

Diet and trophic structure of the fish fauna in a subtropical ecosystem: impoundment effects

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This study examined the diet and trophic structure of the fish fauna, over temporal and spatial scales, as affected by the impoundment of the Iguaçu River in the region of Salto Caxias, Paraná State, Brazil. Sampling was conducted before (March 1997 - February 1998) and after the impoundment (March 1999 - February 2000), at four sampling sites. The stomach contents were analyzed by the volumetric method. The species could be organized in 10 trophic guilds: algívores, carcinófagos, detritívores, herbívores, aquatic insectívores, terrestrial insectívores, invertívores, omnívores, piscívores, and plânctívores; the first and last guilds were represented only in the post-impoundment period. Similarity patterns and feeding changes were summarized by a non-metric Multi-dimensional Scaling (nMDS) analysis and statistically tested by a Permutational multivariate analysis of variance (PERMANOVA). Most species showed feeding changes, except for the piscívores and detritívores. These changes were related to the temporal factor (impoundment phases), such as reduced intake of benthic organisms and allochthonous food, which were usually replaced by resources from the reservoir itself (algae, microcrustaceans, and fish), simplifying the food spectrum of the fish fauna. A different indicator of food resources (IndVal) corroborated these changes in the feeding of the species. The proportions of the trophic guilds evaluated based on the catch per unit of effort (CPUE) and tested by ANOSIM were significantly different before and after the impoundment. Herbívores and piscívores were the guilds that contributed (SIMPER) to these differences, especially the high increase in biomass of the piscívore guild after the impoundment. Variations in the abundance of trophic guilds were more directly related to changes in the feeding habits of the fish fauna than to increases in the number and biomass of the species that constitute these guilds.

Neste estudo foram avaliadas a dieta e a estrutura trófica da ictiofauna em escala temporal e espacial, sob efeito do represamento do rio Iguaçu, na região de Salto Caxias, Paraná, Brasil. Para tanto, foram realizadas amostragens nas fases pré (março/97 a fevereiro/98) e pós represamento (março/99 a fevereiro/00) em quatro pontos de coleta. Os conteúdos estomacais foram avaliados pelo método volumétrico. As espécies foram organizadas em 10 guildas tróficas: algívora, carcinófaga, detritívora, herbívora, insetívora aquática, insetívora terrestre, invertívora, omnívora, piscívora e plânctívora, sendo a primeira e a última representadas apenas após o represamento. Os padrões de similaridade e alterações na dieta foram sintetizados através da ordenação multidimensional não paramétrica (nMDS) e estatisticamente testados pela análise de variância permutacional (PERMANOVA). Foram constatadas alterações na dieta da maioria das espécies, com exceção das piscívoras e detritívoras. Essas alterações foram relacionadas ao fator temporal (fases do represamento), configuradas como redução no consumo de organismos bentônicos e alimentos alóctones, os quais foram geralmente substituídos por recursos provenientes do próprio ambiente (algas, microcrustáceos e peixes), simplificando o espectro alimentar. Diferentes recursos alimentares indicadores (IndVal) corroboram essas alterações na composição alimentar das espécies antes e após o represamento. As proporções na abundância (número e biomassa) das guildas tróficas avaliadas com base na captura por unidade de esforço (CPUE) e testadas pela ANOSIM foram significativamente diferentes antes e após o represamento. As guildas herbívora e piscívora foram as que mais contribuíram (SIMPER) para essas diferenças, especialmente o elevado incremento em biomassa da guilda piscívora após o represamento. As variações na abundância das guildas tróficas foram mais relacionadas às alterações no hábito alimentar da fauna de peixes, do que propriamente aos incrementos em número e em biomassa das espécies que anteriormente compunham tais guildas.

Key words: Feeding, Guilds, Iguaçu River, Reservoir, Temporal changes.

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Introduction

Impoundments are important agents in the reorganization of aquatic communities, and their consequences vary along a longitudinal gradient, with different effects on community structure (Agostinho *et al.*, 2007). Studies of aquatic communities have indicated that the hydrological disturbances resulting from the impoundments are key elements in the reorganization of the local fish assemblages (Agostinho *et al.*, 2008). One of the factors that limit the establishment and initial accommodation of the fish fauna in the new environment is the food supply (Mérona & Vigouroux, 2012). The rapid changes from the flooding and new flow conditions change the diet and the trophic structure of the fish fauna, which may lead to the proliferation of some species and the disappearance of others (Piana *et al.*, 2005; Hahn & Fugi, 2007; Agostinho *et al.*, 2010; Bennemann *et al.*, 2011).

Historically, impoundments have altered the landscape of most rivers worldwide (Alexandre & Almeida, 2010). In Brazil this situation is even more pronounced, due to the wide use of hydroelectric power and the increasing demand for energy (Agostinho *et al.*, 2007; Barletta *et al.*, 2010), and only a few rivers have remained in their natural state. In this country, the impoundments are concentrated in the south and southeast regions, and the main water courses of these regions now consist of cascades of reservoirs (Agostinho *et al.*, 2008).

The impacts of damming are stronger on endemic fish faunas (Liermann *et al.*, 2012), which are very common in rivers with a steep slope and numerous waterfalls, conditions that lead naturally to geographic isolation (Dias *et al.*, 2012). This is the case of the Iguaçu River basin; this sub-basin was isolated from the Paraná River 22 million years ago by the Iguaçu Falls, which served as an effective barrier to the dispersal of fish species (Alcaraz *et al.*, 2009). A high degree of endemism (around 70%) (Baumgartner *et al.*, 2012) and the absence of many families of fish that are common in the Paraná River basin are typical features of the Iguaçu basin (Garavello *et al.*, 1997; Júlio Jr. *et al.*, 1997). Changes in riverine habitats caused by human activities may lead to a risk of mass extinction, in this case at the global scale (Baumgartner *et al.*, 2012).

Although several large reservoirs have been constructed in Brazil, 80% of them since 1960, most studies in these environments were carried out only after the environment had changed, limiting the available information about the resulting impacts (Fièvet *et al.*, 2001; Júlio Jr. *et al.*, 2005; Agostinho *et al.*, 2007). The number of publications concerning these impacts on the diet and trophic structure of fish fauna has increased in recent years (see Hahn & Fugi, 2007). Nevertheless, most of the reports are limited and do not treat the entire fish fauna. In this sense, the challenge for

research in this area is to obtain enough samples to make valid inferences.

The present study assessed the fish fauna of the Iguaçu River, Iguaçu River basin, according to food use, before and after the construction of Salto Caxias Dam. We are based on the hypothesis that abrupt changes in physical, chemical and habitat conditions caused by the impoundment alter the availability of food resources. We predict changes in the diets of the fish fauna as a result of the initial impacts from the impoundment, and consequently changes in the trophic structure (number and biomass) of the fish assemblage, on both temporal and spatial scales.

Material and Methods

Study area

The Iguaçu River has the largest watershed in Paraná State, with an area of approximately 72,000 km². The river flows for about 1,060 km from its headwaters on the western slope of the Serra do Mar, near the city of Curitiba, until it joins the Paraná River. Similarly to other tributaries of the Paraná River, it is a geologically old river that runs from east to west (Maack, 1981).

The original terrain changed markedly in altitude along the course of the river, with a vertical drop from 830 m a.s.l. to 78 m at the outlet in the Paraná River. However, large impoundments constructed along the Iguaçu River in the last 30 years have converted the rapids and waterfalls between União da Vitória city (PR) and the Salto Osório waterfall into a cascade of five reservoirs that flood 515 km² and store about 18.8 x 10⁶ m³ water (Júlio Jr. *et al.*, 1997). Salto Caxias is the fifth and last reservoir of this sequence. The dam was closed in October 1998, and the reservoir filled in four months. The reservoir covers 131 km² of flooded area, is about 20 m deep, and the dam is 67 m high.

For this study, samples were taken before and after the impoundment of the Salto Caxias Reservoir, at four sampling sites: upstream (site 1 - below the mouth of the Chopim River), in the middle region (site 2 - middle part of the stretch analyzed), close to the dam (site 3 - Salto Caxias Dam), and downstream (site 4 - downstream from Salto Caxias Dam) (Fig. 1).

Sampling

Samples were taken monthly from March 1997 through February 1998 (before the impoundment) and quarterly from March 1999 through February 2000 (after the impoundment), using gill nets (mesh sizes from 3.0 to 16.0 cm between opposite knots, 12 simple nets and 3 trammel nets) set near the left and right banks for 24 h, with inspections at dawn, dusk, and during the night.

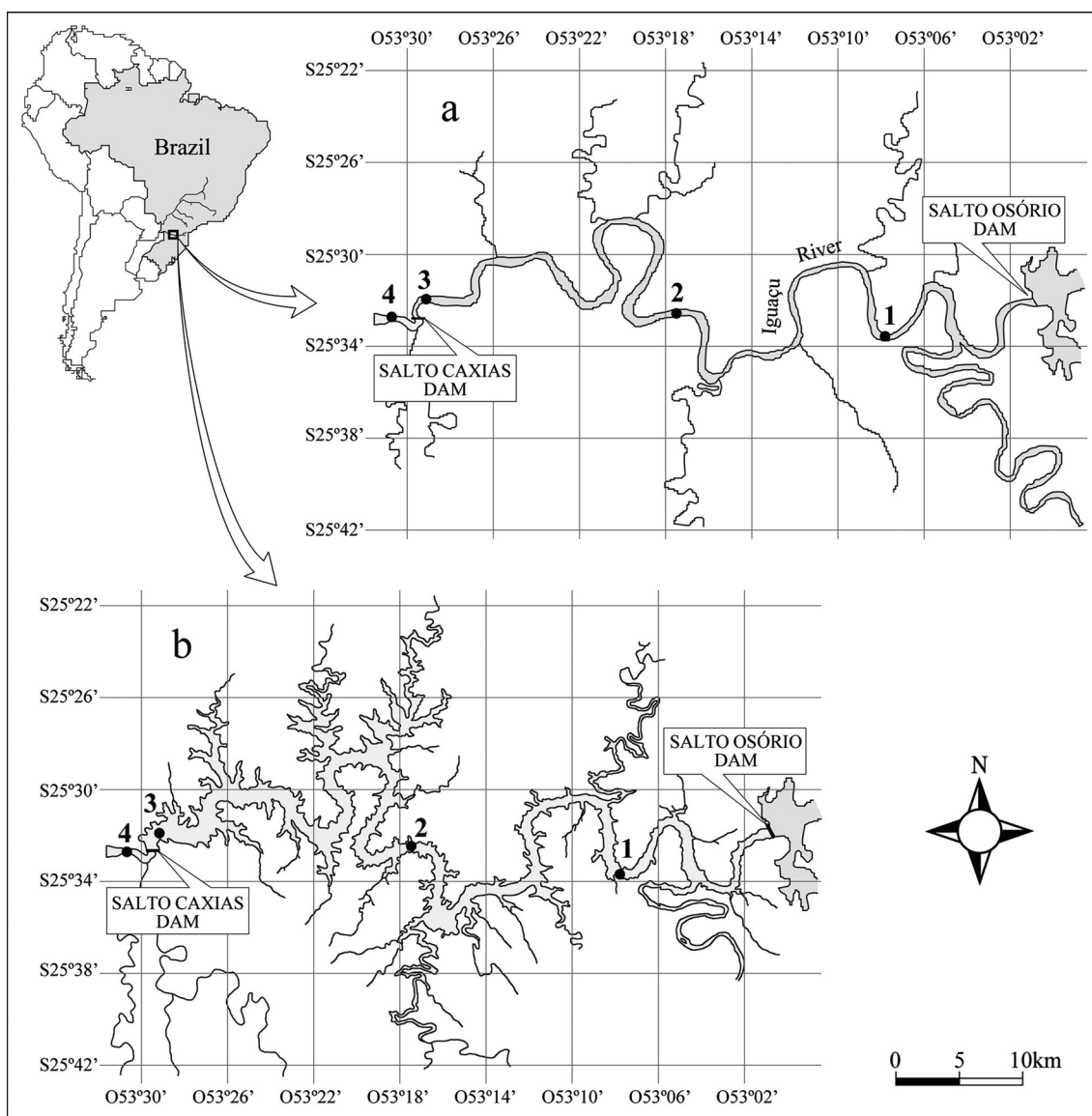


Fig. 1. Location of sampling sites along the longitudinal gradient of the Iguauçu River, in the area influenced by the Salto Caxias Reservoir, Paraná State. a) before the impoundment; b) after the impoundment. (site 1 = upstream; site 2 = middle region; site 3 = dam; site 4 = downstream).

Laboratory procedures

Fish were identified by taxonomists, and voucher specimens (Table 1) were deposited in the Fish Collection of Nupélia (UEM/Maringá). After identification, specimens were measured (total length), weighed (total weight) and gutted; stomachs containing food were fixed in 4% formalin and later transferred to 70% ethanol. 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): the total volume of a food item taken by the fish population is given as a percentage of the total volume of all stomach contents, estimated using graduated test tubes and a glass counting plate (Hellowell & Abel, 1971). For species

with an undifferentiated stomach (Loricariidae), the contents of the anterior third of the digestive tube were examined. For the analysis of stomach contents, we used only species for which we had at least five stomachs in total.

Data analysis

Food items were pooled into broader categories, designated as food resources, consisting of: detritus/sediment (particulate organic matter in different stages of decomposition and with mineral particles present), algae (filamentous and unicellular), terrestrial plants (fruit, seeds and leaves of vascular plants), aquatic plants (bryophytes), fish (muscle, fin rays, and whole fish), terrestrial insects (Coleoptera, Hemiptera, Hymenoptera,

Isoptera, and Orthoptera), aquatic insects (Coleoptera, Diptera, Ephemeroptera, Megaloptera, Odonata, Plecoptera, Trichoptera), decapods (fragments and whole individuals of the crab *Aegla* sp.), microcrustaceans (Copepoda and Cladocera, especially planktonic species), macroinvertebrates (Arachnida, Bivalvia, Gastropoda, Annelida, and Diplopoda) and microinvertebrates (Testacea, Porifera, Rotifera, Bryozoa, Nematoda, Ostracoda).

Trophic guilds were determined from the matrix of stomach contents in each sampling site and phase by an adapted stepwise procedure of Mérona *et al.* (2001): Step 1: more than 50% detritus/sediment in the stomachs: detritivores; Step 2: more than 50% algae in the stomach: algivores; Step 3: more than 50% plant material (supplemented with algae and little proportion or absence of detritus) in the stomachs: herbivores; Step 4: more than 50% plankton in the stomachs: planktivores; Step 5: more than 50% aquatic insects in the stomachs: aquatic insectivores; Step 6: more than 50% terrestrial insects in the stomachs: terrestrial insectivores; Step 7: more than 50% decapods in the stomachs: carcinophages; Step 8: more than 50% or by adding various invertebrates in the stomachs: invertivores; Step 9: more than 50% fish (including scales) in the stomachs: piscivores; Step 10: none of the above statements and adding items of plant and animal origins: omnivores.

To identify trophic patterns and use of food resources by the fish fauna, we used nonmetric multidimensional scaling (nMDS; Kruskal, 1964). The Bray-Curtis index was applied to the matrix of volumetric abundance of food resource, transformed by square root. We obtained a confidence index (Stress) which determines the degree of proximity of the graphical representation to the real data. Stress values below 0.20 allow potential two-dimensional (2D) use of the nMDS (Clarke & Warwick, 2001). Data were randomized 100 times, and the stability criterion was 0.005 standard deviations in the stress after 100 iterations.

To test the null hypothesis of no difference in diet composition of the fish assemblages among sites and periods (spatial and temporal factors) summarized by the nMDS (distance matrix), we used a Permutational Multivariate Analysis of Variance (PERMANOVA - Bray-Curtis index obtained with 9999 random permutations), a nonparametric method to test for multivariate differences among predefined groups (Anderson, 2001). PERMANOVA is sensitive to differences in multivariate dispersion, so we can check if dispersions are significantly different. To estimate the significance of this statistic, we used a Monte Carlo test with 10,000 permutations.

The indicator value method (IndVal) (Dufrene & Legendre, 1997) was employed to detect what food resources were indicative of the diet of the fish fauna before and after the impoundment. An IndVal is based on specificity (the relative

Table 1. List of fish species from the Iguacu River in the area influenced by the Salto Caxias Reservoir, Paraná State. Voucher specimens: Number of voucher lots deposited in the Fish Collection of Nupélia (UEM/Maringá).

Species	Voucher Specimens
<i>Apareiodon vittatus</i> Garavello, 1977	NUP 720; NUP 2049; NUP 2070
<i>Astyanax altiparanae</i> Garutti & Britski, 2000	NUP 2452; NUP 6843
<i>Astyanax bifasciatus</i> Garavello & Sampaio, 2010	NUP 2457
<i>Astyanax dissimilis</i> Garavello & Sampaio, 2010	NUP 6872; NUP 1633
<i>Astyanax gymnodontus</i> (Eigenmann, 1911)	NUP 2050
<i>Astyanax minor</i> Garavello & Sampaio, 2010	NUP 7296; NUP 6873
<i>Bryconamericus ikaa</i> Casciotta, Almirón & Azpelicueta, 2004	NUP 2075
<i>Corydoras</i> aff. <i>paleatus</i> (Jenyns, 1842)	NUP 709; NUP 5763
<i>Crenicichla iguassuensis</i> Haseman, 1911	NUP 1788
<i>Crenicichla</i> sp. 2	NUP 1642
<i>Cyanocharax</i> aff. <i>alburnus</i> (Hensel, 1870)	NUP 6620; NUP 7248
<i>Cyphocharax</i> cf. <i>santacatarinae</i> (Fernández-Yépez, 1948)	NUP 1609
<i>Geophagus brasiliensis</i> (Quoy & Gaimard, 1824)	NUP 704
<i>Glanidium ribeiroi</i> Haseman, 1911	NUP 2443; NUP 5436
<i>Hoplias</i> aff. <i>malabaricus</i> (Bloch, 1794)	NUP 687
<i>Hypostomus myersi</i> (Gosline, 1947)	NUP 5892; NUP 5924
<i>Odontesthes bonariensis</i> (Valenciennes, 1835)	NUP 1610
<i>Oligosarcus longirostris</i> Menezes & Géry, 1983	NUP 721; NUP 1631
<i>Pimelodus britskii</i> Garavello & Shibatta, 2007	NUP 1786; NUP 1826
<i>Pimelodus ortmanni</i> Haseman, 1911	NUP 1664
<i>Rhamdia branneri</i> Haseman, 1911	NUP 2448; NUP 2451
<i>Rhamdia voulezi</i> Haseman, 1911	NUP 1659

abundance of each food resource in each group or factor) and fidelity (the relative frequency of each food resource in each group or factor), and thus incorporates both frequency and occurrence measures, according to the formula (Dufrene & Legendre, 1997): $IndVal_{ij} = A_{ij} \times B_{ij} \times 100$, where: $IndVal_{ij}$ is the indicator value for food resource i in group j , A_{ij} is the relative volume of food resource i in group j , and B_{ij} is the relative frequency of food resource i in group j . We tested the significance of the indicator value for each item with a Monte Carlo randomization procedure with 10,000 permutations (significance level < 0.05).

The trophic structure of the fish fauna was defined here by the proportion of the number and biomass of each trophic guild identified in each phase and sampling site. The data were obtained from the catch per unit of effort (CPUE), expressed as the number and weight of individuals per 1,000 m² net in 24 h. Significant differences in the guild trophic structure before and after the impoundment were identified using one-way analysis of similarity (ANOSIM). This analysis (one-way ANOSIM) was based on two groups defined *a priori* on the temporal factor (before and after impoundment). The significance level was 0.05. Finally, we used discriminant analysis (SIMPER- similarity percentage) to determine which trophic guilds were responsible for dissimilarity between groupings (before and after impoundment) (Clarke, 1993). We used the Jaccard similarity index to discriminate the trophic structure and participation of each guild between different periods (ANOSIM and SIMPER, respectively).

The nMDS and Indval analyses were calculated using PC-ORD (McCune & Mefford, 2006; Peck, 2010). PERMANOVA, ANOSIM and SIMPER were run using the software PAST (version 1.68) (Hammer *et al.* 2001).

Results

Overall diet composition

We analyzed 2,313 stomach contents from individuals sampled before the impoundment and 1,332 after, belonging to 22 species (Table 1), which represented about 99.8% of all individuals captured during the entire study period. Most species incorporated a wide array of resources in their diets, and few of the 22 species consumed only one type of resource. These results allowed us to group species into 10 trophic guilds: detritivores, algivores, herbivores, planktivores, aquatic insectivores, terrestrial insectivores, invertivores, carcinophages, piscivores, and omnivores. Except for the downstream site (42%), in all other sites more than 50% of all species that occurred before and after the impoundment have changed their diets, being classified in different trophic guilds (Tables 2-5).

Temporal and spatial variations in the diet

The stress value (0.13) obtained in non-metric multidimensional scaling analysis (nMDS) gave a potentially useful 2-dimensional picture, allowing the definition of two groups with reduced data dimensionality (before and after impoundment). The analysis recommended three dimensions to explain the majority of variance (87%) among food resources. However, the best dimensionality was represented by the first and second dimensions (Fig. 2). The first dimension (48% variance) gradient contrasted aquatic plants, detritus/

sediment and algae *versus* fish consumption, primarily by detritivorous species and piscivorous species, respectively. Concomitantly, the second and third dimensions (23% and 16% variances) contrasted the resources that are usually available in the benthos, such as aquatic plants, decapods, and macroinvertebrates, *versus* planktonic resources such as microcrustaceans and algae that were consumed after the impoundment. Plants (aquatic and terrestrial), insects (aquatic and terrestrial) and invertebrates grouped together in the multivariate space were derived from the consumption of these resources by species with more generalized diets and omnivores. The results of the two-way PERMANOVA showed that there was no significant interaction between sites and sampling periods ($F = 0.72$; $p = 0.58$), but indicated that the fish before and after the impoundment had significantly different diets ($F = 8.72$; $p = 0.0001$). This result may explain the relationships among objects displayed in the 2-D plot. Piscivorous and detritivorous species did not change their diets, regardless of the impoundment phase. The other species showed varying levels of changes in the diet (see Tables 2-5).

Different indicator food resources (IndVal) corroborated the changes in the feeding composition of most species. Before the impoundment, decapods, aquatic and terrestrial insects, macroinvertebrates, and aquatic and terrestrial plants contributed significantly to the diets of the fish. In contrast, after the impoundment, there were fewer indicator resources, all of autochthonous origin: algae, microcrustaceans and fish (IndVal; Table 6).

Variation in the abundance of the trophic guilds

The proportion of the trophic guilds showed marked spatial and temporal variation (Fig. 3). Before the impoundment, herbivores and piscivores predominated in all sampling sites, in number and biomass, respectively. After the impoundment, the abundance of herbivores decreased (except for site 4) and piscivores increased, with marked increases in biomass, especially at site 3 (dam) (Fig. 3). The ANOSIM showed significant differences in the proportions of the trophic guilds before and after the impoundment, in both number ($R: 0.8021$; $p = 0.026$) and biomass ($R: 0.8021$; $p = 0.034$). The SIMPER analysis also showed that abundance in terms of number and biomass were dissimilar (70.76% and 54.28%, respectively) before and after the impoundment. The trophic guilds that contributed to the differences were herbivores and piscivores, which accounted for more than 72.9% and 64.2% (number and biomass, respectively) of the differences between the periods (Table 7). Also, we recorded a reduction of the terrestrial insectivores and invertivores, and the disappearance of carcinophages from the reservoir sites. Algivores and planktivores were present only after the impoundment (Fig. 3; Table 7).

Table 3. Food resources used by the fish fauna (% volume) at site 2 (intermediate region) in the Iguaçú River, before (be) and after (af) the impoundment of the Salto Caxias Reservoir. FG = feeding guilds (Alg = algivores; Det = detritivores; Her = herbivores; Ain = aquatic insectivores; Tin = terrestrial insectivores; Inv = invertivores; Omn = omnivores; Pis = piscivores; Pla = planktivores; Car = carcinophages); N = number of stomachs analyzed; Food resources (AI = aquatic insects; TI = terrestrial insects; DE = decapods; MC = microcrustaceans; MA = macroinvertebrates; MI = microinvertebrates; FI = fish; FS = fish scales; AP = aquatic plants; TP = terrestrial plants; AL = algae; DS = detritus/sediment). 0 = values < 0.1. * = guild classification considered values greater than 40%, due to small sample size.

Species	FG		N		AI		TI		DE		MC		MA		MI		FI		FS		AP		TP		AI		DS					
	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	be	af				
	Food resources																															
<i>Apareiodon vittatus</i>	Alg		7								0.5														58		41					
<i>Astyanax altiparanae</i>	Her	Omn	40	34	0	5.2	32	19			1	1.1						1.1	1.3	1.2	1.3	0.7		64	44	0.1	0.3		4.3			
<i>Astyanax bifasciatus</i>	Her	Her	55	53	0.5	0.5	16	3.1			1.1	1.4	0.1	0	0			0	0.1	0	0.1	4.2		27	66	1.3	20	0.1	8.8			
<i>Astyanax dissimilis</i>	Omn	Pla	44	18	7.5	14	47	29			54	0.2		0	0			0	1.4	14	19	1.9	12	0	0.3							
<i>Astyanax gymnodontus</i>	Her	Tin	44	56	0.7	1.3	31	53			1.4	0.1		0	3			0.9	40	26	40	3.3		0								
<i>Astyanax minor</i>	Her	Omn	27	28	5.8	16	15	4.7			20	0.4		0	0.1			6.9	59	19	15	0.2	28	0.6	10							
<i>Bryconamericus ikae</i>	Omn	Det*	2	4	37						0.9			0.3				3.2	2.6	13	29	30	22	17	45							
<i>Corydoras aff. paleatus</i>	Inv	Inv	3	18	43	31	0.1			2.5	23			20	9.2		1							4.2	2.1	10	27	26				
<i>Crenicichla iguassuensis</i>	Ain	Ain	1	4	60	96					0.5	40		0.1				77	75	25	0			0.2		2.7						
<i>Crenicichla sp. 2</i>	Pis	Pis	3	5			23				0.3																					
<i>Cyanocharax aff. alburnus</i>	Tin		14	14	17	81					1.8										0.7	0.1										
<i>Cyphocharax cf. santacatarinae</i>	Det	Det	14	14	1	0.3				0.1	3.2			0.7	0.1									0.5	2.2	18	95	79				
<i>Geophagus brasiliensis</i>	Her		7		14						2			2							0	62					22					
<i>Glanidium ribeiroi</i>	Tin	Pis	57	2	6.2	1.4	60	0.4	29					0				98	0	2.9	1.8					0.1						
<i>Hoplias aff. malabaricus</i>	Pis	Pis	11	8														100	100													
<i>Hypostomus myersi</i>	Alg		3		0.1									0.3											52		47					
<i>Odontesthes bonariensis</i>	Pla		4		0.3	15					83							1.5														0.8
<i>Oligosarcus longirostris</i>	Pis	Pis	45	29	0	0.6	28	0.1			0.1	0.9						68	99	0.1	0	3.7	0									
<i>Pimelodus britskii</i>	Omn	Pis	44	21	0.7	0	19	1.7	28	0	0	21		0.2	0			21	90	1.4	0.8	1.3	4.8	7.7	0.2	0	2.5	0.1				
<i>Pimelodus ortmanni</i>	Car	Pis	6	2	7.8	0.3	3.5	0	76									9.2	0	95	0.3	0.1	4.4	0		3.3	0.2					
<i>Rhamdia branneri</i>	Pis		1															100														
<i>Rhamdia voulezi</i>	Pis		4		0.1						0			0				87	12					0.8	0		0.1					

Table 5. Food resources used by the fish fauna (% volume) at site 4 (downstream) in the Iguaçú River, before (be) and after (af) the impoundment of the Salto Caxias Reservoir. FG = feeding guilds (Alg = algivores; Det = detritivores; Her = herbivores; Ain = aquatic insectivores; Tin = terrestrial insectivores; Inv = invertivores; Omn = omnivores; Pis = piscivores; Pla = planktivores; Car = carcinophages); N = number of stomachs analyzed; Food resources (AI = aquatic insects; TI = terrestrial insects; DE = decapods; MC = microcrustaceans; MA = macroinvertebrates; MI = fish; FS = fish scales; AP = aquatic plants; TP = terrestrial plants; AI = algae; DS = detrit/ sediment). 0 = values <0.1.

Species	FG		N		Food resources																													
					AI		TI		DE		MC		MA		MI		FI		FS		AP		TP		AI		DS							
	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	be	af						
<i>Apareiodon vittatus</i>	Her	Det	17	7	0.8	0					0	0.3	0.1									74	0.1				8.5	41	17	59				
<i>Astyanax aliparanae</i>	Her	Her	38	30	0.7	0.2	24	6.9			0.4	0						16	0.1	11	23			51	29	0.1	37	1.1						
<i>Astyanax bifasciatus</i>	Her	Her	54	55	0.7	7	9.4	4.7			0	5.9	0.1	0	0	0	4.8	0	0.3	81	41			9	7.2	0	28	0	1.4					
<i>Astyanax dissimilis</i>	Her	Omn	54	29	6.5	7.5	14	32			20	0.8	0				0.5	0.3	62	1.6	15	28			0.4	8.9	0.4	1.5						
<i>Astyanax gymnodontus</i>	Her	Omn	53	48	1.1	1.6	14	24			2.7	0					28	1.8	49	0.2	37	17				26		0.4						
<i>Astyanax minor</i>	Her	Alg	20	12	3.7	11	5.1	1.8			0	15	0.1	0	0.1			3.8	91	0.2	0.4	6.9				53		7.7						
<i>Bryconamericus ikaa</i>	Det		6		2.2																				28		6.1	52						
<i>Corydoras aff. paleatus</i>	Ain	Det	67	21	51	32	9.6	0.2			2.8	5	1.8	11	1.9										7.2		6.8	7.4	4.9	54				
<i>Crenicichla iguassuensis</i>	Inv	Ain	8	3	24	83								76	2	0.2											5.9	8.2						
<i>Crenicichla sp. 2</i>	Pis	Pis	6	13	2.3	0.3	0	28			0	0	0.6	0	0	69	99	0	0.1								0	0						
<i>Cyanocharax aff. alburnus</i>	Tin		25		35	53								0.4													0	0						
<i>Cyphocharax cf. santacatarinae</i>	Det	Det	7	16							0.1	0.1						13	0.8							0.2	2.1	17	85	82				
<i>Geophagus brasiliensis</i>	Her		4		1.1																				79		3.7	16						
<i>Glanidium ribeiroi</i>	Pis	Pis	83	21	0.2	0.1	21	3	14	28				4.5	0												0	0	4.9	0.1				
<i>Hoplias aff. malabaricus</i>	Pis	Pis	31	33	0	0																					0.1	0.2						
<i>Hypostomus myersi</i>	Det	Det	29	37	0.7	0								0	0.1	0	0.4										1.4	0.2	5.5	12	92	87		
<i>Odontesthes bonariensis</i>	Pis	Pis	6	1	3.7	3.2																					93	100						
<i>Oligosarcus longirostris</i>	Pis	Pis	16	37		31	0																				69	100	0.4					
<i>Pimelodus britskii</i>	Omn	Pis	49	73	2.8	0	5.4	0.1	6.7	6.2	0.1	0	15	2.7	0	0	35	89	2.6	1.3	5.5					11	0.4	0	0.1	16	0.1			
<i>Pimelodus ortmanni</i>	Omn	Pis	21	6	16	1.4	11	1.1	23	31				2.9	0	0	44	65	0.8	0	0.1					1.2	1.4	1.2	0.1					
<i>Rhamdia branneri</i>	Car	Car	5	2		0.1	53	98						42													0.4							
<i>Rhamdia voulezi</i>	Pis	Pis	3	15	0	2.8	0.2	3.7	4.8					9.3													84	95	0.2	0			0.1	

Table 6. Summary of the indicator species analysis showing the Relative Abundances (RA), Relative Frequencies (RF) and indicator values (IndVal) of food resources used by the fish fauna, before and after the impoundment of the Salto Caxias Reservoir, Iguaçu River (only food resources with significant values are listed). Bold font indicates significant indicator values ($p < 0.05$, Monte Carlo permutation test).

Food resources	Relative abundance		Relative Frequency		IndVal		<i>p</i>
	Phase		Phase		Phase		
	Before	After	Before	After	Before	After	
Terrestrial insects	79	21	65	47	51	10	0.0001
Aquatic insects	77	23	65	57	50	13	0.0001
Aquatic plants	98	2	42	2	41	0	0.0001
Terrestrial plants	65	35	53	45	35	16	0.0022
Macroinvertebrates	92	8	19	6	18	0	0.0001
Decapods	75	25	15	6	11	2	0.0059
Microcrustaceans	9	91	5	43	0	39	0.0001
Algae	26	74	27	43	7	32	0.0001
Fish	39	61	23	40	9	24	0.0004
Fish scales	36	64	16	36	6	23	0.0001

Table 7. Results of the SIMPER analyses for the dissimilarity of the proportion in number and biomass (CPUE) of the trophic guilds along the longitudinal gradient of the Salto Caxias Reservoir, Iguaçu River, before and after the impoundment. (Alg = algivores; Det = detritivores; Her = herbivores; Ain = aquatic insectivores; Tin = terrestrial insectivores; Inv = invertivores; Omn = omnivores; Pis = piscivores; Pla = planktivores; Car = carcinophages).

	Guilds	Average dissimilarity	Contribution %	Cumulative Contribution %	Mean abundance	
					Before	After
Individuals Number (70.76)	Her	35.8	50.6	50.6	220.0	2,200.0
	Pis	15.8	22.3	72.9	78.6	490.0
	Omn	6.1	8.7	81.7	51.1	201.0
	Det	4.8	6.8	88.5	44.6	182.0
	Tin	2.5	3.5	92.0	30.7	15.2
	Alg	2.1	2.9	94.9	0.0	68.3
	Pla	1.7	2.5	97.4	0.0	29.4
	Ain	1.3	1.9	99.3	20.5	3.4
	Inv	0.3	0.5	99.8	2.5	4.3
	Car	0.2	0.2	100	1.8	1.9
Biomass (54.28)	Pis	26.0	47.8	47.8	7.1	30.0
	Her	8.9	16.4	64.2	4.1	12.9
	Det	8.7	16.0	80.2	3.5	9.6
	Omn	4.7	8.6	88.9	4.0	1.8
	Alg	3.5	6.4	95.3	0.0	1.5
	Pla	0.8	1.6	96.9	0.0	0.3
	Tin	0.7	1.3	98.2	0.4	0.2
	Car	0.5	0.9	99.1	0.2	0.3
	Ain	0.2	0.5	99.6	0.2	0.1
Inv	0.2	0.4	100	0.1	0.0	

Discussion

In Salto Caxias Reservoir, the fish fauna appears to have used all possible compartments of the habitat, because the fish showed versatility in exploiting about 11 different types of food resources. Most species analyzed in this study exhibited marked changes in their diets after the impoundment, being classified in different trophic guilds. Although food availability has not been measured, we presume that the fish are the best samplers of the available resources (or at least those that are used) because they focus on the resource that they can effectively access (Mérona *et al.*, 2003). The strategy of using the available resources (opportunistic *sensu* Gerking, 1994), is essential to allow the species to persist in impounded environments, because it enables them to broaden their range of resources and thereby tolerate more-severe impacts.

The species whose diets were least affected by the environmental changes were the typical detritivores and piscivores. Similar findings have been reported in other reservoirs (Mérona *et al.*, 2001; Novaes *et al.*, 2004; Fugi *et al.*, 2005; Loureiro-Crippa & Hahn, 2006; Luz-Agostinho *et al.*, 2006; Pacheco *et al.*, 2008). Detritivores and piscivores are trophic specialists with morphological adaptations of the mouth and digestive tract that may prevent them from using other resources. In addition, they may initially benefit from the high availability of detritus and fish after the impoundment (Luz-Agostinho *et al.*, 2006; Hahn & Fugi, 2007; Novakowski *et al.*, 2007; Agostinho *et al.*, 2008; Bennemann *et al.*, 2011).

The more-pronounced changes in the diet of most species were mainly related to the temporal factor, and reflected a trend commonly recorded after the formation of reservoirs, *i.e.*, a reduction in the intake of benthic invertebrates and allochthonous resources such as terrestrial plants and insects, which are usually replaced by resources from the reservoir environment itself, such as algae, microcrustaceans, and small-sized fish (Mérona *et al.*, 2003; Agostinho *et al.*, 2007; Mérona & Vigouroux, 2012). In the pre-impoundment phase, few species exploited these resources exclusively, but they were part of the diets of almost all the species. The amounts of these food categories increase in reservoirs because of the greater supply of nutrients, which increases the overall production, an event known as the trophic upsurge period (Agostinho *et al.*, 2007; Gubiani *et al.*, 2011). In this period, algae, microcrustaceans, and thereafter small-sized fish develop, as described by Araújo-Lima *et al.* (1995) and Agostinho *et al.* (2007) for several Neotropical reservoirs. On the other hand, the settlement of particulate matter in the impounded environments can reduce the diversity of benthic organisms (Ruiz, 1998; Mérona *et al.*, 2001), mainly aquatic plants (bryophytes), decapods, and macroinvertebrates. In addition, the fewer indicator food resources found after the impoundment reflected and corroborate the changes in diet

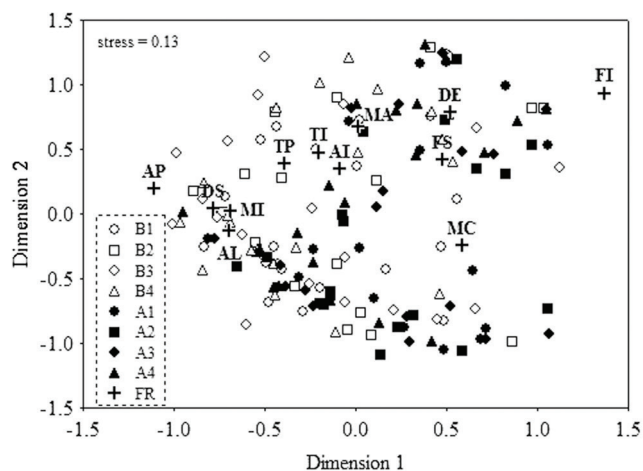


Fig. 2. Graphical representation of the first two axes of the Nonmetric multidimensional scaling (nMDS), demonstrating the food resources used by the fish fauna in the different sites and phases, in the area influenced by the Salto Caxias Reservoir, Iguaçú River. FR = Food resources (AI = aquatic insects; TI = terrestrial insects; DE = decapods; MC = microcrustaceans; MA = macroinvertebrates; MI = microinvertebrates; FI = fish; FS = fish scales; AP = aquatic plants; TP = terrestrial plants; AL = algae; DS = detrit/sediment); B = before impoundment, A = after impoundment; 1 to 4 = sampling sites.

of the species, indicating a general trend for the fish fauna to restrict the food spectrum than in the previous phase. A similar pattern was observed by Mérona *et al.* (2001) in the Tocantins River, where about eight species that were formerly considered non-specialized carnivores have started consuming fish almost exclusively, and five omnivorous species changed diet to consume food of animal or vegetable origin after the reservoir was formed.

Changes in the feeding habits of the fish fauna have markedly affected the abundance of the trophic guilds, since fish species have been classified into different guilds over time and space. These alterations have affected the trophic structure, with increases in the abundance of some guilds and reductions or even the disappearance of others. These changes were observed especially at the dam and downstream, in concordance with the longitudinal zonation generally observed in reservoirs, which is usually influenced by the size and depth of the system and the residence time of the water at the different sites (Hahn *et al.*, 1998; Agostinho *et al.*, 1999; Araújo-Lima *et al.*, 1995; Prchalova *et al.*, 2009). Although this zonation is not pronounced in the Salto Caxias Reservoir, given the physiographic characteristics of the reservoir, it has developed on a smaller scale. The most striking observations were the reduction of guilds that exploit allochthonous resources and benthic organisms, and the increase of the piscivore guild. The predominance of piscivores has been recorded in many reservoirs (Petrere, 1996; Gomes &

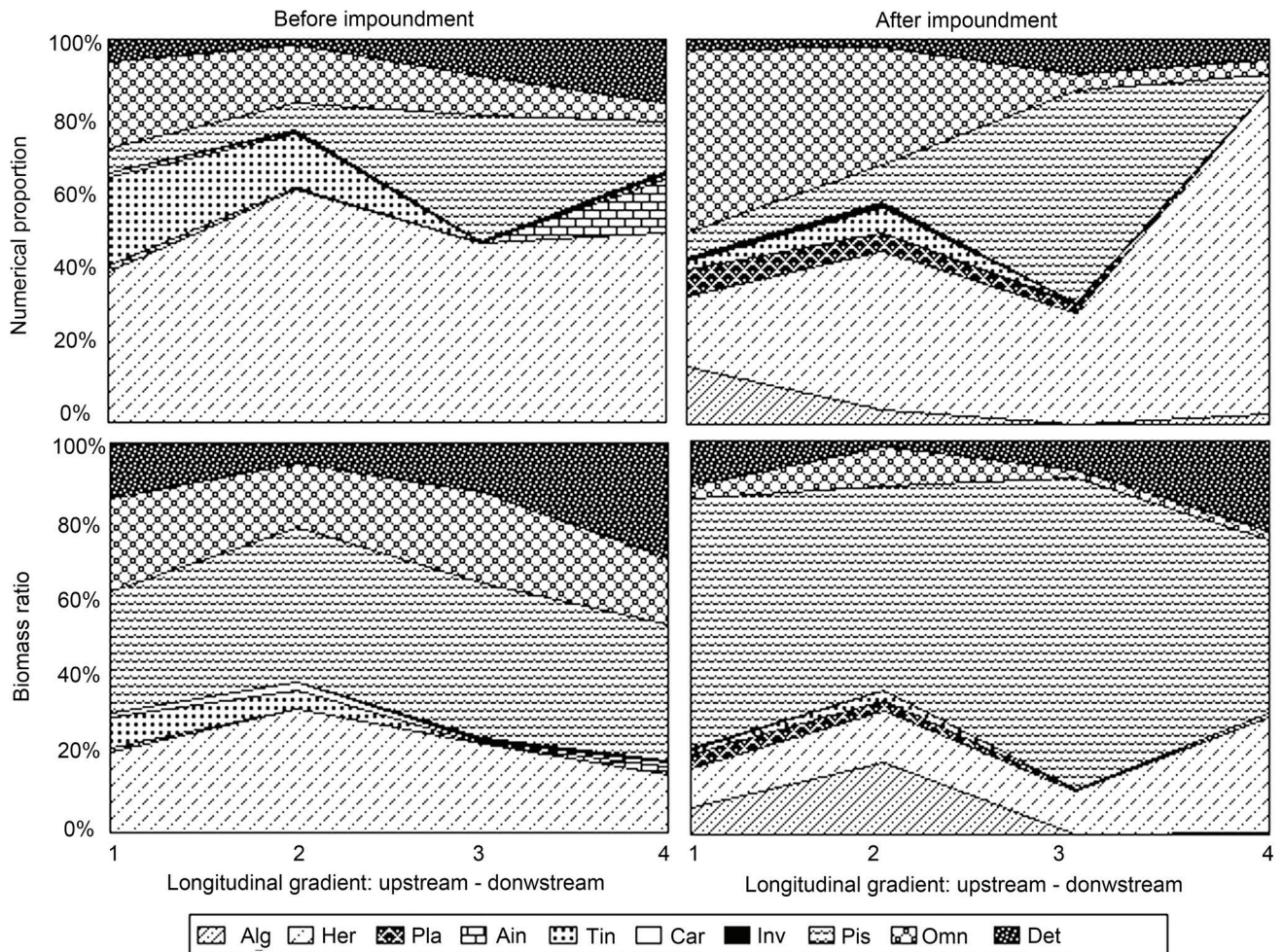


Fig. 3. Proportion in number and biomass (CPUE) of the trophic guilds along the longitudinal gradient of the Salto Caxias Reservoir, Iguaçú River, before and after the impoundment. (1 = upstream; 2 = middle region; 3 = dam; 4 = downstream) (Alg = algivores; Det = detritivores; Her = herbivores; Ain = aquatic insectivores; Tin = terrestrial insectivores; Inv = invertivores; Omn = omnivores; Pis = piscivores; Pla = planktivores; Car = carcinophages).

Miranda, 2001; Abelha *et al.*, 2005; Fugi *et al.*, 2005; Pelicice *et al.*, 2005; Luz-Agostinho *et al.*, 2006; Agostinho *et al.*, 2007; Mol *et al.*, 2007; Bennemann *et al.*, 2011). However, in the present study, the dominance of piscivores was very high, reaching 70% of the catches in biomass and 50% in number near the dam (site 4). The large catches of *Pimelodus britskii* (an omnivorous fish before the impoundment) contributed to the marked dominance of piscivores, especially at the dam site. A high abundance of “lambari” (five species of *Astyanax*, *Bryconamericus ikaa*, and *Cyanocharax aff. alburnus*), along with other small-sized and r-strategist species, characterizes the fish fauna of the Iguaçú River (Baumgartner *et al.*, 2012). The high intrinsic rate of population increase and the ability to quickly colonize disturbed habitats lead to a high turnover of prey individuals (Bailly *et al.*, 2005; Fugi *et al.*, 2005; Pelicice *et al.*, 2005); this explains the high proportion of piscivores found in this study.

In conclusion, the present study showed evidence that the majority of species were flexible, responding almost immediately to the increase in autochthonous resources. The observed alterations in the abundance of trophic guilds were more directly related to changes in the feeding habits of the fish fauna than to increases in the number and biomass of the species that constituted these guilds. This demonstrates that the opportunistic behavior of most species influenced the community trophic structure after the impoundment. So, it corroborates our initial prediction. Additionally, this allows us to speculate that the food supply is not the major constraint impeding the initial colonization of the reservoir. Considering that the feeding strategy is one of the factors that determine the success of fish, especially in impounded environments, it is expected that those species with a more generalist diet and greater ability to exploit temporarily available resources will colonize successfully the Salto Caxias Reservoir.

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