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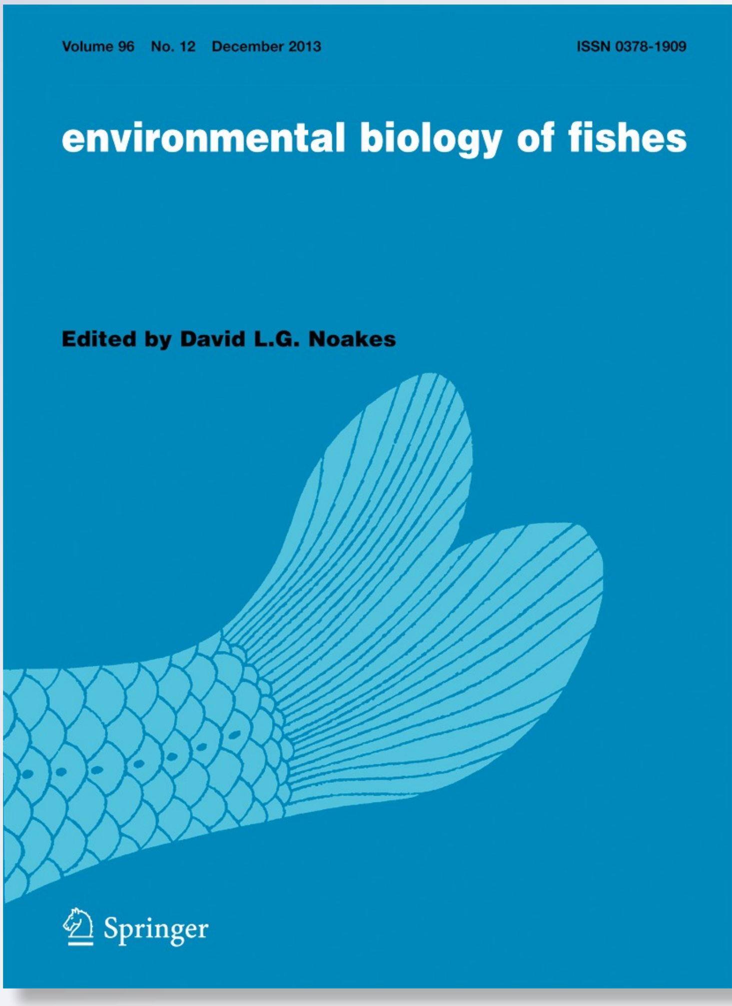

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Seasonal response of fish assemblages to habitat fragmentation caused by an impoundment in a Neotropical river

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Abstract Changes in fish assemblages between the zones above and below Funil dam in Southeastern Brazil were investigated to evaluate the possible impacts of this impoundment in two contrasting seasons: summer/wet and winter/dry. We expect differences in fish assemblage structure and in environmental conditions between seasons and between the reservoir and the zone downriver of the dam. A total of 3,579 individuals comprising 38 species, including six non-natives, were collected. As expected, the comparatively high habitat complexity and water flow regime of the downriver zone favored a richer and more abundant fish assemblage compared with the reservoir, especially in the wet season. In this period, water covers part of the riparian vegetation, increasing habitat availability and nutrient input. Additionally, the dam prevents upriver migration of rheophilics fish species such as the Characiformes *Prochilodus lineatus* and *Leporinus copelandii*, and the Siluriformes *Pimelodus fur and Pimelodus maculatus*, thus increasing shoals below the dam. Although the reservoir represents a simplified ecosystem highly influenced by non-native top predator species (e.g. the Perciformes *Cichla kelberi* and *Plagioscion squamosissimus*), seasonal processes (e.g. water level fluctuations and flood pulses) seem to play a role in structuring of the fish assemblage. Environmental variables, mainly turbidity, temperature, and conductivity were significantly associated to spatial-temporal patterns of fish assemblage. In this freshwater tropical reservoir, the spatial scale, rather than the seasonal changes in environmental variables, was the dominant factor structuring fish assemblage in the reservoir and in the zone downriver of the dam.

Keywords Funil reservoir · Paraíba do Sul River · Ichthyofauna · Spatial-temporal structure · Dams · River fragmentation

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Introduction

Riverine impoundments fragment lotic ecosystems worldwide (Nilsson and Berggren 2000), frequently with deleterious impacts on aquatic systems at multiple spatial and temporal scales (Benke 1990; Poff et al. 1997; Pringle et al. 2000). Because of the negative impacts, reservoirs present a good opportunity for studying and evaluating the effects at local scale of their influence on fish assemblages (Oliveira et al. 2004). Every dam has unique characteristics and, consequently, the nature of environmental changes is highly site-specific (McCartney 2009), with unique impacts for each dam. Differences in biotic and abiotic factors between up and downriver zones of the dam may be a consequence (direct or indirect) of dam construction. Investigations focusing at the local scale (immediately above and below of the dam) are needed and may provide useful clues to mitigate the adverse effects of impoundments. Understanding the effects of impoundments on the ichthyofauna may help environmental mangers to reconcile the socio economic benefits of impoundments with protection of the local aquatic ecology and must fit within the overall river basin management planning process.

Funil Reservoir was built in 1969 in the middle stretch of the Paraíba do Sul River, one of the most used riverine systems in Brazil for many purposes, among them, hydro-power generation, flow regulation and water supply. A major effect of its impoundment is the formation of two contrasting habitats; a lentic environment upstream from the dam, and a tailwater environment downriver of the dam. Other consequences of river impoundments are decreasing of fish richness because of habitat homogenization, changes in artisanal fisheries and introduction of non-native species (Martinez et al. 1994; Hoeinghaus et al. 2009). Dams have increased the cost of fish migration, which reduces energy available for sexual selection and favors a nonmigratory life history, with the reservoirs being a benign environment for many non-native species that are competitors with or predators on native species (Waples et al. 2008). While agency stocking programs encourages sport fisheries and fish culture, local enthusiasm for these activities usually result in illicit introductions of non native species.

Funil Reservoir has seasonal patterns of its environmental characteristics induced mainly by precipitation (Soares et al. 2008), which is directly related to increases in the water level and river inflow during the wet season. Both the reservoir and downriver zones are highly influenced by flood pulses and drought, which cause changes in the availability of physical habitat, food, nutrient inputs and fish migrations (Santos et al. 2010; Terra et al. 2010).

This study aims to elucidate the fish assemblage structure above and below the Funil Dam to evaluate possible impacts of this impoundment, considering two contrasting environmental conditions: summer/wet and winter/dry seasons. We expect differences in fish assemblages and in environmental conditions between the reservoir and the zone downriver of the dam. Since reservoirs bring serious and irreversible alterations in the natural hydrologic regime of rivers, we predict that such changes will affect habitat quality and the dynamics of the biota. Additionally, we also expect that the downriver zone has more fish species and abundance during the wet season because of comparatively higher habitat availability and because migration hindrance of rheophilics fishes that concentrates shoals below the dams (Northcote 1998). Furthermore, we expect more influences of non-native fish species in the reservoir zone, a common consequence of rivers impoundment.

Material and methods

Study area

The Funil Reservoir (Fig. 1) is located mid-way down the Paraiba do Sul River in Southeastern Brazil (22° 31′43.5″S; 43°34′05.7″W). It has a typical branched reservoir area of c.a. 40 km^2, lacking floodplain areas to facilitate lateral connections between the river and marginal lagoons. The hydropower plant, that also controls floods, became operational in 1969. The dam is 385 m long and blocks the entire river course, restraining completely fish movements from up to downriver and vice-versa.

Seasonal rainfall peaks dictate the dynamics of reservoir water level. The reservoir has a maximum depth of 70 m (average of 20 m), a retention time of 10–55 days, and a wide water-level oscillation, which contributes to marginal erosion and sedimentation (Santos et al. 2010). Typical winter and summer flows are 109 m^3 s^{-1} and 950 m^3 s^{-1}, respectively (Marengo and Alves 2005). Annual rainfall ranges from 100 to 300 cm, with the average generally over 200 cm (Carvalho and Torres 2002). Due to large amplitude of the water level oscillations in the reservoir, shore vegetation is very poor featuring an extensive and unprotected shoreline. The surrounding vegetation is degraded, a result of previous agricultural use for coffee plantations and pasture. According to Branco et al. (2002), an increasing eutrophic condition develops in the reservoir due to anthropogenic influences.

On the other hand, the stretch of river below the dam (downriver zone) has a heterogeneous environment with high habitat diversity due to different types of substrate composed of boulder, cobble and gravel associated with high water velocity. The margins are relatively well protected by riparian vegetation and rocky formations (Terra et al. 2010). Water depth is approximately 3 m and the river width ranges between 50 and 100 m.

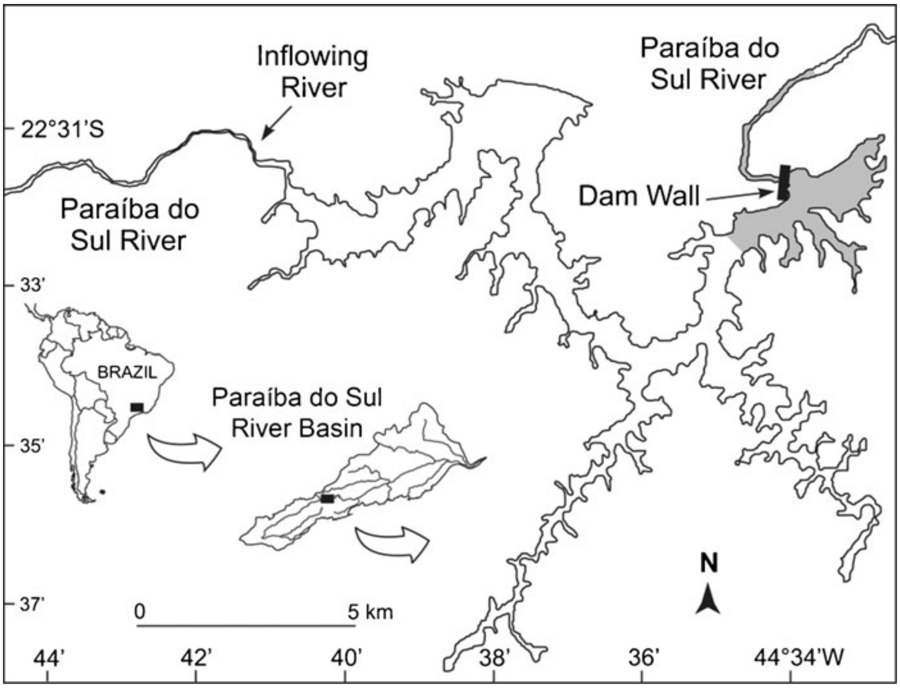

Fig. 1 Map indicating the study area (grey area) in Funil Reservoir – Paraíba do Sul downriver system

Sampling

Eight fish sampling events were carried out over two consecutive years. In each year, two collections were performed during the wet season (January and February/2010; January and March/2011) and two during the dry season (August and September/2010; July and September/2011). A standardized fishing effort was applied in both zones (reservoir and downriver zones), along a stretch of approximately 2 km from the dam. Ten sets of three gillnets (20×2.5 m; 25, 50 and 75 mm mesh size) were randomly distributed within each zone, with a total sampled area of approximately 150 m^2. The sample unit was defined as the sum of all fishes caught by each set of three gillnets. Therefore, our sampling design had a total of 40 samples (10 sets of nets×2 months×2 years) in each zone per season.

Measurements of physico-chemical variables were performed at each fish sampling occasion. Temperature (°C), dissolved oxygen ($mg\times L^{-1}$), conductivity ($\mu S\times cm^{-1}$) and redox potential (mV) were measured using a multisensor Horiba W-21 (Horiba Trading Co., Shanghai). Turbidity (NTU) was taken with a Policontrol turbidimeter model AP2000. Measurements were made during the morning, at a depth of 20 cm below the surface and a distance of approximately 3 m from the margin of the river or reservoir.

Data analysis

Species richness was estimated with individual-based rarefaction curves representing the means of repeated re-sampling of all pooled individuals. Rarefaction curves were calculated for fish assemblage in each zone and season, using the software Estimates 7.5 (Colwell 2005).

The raw data of species abundance was square-root transformed to reduce the contributions of highly-abundant species and used to create a Bray–Curtis similarity matrix. Two-way analysis of similarities (ANOSIM) was performed to assess eventual differences in fish assemblage between zones and seasons. These analyses were performed using PRIMER version 5 (Clarke and Warwick 1994). The Indicator Species Analysis was used to determine which species might be used as indicators, characterizing different zones/seasons. This analysis of species gives an indicator value from 0 to 100 %, where zero indicates that the species is not an indicator for a particular environment and 100 indicates that the occurrence of the species is characteristic of the environment. This method, developed by Dufrêne and Legendre (1997), was applied using the software PCOrd (McCune and Mefford 1999).

Abiotic variables were log-transformed to minimize the differences between units of different variables and compared with the non-parametric Kruskal-Wallis test followed by a Multiple Comparisons of Mean Ranks for all Groups test ($P<0.01$). These analyses were performed using Statistica 7.0 package (Statsoft, Tulsa, Oklahoma, USA).

Canonical Correspondence Analysis (CCA) was performed by using CANOCO version 4.5 (ter Braak and Šmilauer 2002) on fourth-root transformed data to detect joint species distribution and environmental patterns. Statistical significance was assessed by a Monte Carlo permutation test, using 1,000 sample permutations ($P<0.01$). Only species with frequency of occurrence above 15 % were considered in this analysis in order to remove the influence of rare species. Such removal of rare species may prevent the strong dependence of ordination procedures on single outlier species (McCune and Mefford 1999).

Results

Fish assemblages

A total of 3,579 specimens comprising five orders, 15 families, 30 genera and 38 species were caught, including six non-native species (Table 1). A higher richness and abundance was found in the downriver zone (33 spp.; 2,069 individuals) compared with the reservoir zone (23 spp.; 1,510 individuals). Species rarefaction curves showed an increase in the number of species, but did not reach an asymptote (Fig. 2). Nonetheless, similar patterns were depicted with the greatest number of species for the downriver zone in summer/wet season and the lowest for the reservoir in winter/dry season.

According to the ANOSIM, spatial differences of the fish composition were more pronounced during the wet season ($R=0.55$, $P_{1,78}<0.001$) than dry season ($R=0.34$, $P_{1,78}<0.001$). When we consider seasonal differences for each zones, the reservoir had greater fish assemblage changes ($R=0.26$; $P_{1,78}<0.001$) than the downriver zone ($R=0.14$; $P_{1,78}<0.001$). Moreover, each zone/season was characterized by different sets of species (Table 2). According to Species Indicator Analysis, eight species, including the migrants Characiformes *L. copelandii* and *P. lineatus*, and the Siluriformes, *P. maculatus* and *P. fur* were indicators for the downriver zone during wet season. Five species were characteristics of the reservoir zone in the wet season, especially *H. littorale* and two non-native species (the Perciformes *C. kelberi* and *P. squamosissimus*). *Oligosarcus hepsetus* and *P. fur* were typical of the downriver zone during both the wet and dry seasons (Table 2).

Environmental variables and fish assemblages

The temperature was comparatively higher during wet season with the highest values recorded in the reservoir zone irrespective of seasons (Table 3). The dissolved oxygen values were significantly higher in the reservoir zone during the dry season, while the highest turbidity and redox potential values were found in the downriver zone during the wet season. Conductivity was significantly higher in the dry season compared with the wet season in both zones.

The Monte Carlo permutation test was significant for all abiotic variables used in CCA, therefore, no variable was excluded from analysis. The first two axes explained 78.6 % of the total variance in the species-environment correlation (Table 4). The first two canonical axes revealed a well-defined spatial-temporal pattern (Fig. 3). The first axis explained 51.4 % of the species-environment relationship, and separated the reservoir and downriver samples (i.e., spatial dimension). The second axis explained 27.5 % and distinguished the wet and dry samples (i.e., seasonal dimension). According to the CCA, the non-native predator species (*P. squamosissimus* and *C. kelberi*) were associated with higher values of temperature and turbidity, typical of the wet-season samples. In contrast, the conductivity was the main variable related to the dry-season samples and was directly associated with the occurrence of *P. fur, P adspersus* and *P. lineatus* (Fig. 3).

Discussion

Our results showed that changes in fish assemblage structure were more related to the spatial (habitat) characteristics than to the seasonal changes in environmental variables. The largest differences in assemblages between the reservoir and downriver zones were observed during the wet season, especially because of the contribution of

Table 1 Total number of specimens (ΣN), total length range (TL, cm), and frequency of occurrence (%FO) of the fish species in the Funil Reservoir – Paraíba do Sul downriver system

Species	Reservoir (S=23)		Downriver (S=33)		ΣN	TL	%FO
	Wet	Dry	Wet	Dry			
Characiformes							
Anastomidae							
Leporinus copelandii Steindachner, 1875			56	27	83	15.2–51.5	26.3
Leporinus conirostris Steindachner, 1875	1		8		9	23–34	1.9
Leporinus mormyrops Steindachner, 1875			7	3	10	13–23.3	2.5
Characidae							
Astyanax bimaculatus (Linnaeus, 1758)	481	250	242	141	1114	4.5–15.5	77.5
Astyanax parahybae (Eigenmann, 1908)		2	235	18	255	8–16	20
Astyanax scabripinnis (Jenyns, 1842)			54		54	9–13	2.5
Astyanax sp.			116	2	118	9–14.3	7.5
Brycon insignis Steindachner, 1877				1	1	28.5	0.6
Oligosarcus hepsetus (Curvier, 1829)	2	1	81	54	138	16–29.7	25.7
Metynnis maculatus (Kner, 1858)[a]	8	11	1		20	7–15.3	5.6
Piaractus mesopotamicus (Holmberg, 1887)[a]	1				1	70	0.6
Probolodus heterostomus Eigenmann, 1911			5	1	6	11.8–13.5	1.9
Salminus brasiliensis (Curvier, 1816)[a]			4		4	37–38.7	1.3
Crenuchidae							
Characidium lauroi Travassos, 1949	6	2			8	10–13	4.4
Erythrinidae							
Hoplerythrinus unitaeniatus (Agassiz, 1829)		3			3	24–25.5	0.7
Hoplias malabaricus (Bloch, 1794)	9	25	5	21	60	12.5–43	27.5
Prochilodontidae							
Prochilodus lineatus (Valenciennes, 1837)	1	1	30	6	38	15–45.5	16.9
Siluriformes							
Auchenipteridae							
Trachelyopterus striatulus (Steindachner, 1877)			1		1	17	0.6
Callichthyidae							
Callichthys callichthys (Linnaeus, 1758)			1		1	16.5	0.6
Hoplosternum littorale (Hancock, 1828)	66	4	7	4	81	9–29	21.9
Heptapteridae							
Pimelodella eigenmanni (Boulenger, 1891)			1		1	13.5	0.6
Rhamdia quelen (Quoy & Gaimard, 1824)			12	8	20	21–37	10.7
Loricariidae							
Hypostomus affinis (Steindachner, 1877)			22	11	33	15.8–43.8	15.6
Hypostomus auroguttatus Kner, 1854	1		6	6	13	14–34	6.9
Rhinelepis aspera Spix & Agassiz, 1829[a]			33		33	20–38	4.4
Rineloricaria lima (Kner, 1853)	1		13	6	20	12.3–15.5	5.6
Pimelodidae							
Pimelodus fur (Lütken, 1874)	5	5	217	173	400	12–28.5	33.1
Pimelodus maculatus La Cèpede, 1803	70	50	200	51	371	11.5–41.5	58.1
Gymnotiformes							
Gymnotidae							

Table 1 (continued)

Species	Reservoir (S=23)		Downriver (S=33)		ΣN	TL	%FO
	Wet	Dry	Wet	Dry			
Gymnotus carapo Linnaeus, 1758	3	2	11	1	17	15–33.2	8.1
Sternopygidae							
Eigenmannia virescens (Valenciennes, 1842)			37	13	50	12.1–33	13.1
Symbranchiformes							
Synbranchidae							
Synbranchus marmoratus Bloch, 1795	1				1	43	0.6
Perciformes							
Cichlidae							
Australoheros paraibae Ottoni & Costa 2008		9		1	10	8.2–15.5	5.6
Cichla kelberi Kullander & Ferreira, 2006[a]	64	2	1		67	9–40.5	15.6
Crenicichla lacustris (Castelnau, 1855)	6	2	4	7	19	12.5–27	10.6
Geophagus brasiliensis (Quoy & Gaimard, 1824)	17	4	2	3	26	12–26.5	12.5
Tilapia rendalii (Boulenger, 1897)	2				2	11–16.5	0.6
Sciaenidae							
Pachyurus adspersus Steindachner, 1879	55	22	7	8	92	12.5–28	23.1
Plagioscion squamosissimus (Heckel, 1840)[a]	258	57	64	20	399	6–45	58.8
Total	1058	452	1483	586	3579		

S=species richness

[a] non-native species

migratory fishes (e.g., *Leporinus copelandii*, *Pimelodus maculatus*, *Prochilodus lineatus* and *Pimelodus fur*) in the downriver zone, and reservoir-tolerant native (*H. littorale*) and non-native fishes (e.g., *C. kelberi* and *P. squamosissimus*) in the reservoir. Generally, the reproduction of most Neotropical fish species, particularly those migrants, coincides with the wet/rainy season and high temperatures (Lowe-McConnell 1987; Vazzoler et al. 1997). Despite the existence of several triggers for reproduction of rheophilic fishes, one of the most important in the Neotropical region is the increase in water flow during the rainy season, a condition that is strongly altered by river damming (Agostinho et al. 2004). In this study, we rarely recorded rheophilic species in the reservoir, except *P. maculatus*, which confirms that the lentic habitat is unsuitable for these species.

The accumulation of migratory fishes immediately below dams is well documented (Taylor et al. 2001; Gehrke et al. 2002), and these interruptions are the main factor that affects the abundance of migratory fishes, mostly in downriver sections (Bayley and Petrere 1989; Northcote 1998; Agostinho et al. 2005; Roscoe and Hinch 2010). According to Leeuw and Winter (2008) some rheophilic fishes reside in the areas immediately downriver of dams during the spawning season, although it was unclear to what extent these reflected habitat choice or barriers to migration. We detected that rheophilic species were associated with the downriver zone during the wet season, which probably is associated with the river blockage by the dam.

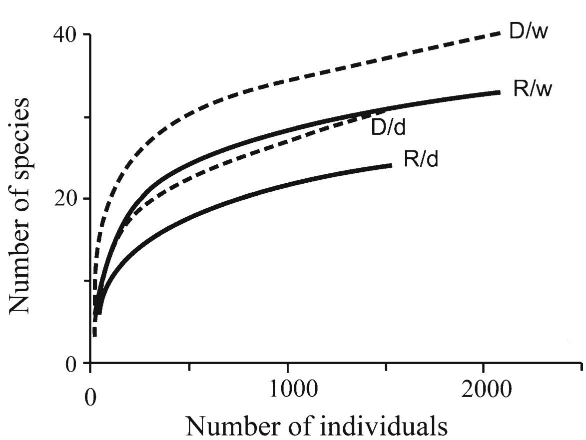

Fig. 2 Individual-based rarefaction curves for species richness in Funil Reservoir – Paraíba do Sul downriver system. Codes: R/w, reservoir in wet season; R/d, reservoir in dry season; D/w, downriver zone in wet season; D/d, downriver zone in dry season

Table 2 Significant values of the Indicator Species Analysis for the fish assemblage in the Funil Reservoir – Paraíba do Sul downriver system

Species	Indicator value	*P*	Zone/season
Astyanax bimaculatus	38.9	< 0.001	R/w
Cichla kelberi	52.5	< 0.001	R/w
Hoplosternum littorale	55	< 0.001	R/w
Pachyurus adspersus	26.9	< 0.001	R/w
Plagioscion squamosissimus	55	< 0.001	R/w
Astyanax parahybae	48.4	< 0.001	D/w
Hypostomus affinis	25	< 0.001	D/w
Leporinus copelandii	40.5	< 0.001	D/w
Pimelodus maculatus	40.4	< 0.001	D/w
Prochilodus lineatus	39.5	< 0.001	D/w
Oligosarcus hepsetus	24.9	0.002	D/w; D/d
Pimelodus fur	28.3	0.008	D/w; D/d

Zone codes: R=Reservoir; D=Downriver. Season codes: w=wet; d=dry

Tropical regions usually have strong seasonal precipitation that produces seasonal patterns of river discharge, and consequently, temporal patterns of fish distribution (Winemiller and Jepsen 1998). In this study, abiotic variables had a strong influence in the second canonical axis (i.e. seasonal dimension), though they were also directly related to and influenced by the dam/impoundment. High turbidity values were recorded during the wet season, and associated with the highest occurrence of *A. parahybae*, *H. littorale* and carnivorous species (e.g., *P. squamosissimus*, *C. kelberi* and *O. hepsetus*). Increased sedimentary inputs from erosion and algal growth from eutrophication lead to increased turbidity (Gray et al. 2012). Turbid waters can alter visually mediated behaviors in fish, such as foraging (Utne-Palm 2002), avoiding predators (Abrahams and Kattenfeld 1997) and selecting mates (Candolin et al. 2007; Maan et al. 2010). In contrast, high conductivity values were recorded during the dry season. Overall, water conductivity tends to be lower during wet season (Winemiller and Jepsen 1998) because rainfall dilutes the ions present in the water; therefore, conductivity levels decreased during the wet season and increase in the dry season (Matthews 1998; Guarino et al. 2005). These environmental conditions appeared to favor the presence of some bottom-dwelling species (e.g. atipa *Hoplosternum littorale* and the catfishes *P. maculatus* and *P. fur*). However, these relationships are not very consistent, because seasonal environmental changes and anthropogenic interferences can modify existing physico-chemical characteristics affecting directly fish species (Araújo and Tejerina-Garro 2009).

We found higher fish richness and abundance in the downriver zone compared with the reservoir zone, confirming our expectations that the downriver zone supports more fish species than the reservoir. Narrow transversal section of the habitat and the dam obstacle probably contributed to fish agglomeration in the downriver zone, mainly due to reproductive migrations. Structural habitat complexity, which seems to be high in the downriver zone, supports fish diversity both directly and indirectly, because it contributes

Table 3 Abiotic data (mean±s.d.) from Funil Reservoir – Paraíba do Sul downriver system during the wet and dry seasons. Superscript letters indicate significant ($P_{1,158}$<0.001) differences according to Kruskal-Wallis test (a>b>c>d). n=40 for each zone in each season

Zone/season	Temperature (°C)	Dissolved oxygen (mg L^{-1})	Redox potential (mV)	Conductivity (µS cm^{-1})	Turbidity (NTU)
R/w	29 ± 0.7^{a}	6.5 ± 1.5^{b}	247.3 ± 26.8^{b}	73.1 ± 0.2^{b}	23.9 ± 11.4^{b}
D/w	25.9 ± 1.3^{b}	6.3 ± 0.9^{b}	276.7 ± 46.9^{a}	70.3 ± 0.5^{b}	56.2 ± 17.7^{a}
R/d	22.2 ± 1.1^{c}	8.8 ± 0.6^{a}	217.8 ± 40.7^{c}	90.5 ± 0.4^{a}	4.3 ± 2.3^{c}
D/d	20.3 ± 0.6^{d}	5.9 ± 0.3^{b}	269.1 ± 12.0^{b}	89.2 ± 0.3^{a}	3.8 ± 1.8^{c}

Zone codes: R=Reservoir; D=Downriver. Season codes: w=wet; d=dry

Table 4 Summary of Canonical Correspondence Analysis of data for biotic and abiotic factors in the Funil Reservoir – Paraíba do Sul downriver system

Axes	1	2	3	4	Inertia
Temperature	−0.15	−0.56	0.21	−0.02	
Conductivity	−0.29	0.53	−0.22	−0.02	
Dissolved oxygen	−0.32	−0.01	−0.38	0.15	
Redox potential	0.04	0.07	0.34	0.25	
Turbidity	0.34	−0.45	0.13	0.05	
Summary					
Sum of all eigenvalues	0.284	0.152	0.073	0.031	3.282
Sum of all canonical eigenvalues					0.552
Cumulative variance (%)					
Of species data	8.6	13.3	15.5	16.5	
Of species-environment relation	51.4	78.6	92.2	97.8	

to the increase of invertebrate species, preferential food resources for omnivores and young carnivores such as *P. fur* and *O. hepsetus* (Felley and Felley 1987; Peretti and Andrian 2004; Araújo et al. 2005). Ogbeibu and Oribhabor (2002) revealed that sites below reservoirs generally support higher macroinvertebrate diversity than reservoirs, thus increasing food availability for ichthyofauna. Higher food availability and shelter during the wet season is typical of tropical rivers (Angermeier and Karr 1983; Lowe-McConnell 1987), and presumably are related to the increase of fish diversity in both zones.

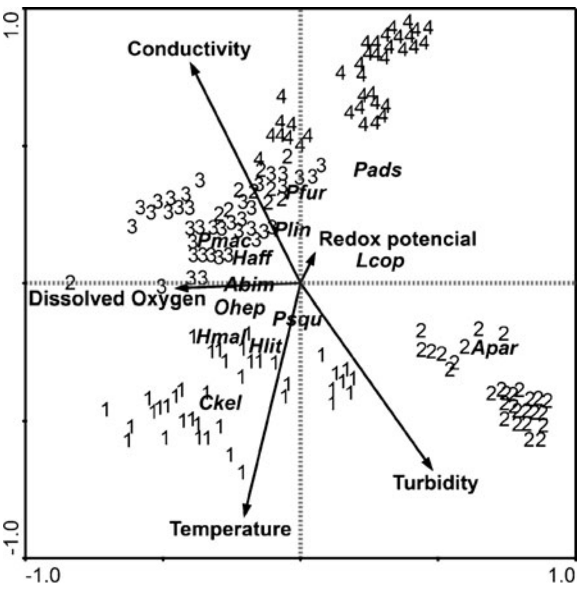

Fig. 3 Triplot of canonical correspondence anayses of the 13 most frequent species with abiotic variables and zones. Codes for Zone/Season: 1, reservoir/wet; 2, downriver/wet; 3, reservoir/dry; 4, downriver/dry. Species codes: *Apar*, *Astyanax parahybae*; *Abim*, *Astyanax bimaculatus*; *Ckel*, *Cichla kelberi*; *Hmal*, *Hoplias malabaricus*; *Hlit*, *Hoplosternum littorale*; *Haff*, *Hypostomus affinis*; *Lcop*, *Leporinus copelandii*; *Ohep*, *Oligosarcus hepsetus*; *Pfur*, *Pimelodus fur*; *Pmac*, *Pimelodus maculatus*; *Pads*, *Pachyurus adspersus*; *Plin*, *Prochilodus lineatus*; *Psqu*, *Plagioscion squamosissimus*

Introduction and establishment of non-native species as result of this impoundment was detected in this study. The non-natives species silver croaker (*Plagioscion squamosissimus*) and the peacock bass (*Cichla kelberi*), both top predator of Amazonian rivers and lakes, were introduced in the reservoir and their establishment is linked to the decrease and displacement of native fish population in this stretch of the Paraiba do Sul River basin. These two predator species were associated with higher values of temperature and turbidity, typical of the wet-season samples and occurred main in the reservoir. They probably take advantage of the highest number of fishes, especially forage species (e.g., *Astyanax bimaculatus*) that are abundant in the reservoir during the wet season. There are strong indications that species of *Cichla* and *P. squamosissimus* exploit resources available in the environment, mainly fish, insects and crustaceans, demonstrating opportunistic behavior (Capra and Bennemann 2009; Villares-Junior and Gomiero 2010). According to Holmquist et al. (1998), non-native fish predators have a higher abundance above than below large dams in tropical streams. Furthermore, in many Brazilian reservoirs the decrease of native river fish populations have been reported as a result of introduction of non-native piscivorous fish species associated with impoundments (Latini and

Petrere 2004; Gomiero and Braga 2004; Bennemann et al. 2006; Pelicice and Agostinho 2009). The deliberate or accidental introduction of non-native species has caused a range of environmental impacts (e.g., predation, competition, parasite dissemination, hybridisation, habitat use), and aquaculture and sport fisheries in reservoirs are the key drivers for the introduction of such species (Peeler et al. 2011).

Hoplosternum littorale was another fish well suited to reservoir conditions during the wet season. The highest amplitude of dissolved oxygen values found in the Funil reservoir zone can be interpreted as a clear evidence of the eutrophication process already reported by Branco et al. (2002). According to Smith et al. (2009), this species is very abundant and adapted to locals with increased concentration of organic loads and low water oxygenation. The ability to breathe atmospheric oxygen and saculiforms structures in intestinal alces (Chagas and Boccardo 2006) ensure greater efficiency during hypoxia and the colonization of this kind of environment.

We conclude that the local habitat constraints are the main force behind fish fauna structure, while temporal shifts seemed to play a secondary role in structuring fish assemblage. The impoundment effect on the fish fauna was documented by differences in assemblages between the reservoir and the zone downriver of the dam. The most typical species of the downriver zone were rheophilics, probably indicating a negative impact of dams for reproductive migration of these fish populations. Additionally, the downriver zone supported more fish species and abundance, mainly due to migration deterrent in wet season, which increases shoals bellow dams. Although it is widely accepted that freshwater tropical fish assemblages are mainly structured by seasonal changes in environmental conditions (Lowe-McConnell 1987; Vazzoler et al. 1997), in this research, the spatial scale was the dominant factor structuring fish assemblage. Further studies on the influence of reservoirs to the fish assemblage are required. A sampling design that encompasses different reservoirs should be implemented to corroborate this study's findings.

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