Influence of hydrology on the fish body condition in a large subtropical floodplain

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With the objective of finding fluctuations on fish body condition in the Middle Paraná River floodplain in different hydrological scenarios, this attribute was analyzed in several trophic groups of a secondary floodplain channel and its associated lakes between 2010 and 2012. Standardized residuals generated by length-weight regressions were calculated for each species and the relative weight (Wr) of the most abundant species per group was examined. A two-way factorial ANOVA was carried out (factors: hydrology and habitats) to evaluate the existence of significant spatial-temporal differences by groups and species. Results showed that body condition in detritivorous, herbivorous and omnivorous species fluctuated significantly depending on hydrology and the environment. Optimal body condition was recorded after the largest flood pulse in most species. Body condition decreased during the low-water period and after two disconnection periods, whereas during the second flood pulse it increased in detritivores, herbivores and omnivores. No floods occurred thereafter, but two flow pulses were registered, and body condition increased under these hydrologic scenarios, with similar or higher values to those recorded after the largest pulse. These results indicate that flow pulses, which are supplementary to flood pulses, may have a positive effect on fish body condition.

Keywords: Flood/flow pulses, Hydrological fluctuations, Ichthyofauna, Middle Paraná River, Trophic groups.

Con el objetivo de conocer la fluctuación de la condición corporal de peces en la planicie de inundación del tramo medio del río Paraná ante diferentes escenarios hidrológicos, se analizó este atributo de diferentes grupos tróficos en un cauce secundario de la planicie y sus lagunas asociadas durante 2010 a 2012. Se calcularon los residuos estandarizados generados por las regresiones longitud-peso para cada especie y se examinó el peso relativo (Wr, por sus siglas en ingles) de las especies más abundantes de cada grupo. Se llevó a cabo un ANOVA factorial de dos vías (factores: hidrología y ambientes) para evaluar la existencia de diferencias significativas espacio-temporales por grupos y por especies. Los resultados mostraron que la condición corporal de las especies detritívoras, herbívoras y omnívoras fluctuó significativamente en función de la hidrología y los ambientes. Óptimas condiciones corporales se registraron en la mayoría de las especies después del mayor pulso de inundación. La condición corporal disminuyó durante el período de aguas bajas y luego de dos períodos de desconexión, mientras que, durante el segundo pulso, aumentó en detritívoros, herbívoros y omnívoros. No hubieron inundaciones luego, pero ocurrieron dos pulsos de flujo y las condiciones corporales se incrementaron bajo estos escenarios hidrológicos, presentando valores similares o incluso mayores a los registrados luego del gran pulso. Esto destaca que los pulsos de flujo complementarios a los pulsos de inundación pueden tener un efecto positivo sobre la condición corporal de peces.

Palabras Clave: Flutuaciones hidrológicas, Grupos tróficos, Ictiofauna, Pulsos de inundación, Rio Paraná médio.

Introduction

Hypothetically, variations in hydrometric levels have a relevant influence on fish body condition. This attribute refers to the length/weight relationship in fish fauna and is understood as its health condition or well-being. Different methods have been developed to describe the effect of biotic and abiotic factors on body condition in fish species (Cone, 1989). Information on body condition is a key element for both research and fishing management (Anderson, Neumann, 1996) and allows for the establishment of relationships between intrinsic and extrinsic variables influencing fish fauna. It also gives information on fertility, reproduction, growth and death rates. Extrinsic factors like food availability and habitat morphology depend on environmental variables such as physical and chemical water characteristics (Holmes, Yousen, 1994). Intrinsic factors like ontogenetic changes (Teixeira de Mello *et al.,*

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2006), gonadal development and fat reserve are closely associated with the physiological state of organisms (Benedito-Cecilio *et al.,* 2005), over which intervene intra and interspecific interactions such as competition (Wyttenbach, Senn, 1993), predation (Dannewitz, Petersson, 2001), disease and parasitism (Machado *et al.,* 2005). Other factors typical of the species such as feeding and reproductive strategies also play a crucial role on fish body condition (Engelhard, Heino, 2006). Junk (1980) postulated that changes in hydrological conditions have an effect on the quantity and quality of available food in the environment. Indeed, food resource availability, its nutritional value and food digestibility are related to the dynamics of river floodplains. Changes in these dynamics can modify the trophic spectrum and feeding habits. They can also have an influence on trophic relationships among species (Lowe-McConnell, 1999).

Esteves, Aranha (1999) have suggested that variations in fish assemblages due to hydrology can explain quantitative and qualitative changes in the diet of different trophic groups (detritivores, herbivores, omnivores, piscivores, planctivores, invertivores and insectivores). For instance, in the case of piscivores, an increment of the duration and magnitude of floods produced a positive effect on the reproductive success of many prey species (Fernandes *et al.,* 2009). However, detritivores, omnivores and herbivores may be adversely affected during flood periods due to transport processes, since flow velocity increases and protein-rich food resources are carried away (Bowen, 1987; Faria, 2007). Thus, the caloric content of a fish belonging to a certain trophic level will depend on the environment as well as on the hydrological alterations (Benedito-Cecilio *et al.,* 2005).

Though the effect of floods on floodplain regulation over fish populations have been analyzed in different publications worldwide (*e.g.,* Welcomme, 1979; Lowe-McConnell, 1999), essentially only reproductive characteristics, recruitment and changes in structure have been referred to. Few of these traits are associated with the trophic nature of the ichthyofauna (Luz-Agostinho *et al.,* 2009). Some of those studies focus on the nutritional state of the fauna but are mono-specific (Gomes, Agostinho, 1997), only related to a particular trophic group (Luz-Agostinho *et al.,* 2008), or include species of a unique genus (Jepsen *et al.,* 1999). Finally, Abujanra *et al.* (2009) studied the influence of different hydrological cycles on the body condition of fish belonging to different trophic groups in the Upper Paraná River floodplain. The great alluvial plain of the Upper Paraná River in Brazil, where numerous dams were built since the end of the 1960s, differs from the Middle Paraná River in that the latter is a free-flowing water current (undammed and unregulated). In the middle reach of this river, Rossi *et al.* (2007) qualitatively underline the importance of floodplain habitats and their changes due to flood pulses for the feeding, reproduction and shelter of the different fish species.

It is important to understand the ecological role and effects of flow pulses, understudied in comparison with flood events, and they should be even more intensively studied and better understood (Espínola *et al.,* 2016) in relation with fish body condition. Contributing to the knowledge of the fluctuations of fish body condition in large floodplains and the effect of hydrological dynamics is of utmost importance for the conservation of fish fauna and for the proposal of management measures, as well as the evaluation of fishery resource plans.

In this study, it was expected that fish body condition in the Middle Paraná River floodplain would fluctuate under different hydrological scenarios, based on the assumption that the quality and quantity of food resources change with the flood/flow pulses. To evaluate this hypothesis, several trophic groups of the most frequent and abundant species living in lotic and lentic habitats were considered. Finally, observations were made about the functioning of the Paraná River ecosystem, highlighting the possible availability of food resources, regardless of the hydrologic changes, at least in the studied period. Guidelines about future research are also given.

Material and Methods

Study area. The Paraná River ranks ninth among the largest rivers in the world according to its mean annual discharge into the sea (18,000 m^3s^{-1}; Latrubesse, 2008). It shows seasonal changes in temperature, with the highest values recorded in December-March and the lowest in June-August (Drago, 1984). In its middle reach, the plain is characterized by an anastomosed pattern with an intricate drainage network in lotic-lentic environments (primary, secondary and tertiary courses, lakes and swamps with different degrees of connectivity; Paira, Drago, 2007). The typical hydrometric regime is marked by a high-water period in summer-autumn (December-April), and a low-water period in early spring (September-October) (Giacosa *et al.,* 2000).

This study extended from August 2010 to December 2012. The area under consideration is located in the alluvial plain of the middle reach of the Paraná River, within a secondary course known as Arroyo Catarata. This brook is situated on the left bank of the Coronda River, downstream from the Salado del Norte River mouth and 2.300 m to the southwest of the city of Santa Fe (Fig. 1). This minor channel is about 50 m wide, with an average depth of 5 m, and discharges measured during the study period ranged from 50 m^3s^{-1} (December 2010) to 300 m^3s^{-1} (April 2011).

In the lotic study area, two sampling stations were selected. They were separated from each other by a distance of 1.5 km. Lentic environments consisted of two lakes situated at a distance of 750 m and 850 m downstream from the first and second lotic sampling stations, respectively. These were located on the brook's left bank and were directly connected to it.
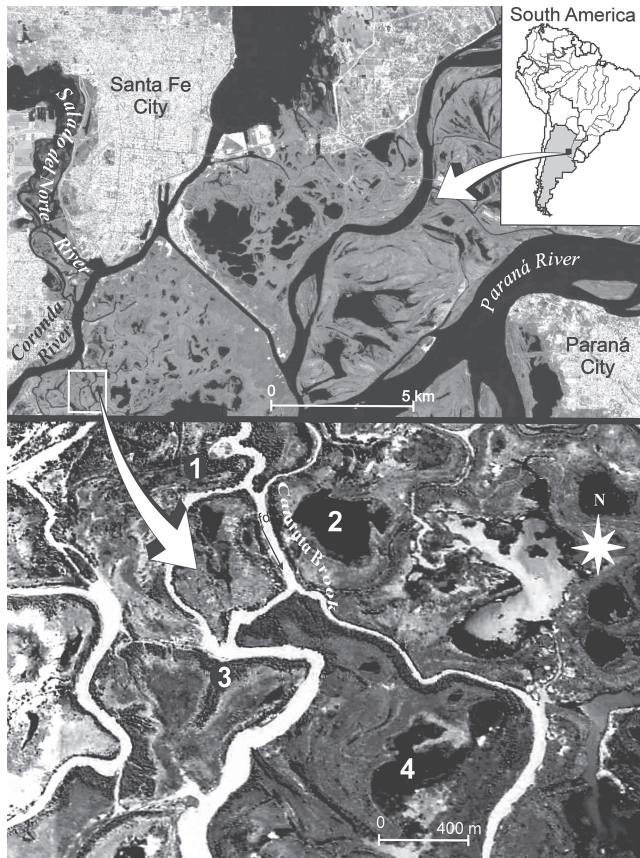
Fig. 1. Study area in the alluvial plain of the Paraná River and sampling sites (1 and 3: lotic habitats; 2 and 4: lentic habitats) located in the Catarata brook; fd=flow direction-modified from Espínola *et al.* (2014).

Fish collection was carried out on August and December 2010, April and August 2011, and March, August and December 2012. Effort, sampling frequency and fishing gear were standardized among surveys. Gillnets of different mesh sizes (3 cm to 16 cm between opposite knots) were used for fish capture. They were laid out for a period of 24 hours and checked every 8 hours. Caught fish were anaesthetized with 5% benzocaine and sacrificed. Specimens representative of the local fauna were deposited in the scientific collection of the Laboratorio de Hidroecología (LH; INALI-CONICET). All specimens were identified up to the species level using identification keys (*e.g.,* Ringuelet *et al.,* 1967; Graça, Pavanelli, 2007; Almirón *et al.,* 2008), and common biometric data was processed in the field [total length (Lt; cm), standard length (Ls; cm), total weight (Wt; gr)]. Moreover, on two sampling dates, sedimentological measures were carried out by gathering organic matter samples with an instantaneous collector (Van Dorn bottle; mg.l^{-1}).

Hydrological regime. Daily hydrological levels of the Paraná River at the Santa Fe Port were supplied by the Dirección Nacional de Vías Navegables de Argentina. During the study period, the hydrometric level's range of

variation was 4.45 m (minimum: 1.53 m on 18/5/2009; maximum: 6.02 m on 9/2/2010). The 4.50 m overflow level is the threshold above which the current starts to flood the plain in the study area (flood pulse), and 2.30 m is the level of disconnection (isolation) of most lentic bodies from the main course (Paira, 2003). Between floods and low-water periods, high-water level periods occur below the bank overflow (high magnitude variations of the hydrometric level within the channel banks). These fluctuations are referred to as flow pulses by Tockner *et al.* (2000). In the present study, flow pulses were considered as the hydrological variations below 4.5 m and up to 3.2 m.

Hydrometric levels were analyzed since January 2008 for a more general hydrologic context. Then, from 2010 to 2012 the hydrologic connectivity was quantified as the ratio between days with water levels higher and lower than 3.2 m (Tab. 1). It was decided to use the 3.2 m value instead of the overflow level of 4.5 m (suggested by Neiff, 1990) to highlight the influence of flow pulses on the connectivity with the nearby floodplain in the area of study. The 3.2 m level is an arbitrary value chosen to achieve this purpose and is equal to the average water level between 2008 and 2012.

Data analysis by trophic groups. Species richness (number of species captured) and fish abundance were calculated by catch per unit effort (CPUE: number of individuals/1.000 m^2 of gillnets in 24 hours) and were used to characterize fish assemblages. Captured species were classified according to feeding pattern into seven trophic groups (Fig. 2), in line with the existing knowledge about the Paraná River (*e.g.,* Ringuelet *et al.,* 1967; Hahn *et al.,* 2004; Almirón *et al.,* 2008). These trophic groups consisted of detritivores, herbivores, omnivores, piscivores, insectivores, planctivores and invertivores (Ringuelet *et al.,* 1967; Bechara *et al.,* 1999; Almirón *et al.,* 2008). The last three groups did not reach the minimum number of samples to be analyzed and thus were excluded from the study. Twenty-one species were selected considering their abundance and frequency in the fish catch (Tab. 2).
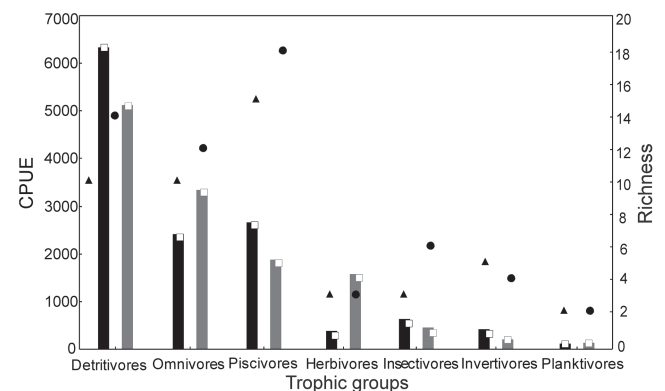
Fig. 2. Total fish abundance (CPUE: black bars = lentic; gray bars = lotic) and richness (species number: ● lotic; ▲ lentic) per trophic groups and per habitats along the period of study.

Tab. 1. Values of hydrological attributes in the area of study by sampling date from 2010 to 2012 (Isolation < 2.3 m; Midwater: between 2.3 and 3.2 m; Flow P=Flow pulse: between 3.2 and 4.5 m; Flood P=Flood pulse > 4.5 m). (*) There were no days with water levels lower than 3.2 m in the first half of 2010. Thus, it is not possible to obtain a quantitative value with the expression used for the computation of connectivity but it was the maximum through the entire period of study.

Attributes	Periods						
	2010		2011		2012		
Annual connect.	1.25		3.10		0.16		
Semestral connect.	MAX[(*)]	0.14	3.31	2.91	0.03		0.32
	Aug-10	Dec-10	Apr-11	Aug-11	Mar-12	Aug-12	Dec-12
Mean (month, m)	2.97	2.79	4.81	3.71	2.51	3.18	2.53
Mean (m)	3.13	2.55	4.74	3.49	2.43	3.18	2.28
Maximum (m)	3.16	2.68	4.77	3.49	2.45	3.24	2.3
Minimum (m)	3.09	2.55	4.7	3.49	2.42	3.1	2.27
Sampling dates	Midwater	Isolation	Flood P	Flow P	Midwater	Flow P	Isolation

Tab. 2. Species by trophic group in the 2010-2012 samples and the respective catalog number of voucher specimens of each specie. Rang of Ls variation (cm) by species per trophic group considering sizes obtained throughout the study period. Species selected for analyses by species are indicated in bold.

Trophic groups	Species	Catalog	Rang of variation Ls
Detritivores	**Cyphocharax platanus (Günther, 1880)**	LH11	7.1 - 16.1
	Cyphocharax voga (Hensel, 1870)	LH13	7.3 - 25.5
	Hypostomus commersoni Valenciennes, 1836	LH55	9.6 - 48.5
	Loricariichthys melanocheilus Reis, Pereira, 2000	LH58	14 - 39.5
	Loricariichthys platymetopon Isbrücker, Nijssen, 1979	LH59	12.2 - 37.5
	Prochilodus lineatus (Valenciennes, 1837)	LH20	9.4 - 43.5
Herbivores	**Schizodon borellii (Boulenger, 1900)**		13.5 - 35
	Schizodon platae (Garman, 1890)	LH27	7.5 - 38.4
Omnivores	**Astyanax abramis (Jenyns, 1842)**	LH4	5.8 - 13.5
	Astyanax asuncionensis Géry, 1972	LH5	6.7 - 17.5
	Astyanax rutilus (Jenyns, 1842)	LH7	8 - 9
	Megaleporinus obtusidens (Valenciennes, 1837)	LH15	7.4 - 40.1
	Pimelodus maculatus Lacepède, 1803	LH62	8.4 - 27
	Pterodoras granulosus (Valenciennes, 1821)	LH66	9.8 - 31.5
Piscivores	**Acestrorhynchus pantaneiro Menezes, 1992**	LH2	11.5 - 30
	Cynopotamus argenteus (Valenciennes, 1836)	LH10	6.5 - 24
	Hoplias aff. malabaricus (Bloch, 1794)		16.1 - 49
	Pygocentrus nattereri Kner, 1858	LH22	12.5 - 31
	Rhaphiodon vulpinus Spix, Agassiz, 1829	LH23	9.9 - 56.4
	Salminus brasiliensis (Cuvier, 1816)	LH26	18.4 - 54.5
	Serrasalmus maculatus Kner, 1858	LH28	7.5 - 21.5

Mean body condition was calculated taking into consideration the standardized residuals generated by regressions between the Wt and Ls logarithms in each species, according to Abujanra *et al.* (2009). To avoid misunderstandings about the effects of hydrology over the trophic groups, only the most abundant and frequent species recorded in all sample months throughout the period of study were considered for each group. This species subset was the same in all sampling periods. On the other hand, only months with sample numbers equal or higher than 5 were considered for groups. Use of standardized effort was performed to eliminate the effect of species that make up each trophic group. As the number

of samples was not enough, different statistical analysis for males and females could not be done.

Since assumptions of homoscedasticity and normality were fulfilled in all cases, a two-way factorial ANOVA of the standardized residuals, obtained independently for each species in each trophic group by hydrological phase and environment, was applied in order to evaluate whether there were significant spatial-temporal differences. A *post hoc* test, Tukey HSD (Honestly-significant-difference; Tukey, 1953) was carried out to identify these possible differences. Pearson´s correlations between body condition per trophic group and hydrometric level (m) and connectivity were assessed during sampling dates.

Data analysis by species. The most abundant species in each trophic group were selected (4 detritivores, 2 herbivores, 4 omnivores and 5 piscivores) to study their specific body condition (Tab. 2). No species were selected from the insectivore, invertivore and planctivore groups, because none of them reached the minimum number of samples required for analysis (Fig. 2). Relative weight (Wr) (Wege, Anderson, 1978) was used for the analysis of fish body condition by species. This method allows direct comparisons between different sizes in the same species, in accordance with Murphy´s equation (Murphy *et al*., 1990), developed from the method proposed by Wege, Anderson (1978). Relative weight was estimated through the following equation:

$$Wr = (W/Ws) \times 100$$

where: W is the specimen's observed weight, and Ws is calculated using the 75th-regression-line-percentile (RLP) technique (Murphy *et al.,* 1990), which is a length-specific standard weight predicted through a weight-length regression and constructed to represent the species (Anderson, Neumann, 1996). The form of the equation for Ws is:

$$Ws = a´ + b * \log_{10} (ls)\ 100$$

where: a´ is the intercept value, b is the slope of the $\log_{10}$(weight) - $\log_{10}$(length) regression, and ls is the standard fish length.

The objective of the Wr analysis is to provide a convenient, integrated measure for the physiological status of fish populations. Condition indices for fish, if carefully interpreted, can provide insights into the status of the ecosystem (Murphy *et al.,* 1990).

A basic concept for the interpretation of Wr is that the standard weight should describe the inherent shape of a fish in its "average" condition (median values are used here to denote "average"). When Wr values are well below 100 for an individual or a group, it is considered they are not in good condition (below the median), and when Wr values are well above 100, the individual or group are considered to be in good condition (above the median). When Wr values are near 100, fish are at the median condition for the population (or the condition representative of the average if another definition of "average" is used; Murphy *et al.,* 1991).

To evaluate spatial-temporal differences in each species, a two-way factorial ANOVA of the average Wr in each species and in each hydrological phase and by habitats was performed. Species belonging to the same genera were brought together for graphic representation. Moreover, spatial variation in *Schizodon spp.* and *Prochilodus lineatus* is presented separately, since they were the only species that showed significant spatial differences. For all analyses, the adopted significance level was p<0.05. Analyses were performed with R-statistical software (R Development Core Team, 2011).

Results

Hydrological and hydraulic fluctuations. Two flood pulses occurred as depicted by the hydrometric levels between January 2008 and December 2012 (Fig. 3). They had different intensities, durations and timing. The first one began on November 2009 and finished on May 2010, and remained 195 days above the 4.50 m level. Peak level was 6.02 m on February 2010. The second flood pulse started at the beginning of April and ended on May 2011. It had a shorter duration and a lower peak level: 47 days above 4.50 m and 5.10 m at the end of April, respectively. Flood pulses did not occur during 2012, but values below the disconnection level were recorded during 58 days (Fig. 3). Two remarkable flow pulses could be seen on August 2011 and July 2012, with maximum levels of 4.17 m and 3.97 m, respectively.
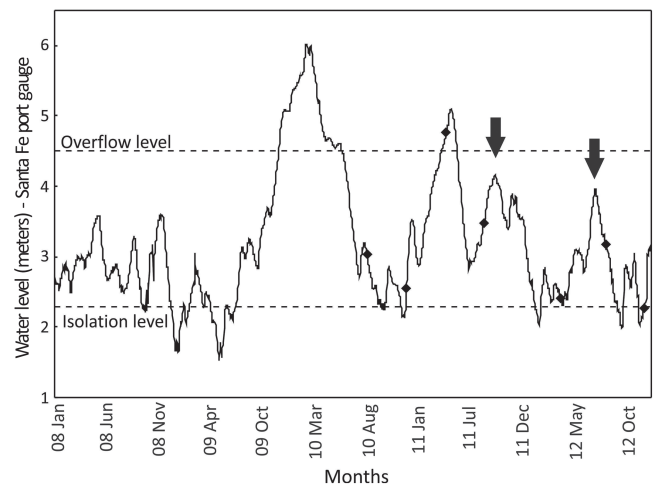

Fig. 3. Daily water levels between January 2008 and December 2012. Full circles: fish samplings. Arrows: 2011 and 2012 flow pulses with hydrometric levels above 3.2 m and below the overflow level.

Variations in hydrologic connectivity as a result of the water fluctuations mentioned above are shown in Tab. 2, computed annually and every 6 months. On the other hand, values in suspended organic matter showed a reduction during flood pulse events (10.73 and 6.85 mg.l^{-1} on August 2010 and April 2011, respectively).

Spatial-temporal variation in body condition by trophic groups. During this study, a total of 4.334 individuals belonging to 65 species were caught, and then separated into seven distinct trophic groups. Were selected 21 species, including herbivores, detritivores, omnivores and piscivores, which represented 93% of all specimens caught during the three years of the investigation. These belonged to 2 orders (Characiformes and Siluriformes) and 10 families. Detritivores, omnivores and piscivores were dominant in regard to richness and biomass density in the area (Fig. 2; Tab. 3).

Tab. 3. Number of specimens (N°) and species (S) per trophic group recorded by sampling date considered for the analysis of the mean and standard error of the standardized residuals (Fig. 4).

Months	Herbivores		Detritivores		Omnivores		Piscivores	
	S	N°	S	N°	S	N°	S	N°
Aug.10	2	194	5	1042	4	426	7	258
Dec.10	2	58	6	438	4	157	7	100
Apr.11	2	8	6	58	5	34	6	16
Aug.11	2	22	5	22	5	165	4	14
Mar.12	2	16	5	69	3	35	7	107
Aug.12	2	18	6	127	3	52	6	77
Dec.12	2	17	6	56	5	16	7	109
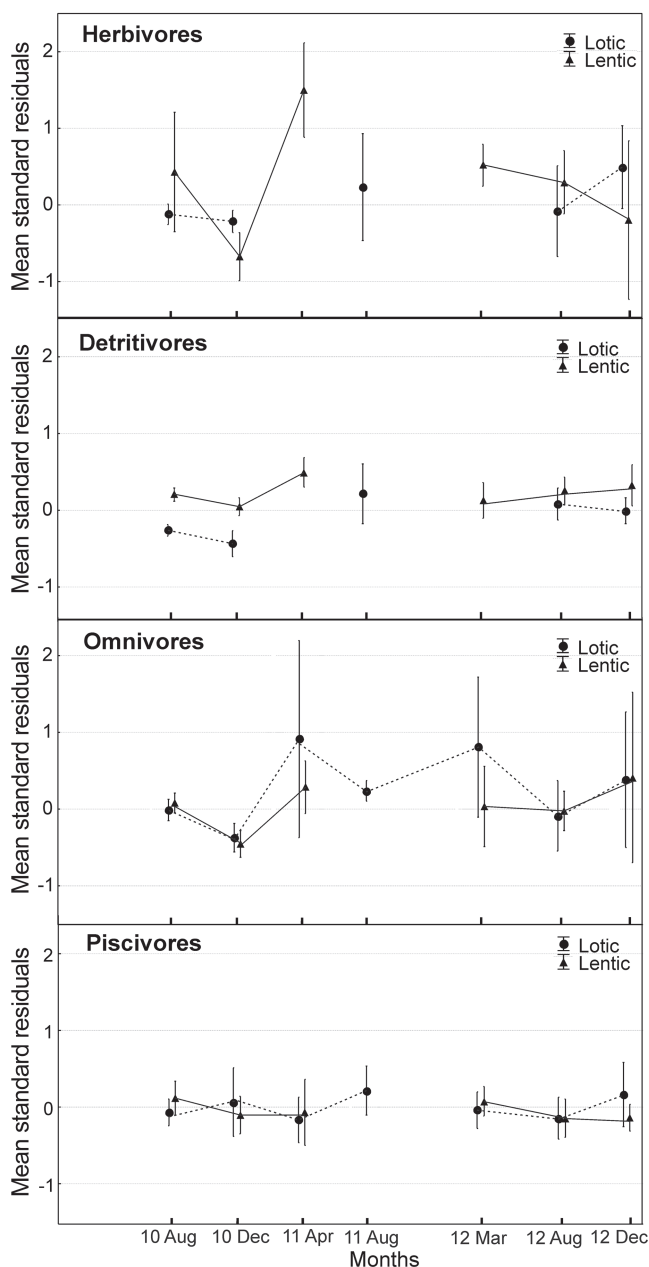
Fig. 4. Mean and standard error of standardized residuals for fish trophic groups by environments during the study period.

Detritivores showed significant spatial (F=85.928, p<0.001) and temporal differences (F=4.691, p<0.001) in body condition. The spatial-temporal interaction with body condition was significant in herbivores (F=3.089, p=0.027). In omnivores, body condition showed significant temporal differences (F=8.592, p<0.001). Piscivores did not present statistically significant space-time changes in body condition, although body condition increased during the first flow pulse (in lotic habitats; Fig. 4).

A highly significant temporal increase in body condition occurred during the flood pulse in detritivores (April 2011, in lentic habitats) compared to August (p<0.001) and December 2010 (p<0.001) (Fig. 4). Herbivores showed the most significant spatial-temporal variation in body condition (Fig. 4). A considerable rise in lakes during the flood pulse compared to August (p<0.001) and December (p<0.001) of 2010, and on August (p=0.014) and December (p=0.045) of 2012 must be taken into consideration.

In general, omnivores displayed similar values through the months and among the environments (Fig. 4). On December 2010, a less significant difference in body condition between lentic-lotic environments was determined, as compared to that of August 2010 (p<0.001), during 2011 (p<0.001) and on March and December 2012 (p=0.015; p=0.017). The body condition increased during the flood pulse.

Correlations performed between the mean hydrometric level (m) for each sampling campaign and the semestral connectivity with the body condition by trophic groups were significantly positive for herbivores (r=0.219, p<0.001; r=0.302, p<0.001) and omnivores (r=0.159, p<0.001; r=0.133, p<0.001), and to a lesser extent for detritivores (r=0.085, p<0.001; r=0.112, p<0.001). Correlations were not significant in piscivores (r=0.051, p=0.184; r=-0.004, p=0.905).
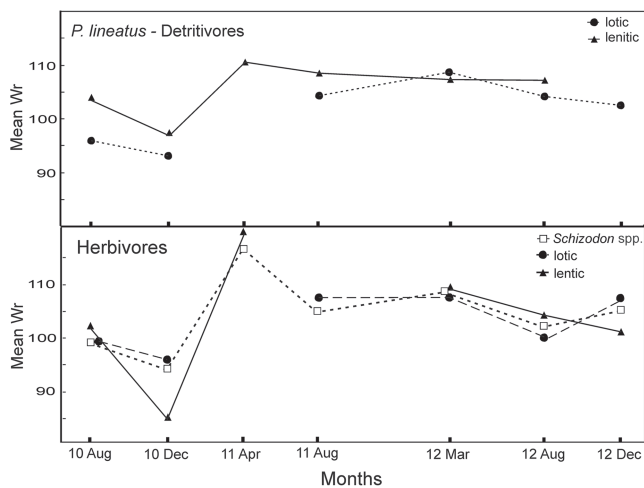
Spatial-temporal variation in body condition by species. Different tendencies in body condition between the studied species were observed in detritivores over time (Fig. 5). *Loricariichthys platymetopon* did not show significant spatial and/or temporal differences (Fig. 5). The *Cyphocharax* genus (*C. voga* and *C. platanus*) presented an increase in body condition during the first flow pulse (August 2011) (Fig. 5). *Prochilodus lineatus* showed temporal (F=12.983, p<0.001) and spatial differences (F=75.215, p<0.001; Fig. 6). Body condition in *P. lineatus* increased during the flood pulse (April 2011). Values for these attributes registered in lakes were higher than those recorded in lotic environments (Fig. 6).

The omnivorous species *Megaleporinus obtusidens* (F=5.537, p<0.001), as well as species in the *Astyanax* genus *(A. asuncionensis,* F=12.651, p<0.001; *A. abramis,* F=5.536, p=0.001) showed temporal differences. Piscivores did not present significant spatial-temporal differences. Temporal variation in body condition in the five most abundant species changed considerably

among them (Fig. 5). *Hoplias* aff. *malabaricus* (F=9.586, p<0.001), *Salminus brasiliensis* (F=5.594, p<0.001) and *Cynopotamus argenteus* (F=2.221, p=0.05) displayed significant temporal differences. *Salminus brasiliensis* exhibited below average body condition values during low-water periods (Fig. 5). In the case of herbivores, two species of the *Schizodon* genus were analyzed, both showing significant temporal differences (F=5.162, p<0.001; F=11.475, p<0.001). Their body condition increased during the flood pulse (Fig. 6).
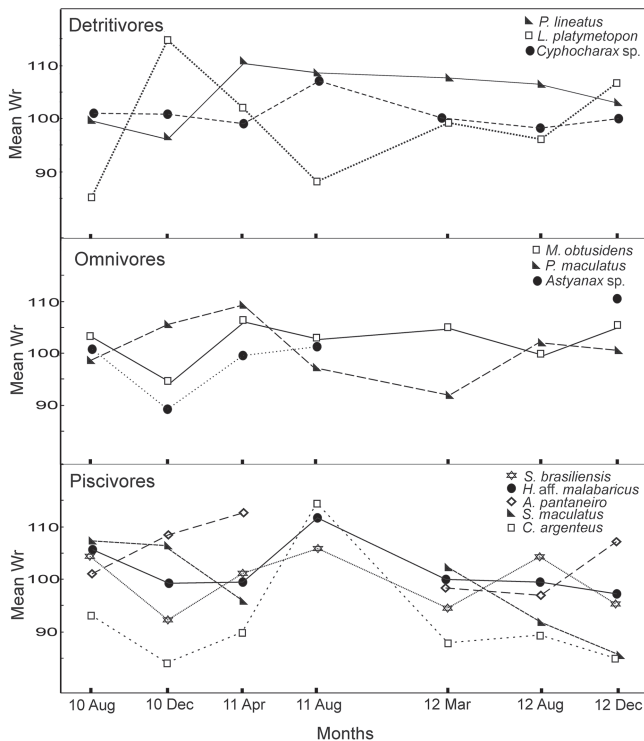
Fig. 5. Temporal variation in mean body condition of selected species for each trophic group.

Fig. 6. Spatial and temporal variation in body condition average in *Prochilodus lineatus* per habitat; *Schizodon* spp. (*S. platae* and *S. borellii*) total and per habitat.

Discussion

Hydrologic connectivity between the main water courses and their nearby floodplain is a crucial factor upon which the proper functioning of river-floodplain ecosystems such as the Paraná River depends (Neiff, 1990). The increasing/decreasing connections between habitats as water levels fluctuate are vital routes for fish and for the transport of the organic/inorganic matter that sustains the biota. Indeed, quantification of this connectivity helped evaluate the nature of the relationship between fish body condition and hydrology.

Biotic and abiotic conditions in the Paraná floodplain are affected by periodical floodings. These floods contribute to the organic matter exchange between lotic and lentic environments, and create new, highly productive zones for aquatic communities (ATTZ, aquatic/terrestrial transition zones, the area that alternates between aquatic and terrestrial environments; Junk *et al.,* 1989). Such transition zones, which are periodically inundated, allow for the rapid recycling of organic matter and nutrients, and this in turn results in high productivity (Junk *et al.,* 1989). Increases in hydrometric level positively affect food availability for fish as allochthonous resources are incorporated into the plain (Abujanra *et al.,* 2009).

In the present case, the first flood pulse produced sustained connectivity between the floodplain environments. In this context, herbivores, omnivores and detritivores exhibited good general body condition (August 2010, mid-water, after the flood pulse), which might be caused by the run-off of large quantities of organic matter as well as the incorporation of allochthonous resources during the flood event. Those groups, especially herbivores, might have taken advantage of the good feeding conditions created by the previous inundation, which gave access to larger flooded areas. These areas contributed with new habitats; these in their stead provided new surface for subsequent vegetative recruitment and growth, and favoured the transport of food resources (nutrients and organic detritus) from the floodplain to the river. They also provided access for allochthonous resources and suspended sediments transported from the river to the floodplain (Tockner *et al.,* 2010).

On the other hand, optimum conditions for fish recruitment were present during the 2010 flood pulse, with high temperature values, a long duration and the covering of an extensive floodplain area (King *et al.,* 2003). Abrial *et al.* (2014), in the same study area, registered higher richness and fish abundance values after this flooding, and individuals were mainly small in size (juveniles), a fact associated with the previous greater connectivity in the floodplain. This event was likely to have favored the reproductive processes of most migratory species, such as *Prochilodus lineatus, Pterodoras granulosus* (LM: large migrations), *Cynopotamus argenteus* and *Schizodon platae* (SM: short migrations) (Abrial *et al.,* 2014). Such periods

of large recruitment in the floodplain can give place to strong competition, modifying patterns in body condition variation per trophic groups.

Low values in body condition recorded on December 2010 for herbivores, detritivores and omnivores are the result of the low connectivity period registered in the plain, which sustained six months of average and disconnection water levels. It must be pointed out that the period of reduced food availability, at least for detritivores and omnivores, coincides with the low-water phase (Tello *et al.*, 1992). These variations (low/high connectivity periods) allow for a differentiation in fish body condition (increase and/or decrease) in trophic groups and their more frequent and abundant species, in response to the hydrological fluctuation. Ground food resources (Hahn *et al.*, 2004) have an important role in regions ruled by flood pulses and characterized by impounded floodplain areas. Connectivity in these plains has an important role in the ecology of fish communities, and the importance of ground resources varies with the season (Hahn *et al.*, 2004). Variation trends in body condition do not have the same pattern in all fish species. For this reason, Bechara *et al.* (1999) were not able to establish a clear pattern for fluctuations in body condition in different fish species of the upper reach of the Paraná River (Misiones).

Detritivores registered a lower body condition in 2010 as compared to that of 2011, but similar to that of the year 2012 (during which a flow pulse occurred). The temporal tendency observed in this group is mainly influenced by *Prochilodus lineatus* (Fig. 6), which represents the highest biomass in the system. During the second flood pulse, on April 2011, as well as during the flow pulses, an increase in body condition was observed, especially in the case of *P. lineatus*. Tello *et al.* (1992) assumed that this group may have higher food availability during the mid-water period, when decomposing organic matter provided by the flooded area is exploited by the fish community before the isolation period. Furthermore, higher body condition recorded since 2011 in both environments would indicate that flood delay has a positive effect on weight increase, a fact that is in line with the observations made by Abujanra *et al.* (2009).

As to piscivores, the duration and magnitude of floods have a positive effect on the reproductive success of many prey species, increasing food availability for this group (Fernandes *et al.*, 2009). The 2009-2010 pulse presented characteristics that favored juvenile recruitment in most species of the Middle Paraná River floodplain (Abrial *et al.*, 2014). An example was *Salminus brasiliensis,* which registered high body condition after the flood pulse and lower values on December 2010, after four months (from mid-September to mid-December) of low-water levels (below 3.00 m in the Santa Fe Port), with a total of 30 days of complete disconnection. Good body condition is necessary to achieve reproductive success (Engelhard, Heino, 2006; Thorsen *et al.*, 2006).

Concerning detritivores, their ability to change their diet according to food availability would be affected by flood pulses, the same as in omnivores. Food ingested by these trophic guilds in the upper reach of the Paraná River during flood pulses contain less energy and fewer proteins (Faria, 2007). Hence, the nutritional value of the resources consumed by these groups has a spatial (Bowen, 1987) and temporal (Abujanra *et al.,* 2009) pattern of variation. Even though suspended organic matter decreased during the flood pulse, the body condition in *Megaleporinus obtusidens* (an omnivore) increased during flood and flow pulses, maintaining above average values even in 2012. In agreement with Gomes, Agostinho (1997), high hydrometric levels favor detritivorous and omnivorous species that find greater food and shelter availability in the floodplain, and disfavor large predators (piscivores).

In regard to herbivores, as well as omnivores and detritivores, body condition increased during the second flood pulse in lakes. This may explain the fact that groups take advantage of floods in order to gain access to the plain's lentic environments to feed. In addition, throughout the study period, body condition in detritivores (more precisely, in *P. lineatus*) was higher in lakes, with the exception of the year 2012, when values were similar between environments. This tendency shows that, after floods, detritivores would opt to dwell in lakes instead of lotic ecosystems. Two hypotheses could explain this: a) high connectivity in the floodplain gives access to the lakes, which are rich feeding places; and b) the energetic cost of swimming is lower in lentic systems.

As to piscivores, body condition increased on August 2011, after the flood and during the flow pulse. At the species level, this is the case in *Cynopotamus argenteus* and *Hoplias* aff. *malabaricus*. Despite these increases, it is appropriate to remark that both the spatial-temporal fluctuations and the correlations between body condition and hydrological attributes were not significant. This could be attributed to the lower variability in the nutritional value of food resources (preys) available for piscivores (Abujanra *et al.,* 2009), independently of the hydrometric level.

Piscivores, as well as detritivores, showed similar tendencies in body condition between habitats and time, presenting the lowest variation of all. Conversely, herbivores showed the highest space-time variation in body condition. According to Goulding (1980), this group does not exhibit a particular strategy regarding food intake. Hence, depending on their resources, herbivores could either feed throughout the entire year, or only through certain periods that depend on food availability and reproductive activity. Furthermore, after a period of high feeding activity, they produce fat to accumulate reserves.

Differences in biological species, such as reproductive and dietary strategies and habitat use, make the analysis more complex, and conclusions about fluctuations in body condition by trophic groups are more difficult to achieve. At the group level, increases were observed in 2011, with

the occurrence of the second flood pulse. Meanwhile, at the species and genus levels, such as in *P. lineatus, Schizodon* spp.*, M. obtusidens* and *S. brasiliensis,* good conditions were recorded in mid waters in 2010 (after the first pulse), in 2011 (during and after the second pulse), and also in 2012, during the flow pulse and disconnection periods.

In this sense, floods are considered beneficial for fish with respect to feeding and nutritional reserve accumulation, due to biomass transported by run-off (Bennemann *et al.,* 1996) and access to new resources in the flooded area (Machado-Allison, 1992; Lowe-McConnell, 1999). On the other hand, although it is well known that flood pulses yield benefits for fish communities, mid-water periods are just as important (Neiff, 1990), and this was made evident in the analysis of the results. In this study, fish groups in general showed good body condition during mid-water phases (even during the year 2012, when there were no floods).

Even though these benefits cannot be only attributed to hydrology, the multiple connections between lotic and lentic environments, generated in the plain during flow pulses, favored access to richer food areas (although not to the same extent as during floods), thus improving fish body condition. In keeping with this idea, these intermediary hydrological phases, which have not been thoroughly studied yet (previous studies focused mainly on flow pulse occurrence), could have a relevant ecological importance for the ichthyofauna.

The need to continue with this research, especially at the species level, must be remarked. This would give detailed knowledge about variations in the body state of floodplain ichthyofauna in relation to hydrological changes such as droughts, intermediary fluctuations and floods, which are essential in the maintenance of large river ecosystems. It follows that it is necessary to carry out this type of studies with the aim of increasing our knowledge about the behavior of fish communities in floodplains like those of the Paraná River in its middle reach. In this way, additional information for future ichthyofauna preservation plans in different environments of the floodplain could be acquired (*e.g.*, habitat loss due to extended low-water periods).

Acknowledgements

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