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Effects of river damming in Neotropical piscivorous and omnivorous fish: feeding, body condition and abundances

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The increase in abundance of small-sized fishes is common after a reservoir is formed. There is an increase in the consumption of fish, from typically piscivorous fish to opportunistic species that take advantage of abundant resources. This study aims to evaluate the effects of diet changes induced by damming on the feeding activity and condition factor of typically piscivorous (*Hoplias* aff. *malabaricus* and *Oligosarcus longirostris*) and opportunistic (*Astyanax lacustris* (ex *Astyanax altiparanae*) and *Pimelodus britskii*). Sampling was conducted before and after the impoundment in the Iguaçu River in the region of Salto Caxias, Paraná State, Brazil. Stomach contents were analysed by the volumetric method. Feeding activity and body condition were inferred by the mean stomach repletion index and the mean condition factor. Typically piscivorous species presented a general tendency of decreased feeding activity and increased condition factor, while opportunistic species, presented a decrease in condition and feeding activity in the most affected sites. The increase in the condition factor of piscivorous fish suggests that these species benefit by the increased abundance of small size prey fish. Some opportunist species that do not have adjustments for the piscivorous diet, regardless of the intensity of consumption and resource availability, can suffer negative reflex when adopting a piscivorous diet.

O aumento na abundância de peixes de pequeno porte é comum logo após a formação de um reservatório, levando a um aumento no consumo de peixes, tanto por peixes piscívoros como oportunistas que se aproveitam do recurso abundante. Esse estudo visa avaliar os efeitos da mudança de dieta induzida pelo represamento na atividade alimentar e condição nutricional, tanto de espécies piscívoras (*Hoplias* aff. *malabaricus* e *Oligosarcus longirostris*) quanto de espécies oportunistas (*Astyanax lacustris* (ex *Astyanax altiparanae*) e *Pimelodus britskii*). Para tanto, foram realizadas amostragens nas fases pré e pós-represamento no rio Iguaçu na região de Salto Caxias, Paraná, Brasil. Os conteúdos estomacais foram avaliados pelo método volumétrico. A atividade alimentar foi determinada pelo índice de repleção estomacal e a condição nutricional através do fator de condição relativo. As espécies tipicamente piscívoras apresentaram, em geral, incremento no fator de condição e queda na atividade alimentar e a espécie mais oportunista apresentou queda no fator de condição e índice de repleção nas regiões mais afetadas pelo represamento. O aumento no fator de condição de espécies piscívoras sugere que estas se beneficiam pelo aumento de abundância das espécies de pequeno porte. Enquanto espécies que não possuem adaptações para uma dieta piscívora, independente da intensidade de consumo e disponibilidade desse recurso, podem sofrer reflexos negativos em sua condição nutricional, em detrimento da ausência de pré-adaptações à piscivoria.

Keywords: Condition factor, Feeding activity, Opportunist diet, Piscivory, Reservoir.

Introduction

Piscivorous fish impact the aquatic community and water quality (Nowlin *et al*., 2006) contributing to the stabilisation of food webs (Rooney *et al*., 2006). Predators may have large impacts on ecological systems as they remove vulnerable organisms from the environment (Lima, 1998).When a predator's foraging behaviour shifts, it can affect the stability of predator-prey population dynamics (DeAngelis *et al*., 1975), spatial distribution of predators (Van Der Meer & Ens, 1997), food chain length (Schmitz, 1992) and the strength of species interactions in complex food webs (Novak & Wootton 2008).

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The formation of reservoirs leads to deep structural changes in fish communities in relation to the original fluvial system. After damming, most rheophilic species disappear and those that persist are confined upstream and in the mouth of tributaries, where the habitat conditions are more similar to the original (Agostinho *et al*., 2008). The new environment is colonised largely by those species with pre-adaptations for the lentic condition (Fernando & Holcik, 1991) and those with opportunistic strategies. Dominant species in a new reservoir are small-sized, with feeding plasticity, low longevity and high reproductive performance (opportunist strategy, *sensu* Winemiller, 1989), denoting advantages in the colonisation process (Agostinho *et al*., 1999). This small sized species become an abundant resource and explains the success of piscivores after impoundments (Luz-Agostinho *et al*., 2006; Hahn & Fugi, 2007; Bennemann *et al*., 2011).

Extensive incorporation of allochthonous material, as invertebrates and plants, during the reservoir filling provides an important contribution of food resources for fish (Loureiro-Crippa & Hahn, 2006). The high availability of allochthonous resource in the environment, may cause a positive effect in the production of all trophic levels, an event known as the trophic upsurge period (Kimmel & Groeger, 1986; O'Brien, 1990; Gubiani *et al*., 2011). The high availability of small body size species in the new environment should increase the frequency of fish with a carnivorous fish diet (Novakowski *et al*., 2007) or even lead some omnivorous species to piscivory (Luz-Agostinho *et al*., 2006; Delariva *et al*., 2007). Although the nutritional quality of a fish-based diet should be higher than one based on other items, such as invertebrates, due to its high protein (Anthony *et al*., 2000) and energy content (Davis *et al*., 1998), the organism's response to this consumption should differ according to the species diet in the natural environment. Typically piscivorous species have pre-adaptations, both morphological (body size, position and size of the mouth opening, adaptations in the digestive tract) and behavioural (capture strategies of prey) (Zavala-Camim, 1996), that provides a greater profit by consuming this abundant resource after the damming than among the less specialized, that consume opportunistically.

An efficient way to determine the energy intake of an individual is the condition factor, which reflects the recent nutritional status of the fish and the expenditure of reserves in activity (Vazzoler, 1996). Such methodology has been used by several authors to describe the impacts of reservoir formation in fish assemblages (Gubiani *et al.,* 2009; Pacheco *et al*., 2009; Abelha *et al*., 2012; Orsi & Britton, 2014). The condition factor expresses individual wellbeing with respect to the environment and it compensates for changes in the form or condition with length (Le Cren, 1951). This index can be used to indicate whether an individual is in better or worse condition than others of the same length (Árnason *et al*., 2009). It also provides valuable information for the understanding of species ecology, as they reflect the prevailing environmental conditions (Abelha *et al*., 2012).

Thus, it is expected that the increase in the abundance of small sized fish should lead to an increase in piscivory and in the nutritional status of fish with pre adaptations to piscivory. In this context, the present study aims to evaluate changes in abundance, as well as in diet and its effect on the nutritional state of the species that presented a piscivorous diet during the first year after Salto Caxias Reservoir formation. The hypothesis is that changes occur in the nutritional status and species that were essentially piscivorus before the impoundment should have higher energy gain in relation to those species in which fish become important in the diet only after damming.

Material and Methods

Sampling. Was carried out before and after the Salto Caxias Reservoir filling, located in Iguaçu River (25º32'35"S/53º29'43"W) and closed in October 1998. Samples were taken quarterly before damming from March 1997 to February 1998, and after the closure of the dam from April 1999 to January 2000.

The 14 sampled sites were selected according to their position in respect to the dam. Including five sites located on tributaries of Iguaçu River 10 to 20 km upstream from their mouth (TU - tributaries upper sections not affected by the reservoir), and five sites in lower sections flooded by the reservoir (TL - tributaries lower sections) in each of the considered tributaries. In addition, there were two sites upstream from the main river (Iguaçu River - UP), one site in the reservoir (RE) and one downstream from the dam (DO) (Fig. 1). It is important to highlight that all sites suffered direct or indirect impacts due to damming, or in a lesser extent, as in the upstream and tributaries upper section areas, or greater as in dam and downstream areas.

Samples were taken using gillnets (mesh sizes ranging from 3.0 to 16.0 cm between opposite knots, 12 simple gillnets and 3 trammel nets) operated for 24 h and checked every 8 h.

Laboratory procedures. Fish were identified by taxonomists and vouchers specimens were deposited in the Fish Collection of Nupélia (UEM/Maringá/Numbers: NUP 2452, NUP 687, NUP 721, NUP 1786). After identification, specimens were measured (total and standard length), weighed (total weight) and gutted; stomachs containing food were fixed in 4% formalin and later transferred to ethanol 70%. The stomach contents were examined to identify food items under a stereomicroscope and optical microscope. The contents were measured by the volumetric method (Hyslop, 1980; Ahlbeck *et al*., 2012): the total volume of a food item taken by the fish population is given as a percentage of the total volume of all stomachs contents, estimated using graduated test tubes and a glass counting plate (Hellawell & Abel, 1971).

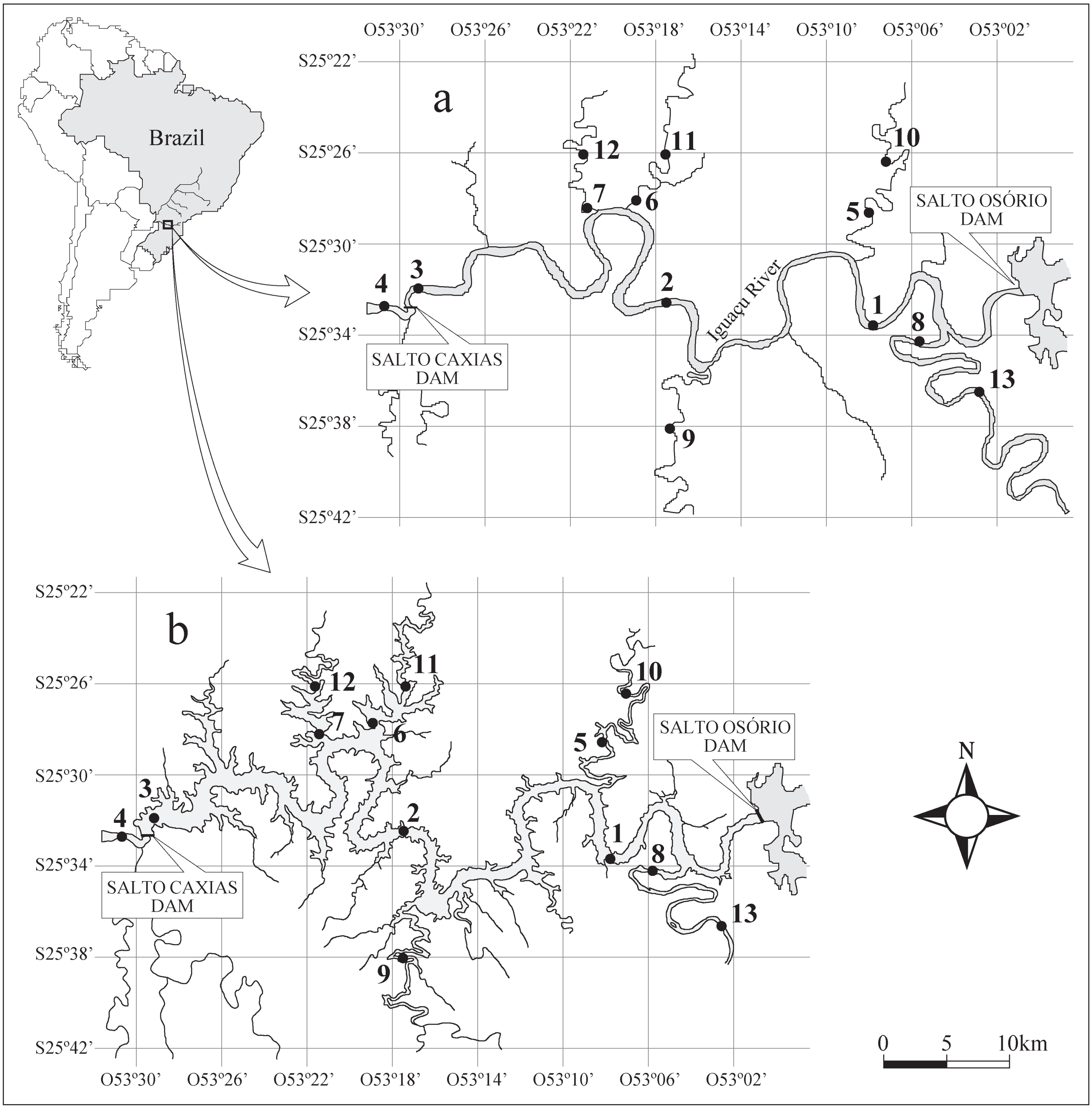

Fig. 1. Location of the sample stations in the Iguaçu River and the dam influence area. a) Before damming. b) After damming. [Point 1-2 = upstream from the Iguaçu river (UP); point 3 = reservoir region (RE); point 4 = downstream (DO); 5-9 = tributaries low section (TL); 10-14= tributaries upper section (TU)].

Data analysis. The chosen species were *Astyanax lacustris* (Lütken, 1875) (ex *Astyanax altiparanae* Garutti & Britski, 2000 (Lucena & Soares, 2016)), *Hoplias* aff. *malabaricus*, *Oligosarcus longirostris* Menezes & Géry, 1983 and *Pimelodus britskii* Garavello & Shibatta, 2007, all of which were selected on the basis of their abundance and feeding habits. *Astyanax lacustris* and *P. britskii* as opportunistic species and *H.* aff. *malabaricus* and *O. longirostris* as tipically piscivorous.

The fish abundance was indexed as catch per unit effort (CPUE), estimated by the ratio between the number of individuals collected by day and the area of the nets used in the sampling, multiplied by 1000 (unit: number of individuals/1000 m² net set for 24h). To evaluate the differences in the species abundance before and after damming, a non-parametric Scheirer-Ray-Hare test (Dytham, 2011) was applied to the data. Period (before and after damming) and sites were used as factor and the CPUE as the dependent variable.

Possible differences in species diet before and after damming were evaluated by a Permutational Multivariate Analysis of Variance (Permanova, Anderson, 2006) using period and sites as factor and diet data, log +1 transformed, as dependent variable.

Food items were pooled into broader categories, named detritus/sediment (particulate organic matter in different stages of decomposition and with mineral particles present), algae (filamentous and unicellular), plants (fruit, seeds and leaves of vascular plants and bryophytes), insects (Coleoptera, Diptera, Ephemeroptera, Hemiptera, Hymenoptera, Isoptera, Megaloptera, Odonata, Orthoptera, Plecoptera and Thichoptera), microcrustaceans (Copepoda and Cladocera, especially planktonic species), macroinvertebrates (Arachnida, Bivalvia, Gastropoda, Annelida and Diplopoda), microinvertebrates (Testacea, Porifera, Rotifera, bryozoa, Nematoda and Ostracoda) and fish (identified to the lowest taxonomic level possible).

The nutritional status was given by the relative condition factor (K; Le Cren, 1951) and the feeding activity was determined using averages of the repletion index (RI). The repletion index (RI) was estimated for each individual through the relative contribution of stomach weight (We) to total weight (Wt) (RI=We/Wt x 100). Each of these index estimated the nutritional state of the individuals in different time scales; repletion index estimates the amount of food ingested in a short temporal scale and the condition factor represents the nutritional state of an individual in a larger scale. Finally, the degree of changes in the feeding habit was based on the volumetric proportion of fish included in the diet (piscivory) in each period.

Variations in the condition factor were evaluated for each individual based on the relative condition means, which were calculated using the equation: K=Wt/Wt', where Wt is the individual weight and Wt' is the estimated weight based on the standard length (Ls) and weight relationship. The Wt' represents the expected weight that a fish with a determined Ls is expected to possess, instead of the observed weight (Wt) (Le Cren, 1951).

The parameters of the Ls × Wt relationship, needed to estimate the condition factor, considered all individuals captured for each species. Differences between the sexes were tested using analysis of covariance (ANCOVA), with weight as the dependent variable, length as the predictive variable and sex as the covariate; if differences between sexes were significant, the relationship Ls x Wt was estimated for each sex separated and, after the condition factor was obtained, they were grouped for analysis. The standard length and weight data were log-transformed for fitting in the test assumptions. To reduce the effect of those less represented length classes, the analyzes were performed for the length class covering the largest possible number of adults (Gomes & Agostinho, 1997), by this, analyses were performed for a pre determined class size, after the elimination of young and very small/large adult individuals that did not present sampling sufficiency.

The degree of piscivory was obtained as the percentage of volume of fish consumed in total diet. Also, to evaluate whether the variations in the nutritional condition were directly related to these changes in the feeding habit (piscivory), a Pearson correlation was applied to the percentage of fish consumed in total diet by each species for period and the condition factor of each analysed species (Dytham, 2011). To test possible differences in the condition factor and the repletion index between periods and sites, a factorial analysis of variance (ANOVA) was applied to both variables, with period (before and after damming) and sampling sites (downstream, reservoir, upstream, tributaries lower section and tributaries upper section) being used as factors. Finally, to evaluate if changes in the condition factor are related to the amount of ingested food or if it is related to other environmental changes, a Pearson correlation between repletion index and condition factor was applied.

The statistical tests were performed with the R Programming Environment (The R Project for Statistical Computing, http://www.r-project.org/) using the Vegan package (Oksanen *et al*., 2015) and the graphics in Statistica Statsoft 10 (StatSoft Inc., 2011).

Results

All species considered in this study presented significant increases in abundance (CPUE), after damming. The Scheirer-Ray-Hare test detected significant interaction for sites and periods for all species, except *P. brtskii* that presented significant differences for sites and periods (Table 1). The studied species that had a greater increase in the general abundance (CPUE) was *A. lacustris,* with an abundance (CPUE) 30 times higher in the period after damming than the period before damming. *Hoplias* aff. *malabaricus* and *O. longirostris* presented, in average, an increase in abundance (CPUE) four times higher than the period before damming. *Pimelodus britskii* abundance (CPUE) was the one that showed less increase in the after damming period, only two times the abundance (CPUE) of the before damming period.

Table 1. Scheirer-Ray-Hare test and Permutational Multivariate Analysis of Variance applied to abundance (CPUE) and diet, respectively, for sites and periods for the analysed species in the Iguaçu River and its tributaries, in the Salto Caxias Reservoir region.

Species	Factor	Abundance (CPUE)		Diet	
		SHR	p	*pseudo*-F	p
A. lacustris	Site	17.35	<0.001	0.0535	0.001
	Period	12.29	<0.001	0.0154	0.011
	Site*Period	6.02	0.014	0.01727	0.005
H. aff. *malabaricus*	Site	9.84	0.001	0.03306	0.001
	Period	13.03	0.003	0.03828	0.001
	Site*Period	4.71	0.029	0.02865	0.001
O. longirostris	Site	18.5	<0.001	0.02172	0.001
	Period	2.7	0.09	0.03415	0.001
	Site*Period	7.99	0.004	0.02431	0.001
P. britskii	Site	5.22	0.022	0.03278	0.001
	Period	24.59	<0.001	0.02026	0.001
	Site*Period	3.24	0.07	0.01253	0.001

When considering sites *H.* aff. *malabaricus* presented a higher increase after damming in the downstream and lower tributaries regions, *O. longirostris* in the downstream, reservoir and upstream sites and *A. lacustris* and *P. britskii* in the reservoir and downstream sites. The abundance (CPUE) of fish species used as prey increased especially in the downstream and reservoir sites (Fig. 2).

All species presented significant differences in diet after damming according to site (Table 1). Before the impoundment, *A. lacustris* consumed high proportions of plants and very low proportions of fish (only fish scales). After the dam closing, this species also consumed large amounts of fish, mainly in reservoir areas and downstream the dam (Table 2). Fish consumed by this species could not be identified because they consisted only of partially digested fragments (fish pieces) and fish scales. *Hoplias* aff. *malabaricus* presented a diet exclusively based on fish in both periods, with a notable exchange of Ciclidae by Curimatidae (*Cyphocharax* cf. *santacatarinae* - Table 3). *Oligosarcus longirostris* and *P. britskii,* showed diets based mainly on insects and fish before damming, and exhibited a diet essentially based on fish in the period after damming (Table 2).

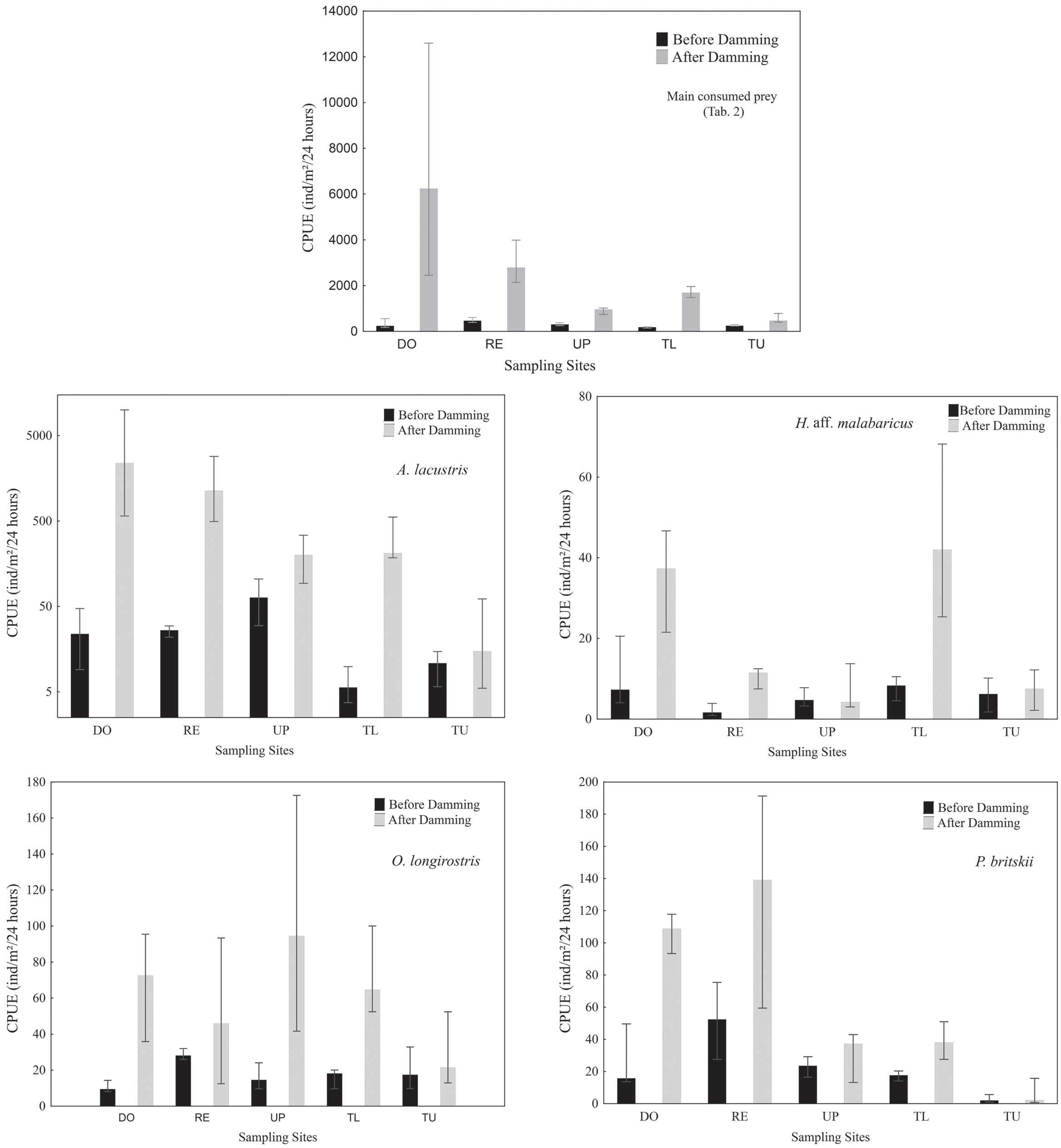

Fig. 2. Median abundance (Capture per unit effort - CPUE; unit: number of individuals/1,000 m² of nets set for 24 h) of the most consumed prey and analysed species from Iguaçu River in the Salto Caxias Reservoir area of influence, before and after damming (RE - reservoir region; DO - downstream; UP - upstream from the Iguaçu River; TL - tributaries lower section; TU - tributaries upper section). Vertical bars=Min and Max values.

Table 2. Food resources (%volume) used by the analysed species before (bf) and after (af) damming and sites (RE - reservoir region; DO - downstream; UP - upstream from the Iguaçu River; TL - tributaries lower section; TU - tributaries upper section). * Represents values lower than 0.1. MacroInver.= Macro Invertebrates, MicroInver= Micro Invertebrates and MicroCrus= Microcrustaceans.

		N		Decapoda		Insects		MacroInver		MicroInver		MicroCrus		Fish		Algae		Plants		Detritus	
	Site	be	af	be	af	be	af	be	af	be	af	be	af	be	af	be	af	be	af	be	af
A. lacustris	DO	45	35			25.6	7.1	*					0.4	*	26	0.1	35.2	73.2	31.3	1	*
	RE	79	57				18.3		0.6				1.5	1.4	43.7	*	0.2	66.4	32.4	0.8	3.9
	UP	53	12			29.3	25.2	0.9		*			35.5	1.9	3.6	3.7		64.1	35.7	*	
	TL	34	66			4.2	10.9	0.3		*			1.2	0.5	26.5		*	90.3	60.6	4.8	0.8
	TU	26	19			15.8	22.4		*					*	8.7			84.1	66.2	*	2.6
H. aff. *malabaricus*	DO	38	37			*	*							99.8	99.9			0.2			
	RE	19	22											100	100						
	UP	4	8				*							100	99.1				0.9		*
	TL	22	110			*								99.9	100			*	*	*	
	TU	19	8											99.8	100			0.2			
O. longirostris	DO	25	41			29.6	0.1	1.5		0.2				67.5	99.9			0.7		0.4	
	RE	99	42			17.9	0.7	0.5					*	79.8	99.2			1.8		0.1	*
	UP	30	50			8.6	*	0.5						90.4	100					0.5	
	TL	55	67			7.3	0.6	13.7					*	62.8	98.6			16	0.1	0.3	0.7
	TU	57	23			4.3	1.3	0.8	*					89.5	98.1			5.1	12.6	0.3	0.6
P. britskii	DO	56	83	5.8	9.8	7.2	0.2	23.9	2.5	*	*	*	*	35.1	86.4	*	*	0.6	20.5	15.4	0.4
	RE	172	64	19	1.6	17.8	0.8	12		0.1		*	*	25.5	86.1	0.1	*	9	31.5	4.9	2.6
	UP	73	28	5.2		18.2	2.8	18.4		*		*	*	19.1	92.3	*	*	3.9	18.6	7.6	0.9
	TL	64	122	2.7	0.3	10.6	1.6	47.8	0.1	0.1	*	*	*	13.5	77.4	*	*	18.5	5.7	6.7	2.1
	TU	11	11	4.9	0.9	23.8	3	38.5	4.8	*	0.1			0.6	88.9			0.9		26.6	1.4

Table 3. Main fish prey (% volume) used by the analysed species before (bf) and after (af) damming and sites (DO - downstream; RE - reservoir region; UP - upstream of the Iguaçu River; TL - tributaries lower section; TU - tributaries upper section). As= *Astyanax* sp., Ab= *Astyanax bifasciatus*, Al= *Astyanax lacustris*, Am= *Astyanax minor*, Ad= *Astyanax dissimilis*, Cr= *Crenicichla* sp., Ci= *Crenicichla iguassuensis*, Cs= *Cyphocharax* cf. *santacatarinae*, Gb= *Geophagus brasiliensis*, Gc= *Gymnotus carapo*, Pm= *Pimelodus* sp., Ol= *Oligosarcus longirostris*. Others= species with low participation in diet, scales and fish pieces.

		As		Ab		Al		Am		Ad		Cr		Ci		Cs		Gb		Gc		Pm		Ol		Others	
	Site	be	af	be	af	be	af	be	af	be	af	be	af	be	af	be	af	be	af	be	af	be	af	be	af	be	af
	DO	6.5	6.8		2.3	0.7	23.9		23.9		2.1	11.7		9.3			1.6			8.3		8			2.1	55.5	28.3
	DA	14.5	2.2			2.2	24.9		5.4			21.8		5.2			2.2			6.5		2.7			2.5	29.1	45.3
H. aff. *malabaricus*	RI											56.7		16			43									27.4	56.2
	TL		2.1		0.4	15.9	4.3		8.5			2.4					4.3			0.7		14.5				66.4	44.8
	TU	12.9	4.5				11.3					16.2		24.3			18.1	18								28.4	66
	DO	8.8												4.3			45.7			2.4		16.3				46.8	23.9
	DA		5.8		17.4				25.1		15.7	22.2														45.4	36.6
O. longirostris	RI	27.5	1.3				2.8		7.8								76.5			0.5						62.9	6.3
	TL	9.7	3.5		14.9		11.5										3.2	1.1		18						34.4	27.1
	TU	1.2	5.9		8.4							8.2														8.3	83.9
	DO	0.9					5.9		9			0.6					24.3									24	47
	DA		2.9				9.9		4.3								1.3					6.2				28.9	68.1
P. britskii	RI		26.3														33.6									19.8	32.4
	TL		3.9				2.4										33.3									13.5	37.7
	TU		11.2				44.9																			0.6	32.8

Astyanax lacustris and *O. longirostris* were the only species showing differences among sexes in the length weight relationship (Table 4). The estimated weights, necessary for the calculation of K, were obtained by the equations showed in Table 4.

Astyanax lacustris was the unique species presenting negative and significant correlation between the piscivory and condition factor (r= -0.46, p=0.006). *Oligosarcus longirostris* and *P. britskii* presented a positive significant correlation between the fish consumption and the condition factor (r= 0.44, p=0.007 and r= 0.60, p< 0.0001, respectively), while for *H.* aff. *malabaricus,* it was not significant (r= 0.14, p=0.40) (Fig. 3).

The ANOVA detected significant interaction in the condition factor and the repletion index for sites and periods only for *A. lacustris* and *P. britskii*. For *H.* aff. *malabaricus* ANOVA detected significant differences in the condition factor and repletion index for sites and periods while *O. longirostris* presented significant difference only for sites (Table 5).

The condition factor of all species increased after the reservoir formation, with the exception of *A. lacustris,* which decreased in the reservoir and downstream areas (Fig. 4). In all four species repletion index decreased in the lentic sites (RE and TL), while *A. lacustris* increased in the downstream sites. *Hoplias* aff. *malabaricus* presented a reduction in the repletion index in the downstream site, while for *O. longirostris* and *P. britskii,* the values were less affected (Fig. 4). The Pearson correlation index detected a positive significant correlation between the condition factor

Table 4. Length-weight relationship and covariance analysis results for the analysed species in the Iguaçu River and its tributaries, in the Salto Caxias Reservoir region. n-Number of analyzed individuals for the condition factor and repletion index. Min-Minimum standard length (cm) and Max-Maximum standard length (cm).

Species	n Before	n After	min	max	Sex	Equation	F	p
A. lacustris	1459	8976	5,1	9,4	Male	$Wt = 0.028 * Ls^{2.78}$	136,3	<0.001
					Female	$Wt = 0.037 * Ls^{2.95}$		
H. aff. malabaricus	341	921	19,7	31,4	-	$Wt = 0.013 * Ls^{3.068}$	1,44	0,23
O. longirostris	887	768	11,3	21,7	Male	$Wt = 0.012 * Ls^{3.07}$	21,2	<0.001
					Female	$Wt = 0.014 * Ls^{3.12}$		
P. britskii	1305	1835	15,3	27,9	-	$Wt = 0.014 * Ls^{3.11}$	1,5	0,21

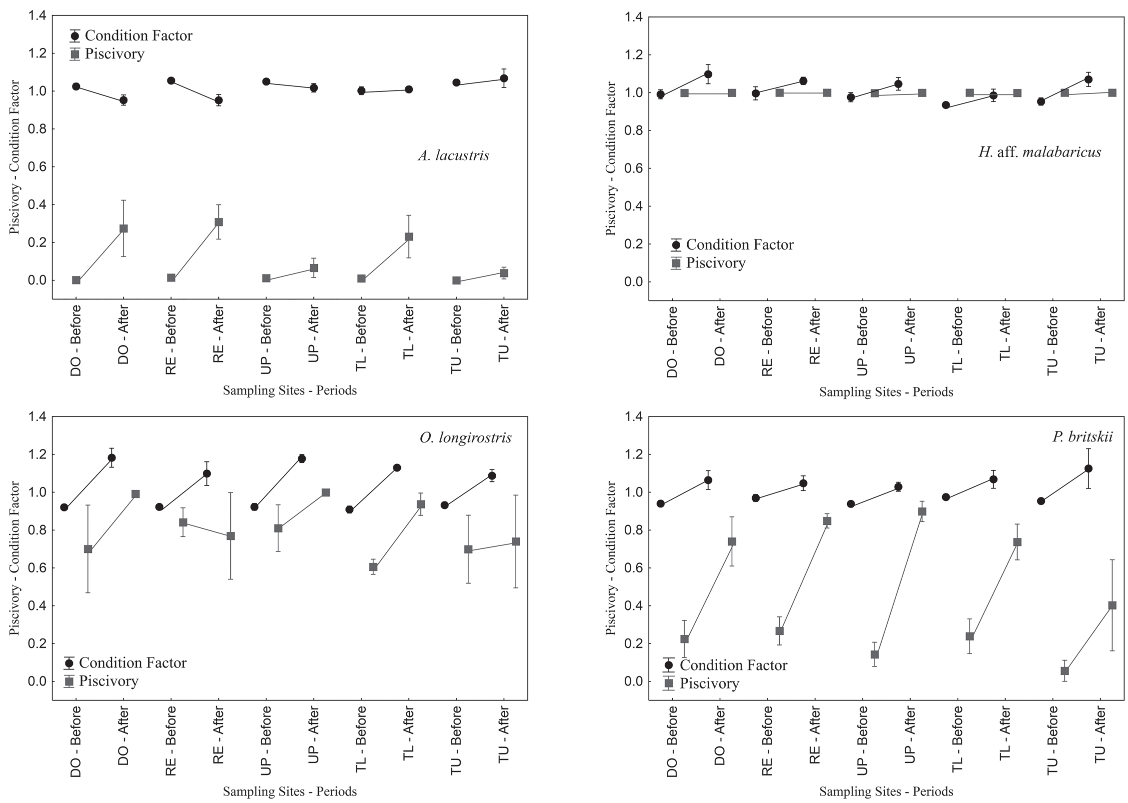

Fig. 3. Piscivory (%) and mean condition factor of the analysed species from Iguaçu River in the Salto Caxias Reservoir influence, before and after damming and sites (RE - reservoir region; DO - downstream; UP - upstream from the Iguaçu River; TL - tributaries lower section; TU - tributaries upper section). Vertical bars= standard error.

and the repletion index for *A. lacustris, H.* aff. *malabaricus* and *O. longirostris* (r=0.3, p < 0.001, r=0.15, p < 0.001 and r =-0.05, p=0.029 respectively). *Pimelodus britskii,* the correlation was not significant (r=0.24, p=0.16).

Table 5. Analysis of Variance applied to the condition factor (K) and repletion index (RI) values for sites and periods for the analysed species in the Iguaçu River and its tributaries, in the Salto Caxias Reservoir region.

Species	Factor	K		RI	
		F	p	F	p
A. lacustris	Site	22.13	<0.001	18.04	<0.001
	Period	61.72	<0.001	25.03	<0.001
	Site*Period	4.52	0.003	30.03	<0.001
H. aff. *malabaricus*	Site	9.74	<0.001	1.08	0.36
	Period	46.53	<0.001	4	0.04
	Site*Period	1.7	0.14	0.3	0.87
O. longirostris	Site	9.41	<0.001	0.31	0.86
	Period	377.6	<0.001	124.18	<0.001
	Site*Period	11.46	<0.001	11.3	<0.001
P. britskii	Site	4.35	<0.001	8.08	<0.001
	Period	347.7	<0.001	162.8	<0.001
	Site*Period	1.24	0.28	43.63	<0.001

Discussion

Proliferation of small-sized fish during the first years after damming and the increase in the prey availability was a clear tendency observed in this study. In response to the increase in prey availability an increase in the piscivorous abundance was observed. Similar patterns have been reported for other reservoirs (Agostinho *et al*., 1999; Luz-Agostinho *et al*., 2006; Bennemann *et al*., 2011). This was also observed in the present study as the sites that presented the higher increases in prey abundance (DO and RE) also presented the higher increases in piscivorous abundance, as observed for *H.* aff. *malabaricus* and *O. longirostris,* specialist piscivorous (Hahn & Fugi, 2008), that do not change their diet despite environmental changes, and for *A. lacustris* and *P. britskii* (opportunist piscivorous), in which the fish consumption was sporadic or even inexistent (Cassemiro *et al*., 2005; Luz-Agostinho *et al*., 2006). This increase in specialist piscivorous abundance can be due to the increase in prey availability, that is highlighted by the great participation of forage species as *Astyanax dissimilis*, *Crenicichla* spp. and *Cyphocharax* cf. *santacatarinae*, in piscivorous species diet after damming.

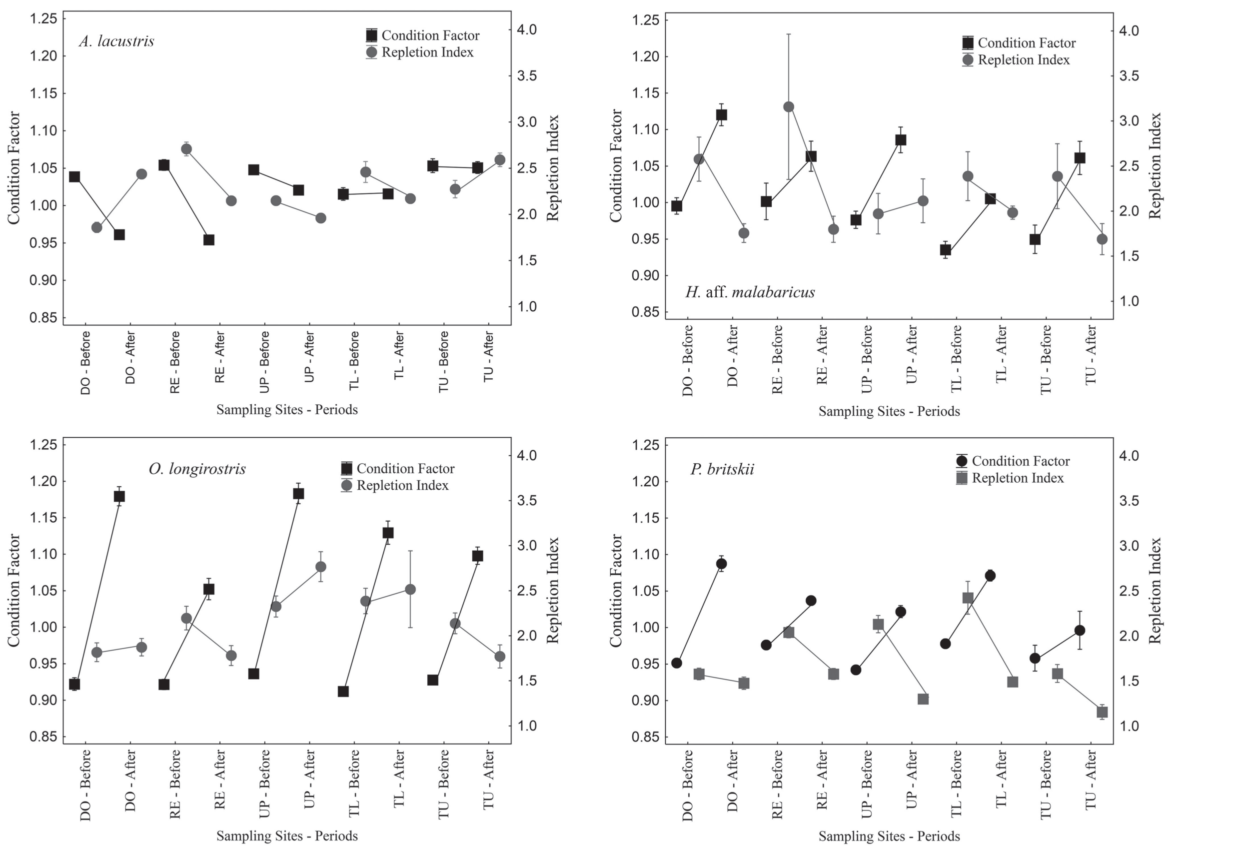

Fig. 4. Repletion Index (righ) and condition factor (left) of the analysed species from Iguaçu River in the Salto Caxias Reservoir influence, before and after damming and sites (RE - reservoir region; DO - downstream; UP - upstream from the Iguaçu River; TL - tributaries lower section; TU - tributaries upper section). Vertical bars= standard error.

Hahn & Fugi (2008) verified that some species eat fish parts after a reservoir is formed, these authors also highlight that species that do not possess the ability of taking away prey parts, due to the lack of morphological adaptations for a piscivorous diet, are characterized as necrophagous. As *A. lacustris* lacks morphological treats that would allow it to pursue, capture and kill fish, the great participation of fish found in this species diet would be an indicative that this species is feeding of dead fish fragments or fish scales, and, if this is true, this species presents a necrophagous behaviour. This hypothesis is, however, based on speculation and as such must be confirmed by more accurate observation of feeding behaviour.

On the other hand, the increase in fish consumption by *P. britskii*, seems to be connected to ontogenetic changes, with adults more inclined to consume fish than young (Delariva *et al.*, 2007) and not only to the necrofagous behaviour. Such hypothesis is enhanced by the fact that, after damming, larger individuals were captured in the dam sites and presented a piscivorous diet with great participation of *Cyphocharax* cf. *santacatarinae*. This fact highlights the opportunistic behaviour of *P. britskii* as it fed in the most available prey in the environment.

In dammed rivers, changing in the diet composition can be associated to changes in feeding resources availability and to the species ability to explore these resources in the novel environment. The feeding plasticity in Neotropical fish has been shown for a great number of species (Hahn *et al.*, 1998; Abelha *et al.*, 2001; Luz-Agostinho *et al.*, 2006). Thus, fish respond to the low availability of preferential resources by changing its behaviour to consume different items as the preferential ones become scarce (Dill, 1983). All species presented an increase in the condition factor, with the exception of *A. lacustris,* especially in those sites that were more influenced by the impoundment (RE) or by flow control (DO) independent of changes in the feeding activity. In *A. lacustris*, the change from a predominantly herbivorous diet to a piscivorous one occurred in different intensities between sites, being more relevant in the reservoir region (RE) and downstream stretches (DO) and less pronounced in the upstream site (UP). The fact that this species showed more pronounced changes in diet composition (herbivory to piscivory) and presented a high decrease in the condition factor suggests that changes in diet composition can have a negative effect on the body condition even when high resource consumption rates are observed.

Hoplias aff. *malabaricus* and *O. longirostris* usually swallow their prey whole (Casatti *et al.*, 2001; Peretti & Andrian, 2008) requiring them to feed less often (Nikolsky, 1963) resulting in low feeding activity. Increased condition factor, despite the decrease in repletion index, might be connected to the lower energetic cost to the capture, manipulation and digestion of the prey, as suggested by the availability of small-sized fish and morpho-physiological adaptations to piscivory.

The fact that *A. lacustris* and *P. britskii,* both opportunistic species, presented different responses in the condition factor with a piscivorous diet, is related with differences in morphology traits between the two species. *Pimelodus* present a very wide mouth opening, ability of store large amount of food in the stomach and histological adaptations to piscivory (Santos *et al.*, 2007; Hahn & Fugi, 2008; Peretti & Andrian, 2008). These features allow eliciting the piscivorous behaviour by such species (Hahn & Fugi, 2008) providing better energy use and increase in the condition factor. On the other hand, *A. lacustris* present terminal and small mouth, delicate stomach and longer intestine (Peretti *et al.*, 2008) associated with a more omnivorous diet specialized for small food items, like algae and insects.

Astyanax lacustris abundance grew thirty times more after damming. This high density combined with the presence of other four abundant *Astyanax* species (Baumgartner *et al.*, 2012) that also fed mostly of plants before damming (Cassemiro *et al.*, 2005; Delariva *et al.,* 2013) and the apparently space segregation between those species (Cassemiro *et al.*, 2005) can cause changes in diet, due, for example, to the lack of preferential resource or competition. According to Agostinho *et al.* (1999), areas upstream from reservoirs are the least affected by dams. In fact, this trend was observed in this study, but still must be considered that the changes were relevant. Therefore, increments in the condition factor in other sites more affected should be evaluated with caution, as they seem more influenced by interannual variables than properly by damming. Thus, if the increase in the upstream site (UP), which is less affected, is considered as a reference and increases verified in the other sites could be, in fact, a reduction in the condition factor.

Hoplias aff. *malabaricus, O. longirostris* and *P. britskii*, had previously, to a greater or lesser extent, consumed a remarkable amount of fishes, being favoured in an environment where this resource became abundant. As a result, they increased the condition factor after damming. For *A. lacustris,* this decrease was evident in all of the sites, being more pronounced in those where the diet changes were higher, independent of the feeding intensity. It can be considered that changes to a piscivorous diet for *A. lacustris*, despite its high protein and energy content and easy digestion, can result in worsening nutritional status.

Astyanax lacustris presented a great increase in abundance despite the observed decrease in condition factor. This is probably connected to the opportunistic reproductive strategy of this species, which possesses a good colonizing ability when facing unpredictable environmental variations (Winnemiller, 1989) being capable of population growth despite the condition factor. Therefore, this low nutritional status can make long term maintenance unsustainable if the species continues on the considered diet. Cassemiro *et al.* (2005) observed that this species returned to a herbivorous diet three years after the reservoir was formed, which may explain the maintenance of a large population in the dammed environment.

It is clear that specialist piscivorous fish will benefit in the early years after damming, mainly because of the increase in fish prey, resulting in better nutritional state and population growth, while for those opportunistic species morphological features will determine if the species will or not have long term advantages in the diet changes, and, for those species that do not possesses such morphological adaptations maintain the large populations, changes to the previous feeding habit will be required.

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