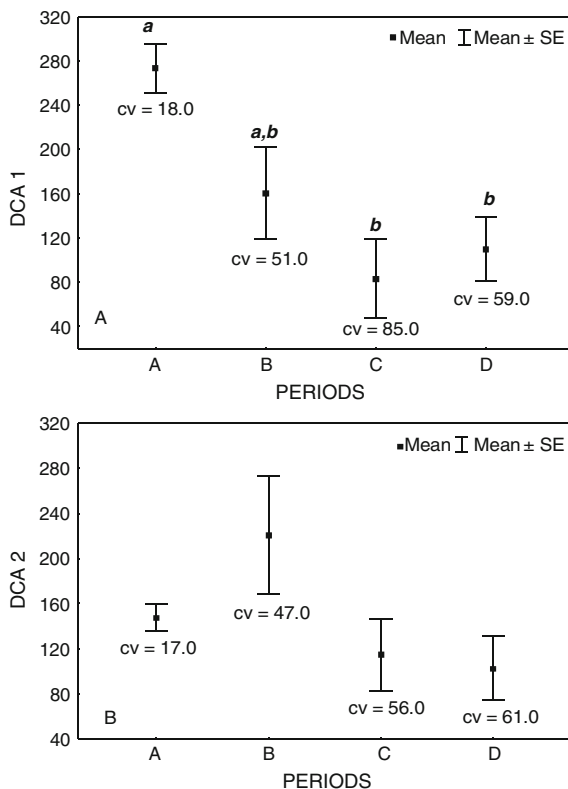
coefficient of variation values, was less pronounced in the first period, with a tendency to increase in subsequent years.

Niche breadth

Feeding niche breadth for the five species combined, based on Levins measure, did not reveal significant differences between periods (ANOVA; df = 3, 12; $F = 0.073$; $P = 0.973$). However, distinct variation patterns did occur among them, with *H.* aff. *malabaricus* being the only species with greater niche breadth in later periods. For this species, the variations resulted from the greater dominance of certain items observed in the first year, since alterations in number of items in the diet were not substantial (Table 2). For the other species, niche breadth was larger in period A, and the decreases observed in periods B or C were due to a reduction in the number of items. Except for *P. squamosissimus*, which showed a progressive decrease in niche breadth, and *S. brasiliensis*, for which no diet analysis was performed in the intermediate periods (no stomach analyzed in 2000 and 2001).

Variations in diet overlap

The Pianka's Index mean values analysis, made by period, revealed that diet overlap for the piscivores was reduced at levels lower than 0.5 on a scale from 0 to 1 (Fig. 4). The highest values were recorded for periods C ($O_{jk} = 0.46$) and A ($O_{jk} = 0.40$), and the lowest for period B ($O_{jk} = 0.21$).

These mean values were low, considering they refer to species in the same trophic category. However, with the exception of period B ($P = 0.35$), these means were significantly higher than expected at random ($P < 0.03$; Table 3). With regard to species pairs in period A, the highest feeding overlap values occurred between *P. squamosissimus* × *S. brasiliensis* ($O_{jk} = 0.598$) and *P. squamosissimus* and *R. vulpinus* ($O_{jk} = 0.576$; Table 4). In this period, the item that increased the overlap for both species pairs was *P. lineatus*. In period B, the greatest overlap occurred between *A. lacustris* × *H.* aff. *malabaricus* ($O_{jk} = 0.479$; Table 4), which consumed *Steindachnerina* spp., followed by *P. squamosissimus* × *R. vulpinus* ($O_{jk} = 0.404$), which consumed *Moenkhausia* spp.

Fig. 3 Mean score values (±standard error) derived from DCA (Detrended Correspondence Analysis) for axes 1 (**A**) and 2 (**B**), for the different sampling periods. Different letters indicate significant differences ($P < 0.05$) by Tukey test (SE = standard error; cv = coefficient of variation; A = 1992–1993, B = 2000, C = 2001, and D = 2002)

Table 2 Trophic niche breadth of five fish species by sampling period (A = 1992–1993, B = 2000, C = 2001, and D = 2002; n = number of prey, B = Levins measure, D = Simpson's dominance)

Species/periods	A			B			C			D		
	n	B	D	n	B	D	n	B	D	n	B	D
A. lacustris	20	6.44	0.16	6	2.45	0.41	7	5.09	0.20	8	5.16	0.19
H. aff. *malabaricus*	24	3.78	0.26	18	6.33	0.16	21	10.13	0.10	19	6.50	0.15
P. squamosissimus	21	4.02	0.25	6	3.81	0.26	5	2.12	0.47	8	2.34	0.43
R. vulpinus	29	7.11	0.14	10	5.77	0.17	6	3.09	0.32	14	6.67	0.15
S. brasiliensis	20	7.60	0.13	–	–	–	–	–		6	3.21	0.31
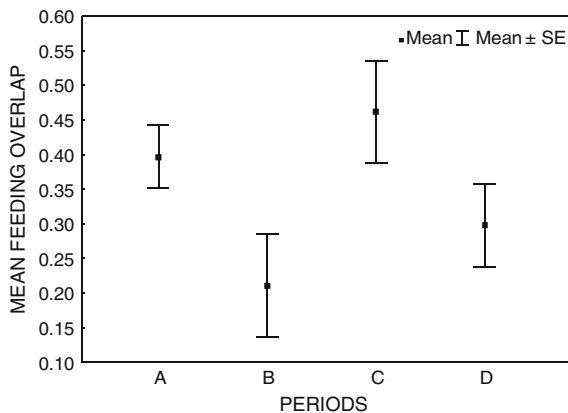
Fig. 4 Mean feeding overlap values (Pianka's Index) for the different periods sampled (A = 1992–1993, B = 2000, C = 2001, and D = 2002) (SE = standard error)

Table 3 Feeding overlap by sampling period (A = 1992–1993, B = 2000, C = 2001, and D = 2002), expressed by the averaged Pianka's overlap Index (O) and standard deviation (SD), calculated from all combination pairs (% volume)

Periods	n	O_{jk}	SD	P
A	432	0.397	0.14	0.0004
B	84	0.211	0.18	0.3460
C	144	0.458	0.18	0.0024
D	148	0.298	0.18	0.0208

Values of $P < 0.05$ indicate that the overlap is more consistent than expected at random (5,000 iterations; Gotelli & Entsminger, 2001); n = number of stomachs analyzed; SD = standard deviation

The greatest overlap value between species was found in period C (Table 4), *P. squamosissimus* × *R. vulpinus* (O_{jk} = 0.687), followed by *H.* aff. *malabaricus* × *P. squamosissimus* (O_{jk} = 0.516) and *H.* aff. *malabaricus* × *R. vulpinus* (O_{jk} = 0.494). The main resource shared by these species was shrimp

(*M. amazonicum*), whereas for *P. squamosissimus* × *R. vulpinus*, the item *Astyanax* spp. also contributed to increased feeding overlap values. In the last period analyzed (period D), the greatest overlap values were recorded for *A. lacustris* × *R. vulpinus* (O_{jk} = 0.605), which consumed *Astyanax* spp. and other characids (not identified because they were in an advanced state of digestion) and *R. vulpinus* × *S. brasiliensis* (O_{jk} = 0.551), which ingested *H.* aff. *malabaricus* and other characids.

Discussion

After the construction of Porto Primavera Dam, the stretch of the Paraná River basin considered in this study became the only remaining segment of the Paraná River in Brazil without dams. According to Agostinho et al. (2004c), the hydrological alterations caused by dams, particularly those related to flood peak attenuations and delays, and daily and weekly flow pulses, have considerable impact downstream. Consequently, dams modify the intensity, duration, and timing of floods, and reduce seasonally flooded areas (Agostinho et al., 2007a, b).

Several authors have found that factors such as habitat characteristics, food availability, and population density exert a pronounced influence on interspecific relations and partitioning of resources (Schoener, 1974; Ross, 1986; Gerking, 1994; Winemiller & Kelso-Winemiller, 1996; Gophen et al., 1998). All these factors are affected by the flooding regime.

The spawning and recruitment of migratory species (such as *P. lineatus*, a seasonal strategist—Winemiller, 1989a) are strongly dependent on flood regimes (Gomes & Agostinho, 1997; Agostinho et al., 2004b). Flooding influences the maturation of oocytes,

Table 4 Feeding overlap (Pianka's Index) between pair of species in different sampling periods (A = 1992–1993, B = 2000, C = 2001, and D = 2002)

	H. aff. *malabaricus*	*P. squamosissimus*	*R. vulpinus*	*S. brasiliensis*
Period A				
A. lacustris	0.221	0.151	0.423	0.366
H. aff. *malabaricus*		0.343	0.333	0.497
P. squamosissimus			**0.576**	**0.598**
R. vulpinus				0.465
Period B				
A. lacustris	**0.479**	0.0530	0.109	
H. aff. *malabaricus*		0.125	0.093	
P. squamosissimus			**0.404**	
R. vulpinus				
Period C				
A. lacustris	0.449	0.127	0.478	
H. aff. *malabaricus*		**0.516**	**0.494**	
P. squamosissimus			**0.687**	
R. vulpinus				
Period D				
A. lacustris	0.423	0.243	**0.605**	0.384
H. aff. *malabaricus*		0.156	0.199	0.087
P. squamosissimus			0.285	0.049
R. vulpinus				**0.551**

Values in bold represent greater overlap values

migration, spawning, drifting of eggs and larvae to nursery areas and initial development of juveniles. In addition, there is a close relationship between recruitment success and timing, duration and intensity of floods (Agostinho et al., 2004c). After the closure of Porto Primavera Dam (in 1998) flooding was extremely rare, and the recruitment of *P. lineatus* was low or did not occur. This affected the availability of this prey, leading to diet alterations in other species, as *P. lineatus* was the main item consumed by all predators in the first year of this study (1992–1993).

Another change observed in flood-restricted years was a reduction in predation of conspecifics (cannibalism) for *H*. aff. *malabaricus*. This may have happened due to the concentration of prey during these periods (Piana et al., 2006). Nevertheless, cannibalistic behavior is likely increased by inadequate or insufficient feeding conditions (Blaxter & Hunter, 1982; Hetch & Appelbaum, 1988). Importantly, this species was the least affected by flood control, as demonstrated by its feeding activity and body mass during that period (unpublished data). The facts that it is an ambush predator and has tolerance for long periods of starvation probably influenced this outcome (Piana et al., 2006; Petry et al., 2007).

A sequence of dry years led to an increase in intraguild predation, as demonstrated by the greater proportion of *H*. aff. *malabaricus* and *P. squamosissimus* in the diet of other piscivorous fish. This was also evident in the *H*. aff. *malabaricus*, which began to eat another piscivore (*Cichla kelberi*) that was introduced into the river basin and became abundant during that period. Due to retracted water levels in the first drought period (2000), prey species were expected to be concentrated and intensely consumed. However, in subsequent years, resources should become depleted and consumption of species with the same feeding habits should increase. While studying peacock bass (*Cichla* spp.) in rivers and reservoirs in Venezuela, Jepsen et al. (1999) reported that predators increased their feeding activities and growth in the low water season. However, this reflects the abundance of resources, which is severely limited by prolonged droughts.

The proportion of shrimp (*M. amazonicum*) in the diet of piscivores was also pronounced in periods of flood restrictions. As this increase involved four of the five piscivore species analyzed, it is assumed that shrimp thrived during dry years. Although Bialetzki et al. (1997) established the relationship between the

shrimp cycle and the flooding regime in the upper Paraná River floodplain, the fact that shrimp is considered an important dietary resource for *C. kelberi* in the Lajes Reservoir (Santos et al., 2001) indicates that the natural flooding regime is not essential for its proliferation. In fact, it has been recorded in greater abundances in the floodplain during the last decade, beginning in years when floods began to be regulated more intensively (A. A. Agostinho, personal observation).

Food items consumed were more diverse during period A (1992–1993), in which more intense and prolonged flooding occurred. However, a strong dominance of some items was observed in the diet of *H.* aff. *malabaricus*. This led to low niche breadth value for the period. It should be highlighted that *H.* aff. *malabaricus* uses more structured environments (macrophyte stands), which are generally more abundant during droughts. In macrophyte stands, where prey heterogeneity (number of species) is high, an effective ambush predator has favored conditions when compared with *P. squamosissimus*, a species that occupies more open areas (where there are less prey species; Agostinho et al., 2007b).

In addition to being the only ambusher species among the piscivores analyzed, *H.* aff. *malabaricus* was also the only species that did not show a relevant decrease in number of prey during drought periods in comparison to flooding periods. Unlike the other fishes, it had a lower niche breadth value in the first year. This fact could be attributed to the greater dominance of migratory species (*P. lineatus* and *Leporinus* spp.) and high abundance of *H.* aff *malabaricus* (cannibalism). During floods, when the reproductive success of migratory species is greater, the young seek shelter in the flooded vegetation and macrophyte banks (Delariva et al., 1994; Súarez et al., 2001) where this predator feeds.

For the other species, which capture their prey using a pursuit strategy, the number of species consumed was consistently higher in the flooding period, with lower dominance (*D*). The fact that these fish exploit open areas more intensely, where more abundant species are likely more vulnerable during drought periods, should explain high dominance (*D*) in their diets. However, the decrease in prey diversity may reflect the decrease observed in the environment as a result of adverse limnological conditions, predation itself, and a lack of connectivity, which

would allow other species to enter the system. The tendency for higher specialization during drought periods has been highlighted by several authors (Lowe-McConnell, 1964; Zaret & Rand, 1971; Winemiller, 1989b; Machado-Allison, 1992).

The fact that these species inhabit the same area, are subject to the same ecological conditions, belong to the same trophic category, and exploit the same environments would lead one to expect diet overlap to be high (Almeida et al., 1997). However, although the estimated overlap values were higher than expected at random in three of the four periods, these values were still low. The smallest overlaps were between *H.* aff. *malabaricus* and the other species. This was expected, due to distinct habitat that *H.* aff. *malabaricus* occupies (structured areas) and the feeding strategy it adopts (ambush predator). A similar pattern was recorded by Winemiller (1989b) in Venezuela. The greatest overlaps were recorded between *R. vulpinus* and *P. squamosissimus*, both with a pelagic or midwater and pursuing habit.

In this study, fluctuations in food resource availability probably led to marked variations in resource sharing levels and consequently, in diet overlap. Diet overlap among the piscivores was lowest in the first drought year (period B) suggesting that diet segregation occurred. This may have resulted from the fact that the resources were more available and diversified, as expected during low-water periods following great flooding periods (floods were pronounced in the preceding hydrological cycle). Lowe-McConnell (1999) suggests that, in general, competition is potentially stronger at the end of the flooding season and during drought in floodplains.

The variation in mean overlap values between periods leads us to believe that overlap is lower under conditions of greater resource availability. This possibility is indicated by: (i) very low overlap in the first year of drought after floods—resources are concentrated; (ii) low values in the last period—small peak of floods; (iii) intermediate value in the year with the greatest flooding—low resource availability due to dilution and shelter; and (iv) greater overlap value in the driest year, after consecutive droughts—depletion of resources.

The flood pulse alterations caused by upstream impoundments have a remarkable influence on trophic aspects of piscivore species of the upper Paraná River floodplain. Diet composition is altered

due to effects on the reproduction of seasonal species (sensu Winemiller, 1989a), and niche breadth is influenced by changes in the proportion between structured and non-structured habitats. Flow manipulation also affects diet overlap due to changes in the availability of resources via concentration/dilution of the water level and shelter supply. Therefore, downstream impacts of dams may be greater than previously considered, especially in floodplain areas.

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