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Influences of dams with different levels of river connectivity on the fish community structure along a tropical river in Southeastern Brazil

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Summary

The influence of three types of dams with different degrees of river connectivity on the structure of fish communities along the Paraíba do Sul River was studied: total blockage (Dam 1); partial blockage allowed by a permanent lateral channel (Dam 2); and total blockage, but with a mechanism operating in the summer for fish passage (Dam 3). The tested hypothesis is that the degree of river connectivity influences the fish community. The largest differences in fish fauna were expected between the reservoir and downriver stretch in Dam 1 with total blockage; an intermediate difference in Dam 3 with total blockage but with a fish passage; and the least difference in Dam 2 with partial blockage. Fish were caught by gill nets between January and March 2010 and between January and February 2011 (wet seasons) in two zones: the reservoir and the downriver stretch from the dam. A total of 43 fish species was recorded, including eight non-native and two marine species. The 13 most abundant species (n > 100; frequency of occurrence >20%) occurred in all three stretches of the river. The community structure changed significantly between the reservoir and associated downriver stretch, with higher richness downriver compared to the reservoir zone. A trend for higher occurrence of migratory fishes (e.g. *Pimelodus maculatus, Pimelodus fur, Leporinus copelandii* and *Prochilodus lineatus*) was found in the downriver zone, suggesting the influence of dams on their upriver migration. The predictions were not fully matched. Although the most significant difference in the fish community structure between the reservoir and the downriver was found for Dam 1, the partial blockage in Dam 2 showed broader differences in the fish fauna than the total blockage in Dam 3 with the fish ladder, which may indicate that the latter is not a guarantee that species and genetic flux will be interchanged, since the water velocity may be a constraint to upriver fish migration.

Introduction

It is well accepted that fragmentation on the continuity of rivers caused by dams results in serious impacts on the fish community structure (Joy and Death, 2001; Freeman et al., 2003; Park et al., 2003; Fukushima, 2005). Nowadays, efforts are toward a congenial design and operation of dams and weirs, aiming to reconcile economic and environmental aspirations. Many authors have assessed the changes in fish assemblages in main-channel tailwaters – downriver of dams – (Poff et al., 1997; Poff and Hart, 2002) in the longitudinal extent or river-dam gradient (Oliveira et al., 2003; Vehanen et al., 2005) and transversal or upriver-downriver gradients of the tributaries (Oliveira et al., 2004; Matthews and Marsh-Matthews, 2007). Nevertheless, local investigations, i.e. immediately above and below the dams, are lacking; this new kind of approach has the advantage of focusing more directly on where the influence of damming is most effective.

The Paraíba do Sul River is fragmented by dams for various purposes (e.g. energy sources, flood control and water supply) along its extended 1100 km. Seven impoundments are currently in operation and another three are planned, fragmenting to different extents the contiguity of the river, thus providing conditions to assess the influence of dams on fish assemblages. The river has a catchment area of ca. 55 500 km^2, draining one of the most developed areas in Brazil. Several studies have been carried out to assess the fish community structure in the river (Teixeira et al., 2005; Araújo et al., 2009; Terra et al., 2010), however, information on the effects of dams on the structure of the fish community are lacking.

This study focus on three dams in Paraíba do Sul River characterized by different degrees of river connectivity for fish: Dam 1 has a total blockage with a typical lentic reservoir, no mechanism for fish passage, and with water flowing through turbines which can limit survival chances even for eggs and larvae (Agostinho et al., 2007); Dam 2 has a partial blockage with a lotic reservoir, no turbines and a permanently open 4-m wide gate allowing water passage at an average velocity of ca. 5 m s^{-1}; Dam 3 has a total blockage and a lotic reservoir, with water flowing through turbines and a fish ladder allowing fish migration when the device is opened during the wet season. The objective of this study was to identify the influence of dams having different degrees of river connectivity on the fish community structure, by comparing reservoir communities and their associated communities downriver. The tested hypothesis is that the degree of river connectivity influences the fish community. The greatest difference in fish fauna was expected in Dam 1, between the reservoir and the downriver stretch having total blockage; the least difference was expected in Dam 2, having partial blockage; and Dam 3 with the fish passage, expected to have an intermediate difference in total blockage.

Materials and methods

Study area

Dam 1 (22°31′43.5″S; 43°34′05.7″W) has a large, branched lentic reservoir of ca. 40 km^2. The Funil reservoir was constructed for hydroelectric generation and flood control, and became operational in 1969. The dam is 385 m long and blocks the entire river course, completely restraining fish

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migration downriver and, conversely, fish downriver the dam to migrate to the reservoir. All water flow is through the turbines. The reservoir has a maximum depth of 70 m, average depth being 20 m (Terra et al., 2010). According to Branco et al. (2002), an increasing eutrophic condition developed in this reservoir due to anthropogenic influences. The vegetation around the reservoir is very poor, a result of previous agricultural use for coffee plantations and pasture (Fig. 1; Table 1).

On the other hand, the stretch of river below the dam (downriver) has lotic conditions and a variety of habitat features. Depth is ca. 3 m, with high habitat complexity due to stony, rocky and gravelly substrate. The margins are relatively well protected by riparian vegetation and rocky formations (Terra et al., 2010).

The Paraíba do Sul segment in the stretch between Funil (Dam 1) and Santa Cecília (Dam 2) reservoirs is ca. 120 km long. Santa Cecília is a run-of-the-river reservoir (22°28′52.6″S; 43°50′20.2″W) with a low-head dam built in 1952 and no turbines since the main purpose was accumulating water pumped from the Paraíba do Sul (ca. 160 $m^3 s^{-1}$) by the Light Electrical Co., leaving approximately one-third of the original flow to the river.

The dam comprises eight floodgates, but a lateral channel is kept open permanently, since there is a compulsory minimum flow release of 90 $m^3 s^{-1}$ according to Brazilian legislation. The downriver zone has an average depth of 3 m, with margins degraded by human settlements. In extreme high flood periods, river waters partially flood the nearby city.

Dam 3 is located ca. 180 km downriver from Dam 2. Built in 1924, Ilha dos Pombos reservoir (21°51′11.6″S; 42°36′24.6″W) is the oldest of the three dams, and located ca. 190 km from the river estuary to the Atlantic Ocean. The reservoir has an area of only 4.3 km² with a maximum depth of 32 m and average depth of 12 m (Aguiar, 2008). The fish passage mechanism (8 m high × 1.5 m wide fish ladder) operates only during the wet season, probably providing a one-way upriver route. The downriver fish route is solely through the turbines. The downriver zone has a maximum width of 110 m, an average depth of 3.5 m and runs embedded in bedrock, where rocky outcrops are very evident in this stretch. Pastureland with grass and some trees are the main riparian cover.

Table 1
Physical features of three studied reservoirs: Funil (Dam 1), Santa Cecília (Dam 2) and Ilha dos Pombos (Dam 3)

Features/reservoir	Dam 1	Dam 2	Dam 3
Location	Itatiaia, RJ	Barra do Piraí, RJ	Carmo, RJ
Opening year	1969	1952	1924
Capacity (MW)	216	–	164
Maximum height (m)	85	–	12
Usable volume (hm^3)	6200	2.17	6.77
Dam length (m)	385	176	514
Reservoir area (km^2)	40	2.70	4.26
Reservoir volume (10^6 m^3)	890	4.35	7.87
Altitude (above sea level)	440	353	108
Water retention time (days)	10–55	<1	<1

Sampling

Fish collections were carried out between January and March 2010 and between January and February 2011 (wet seasons). According to Pinto and Araújo (2002), there is a well-characterized precipitation regime in the middle reaches of the Paraíba do Sul River, with the highest rainfall occurring between November and February. June through August is the driest season (Carvalho and Torres, 2002). A standardized fishing effort was applied in both the reservoir and

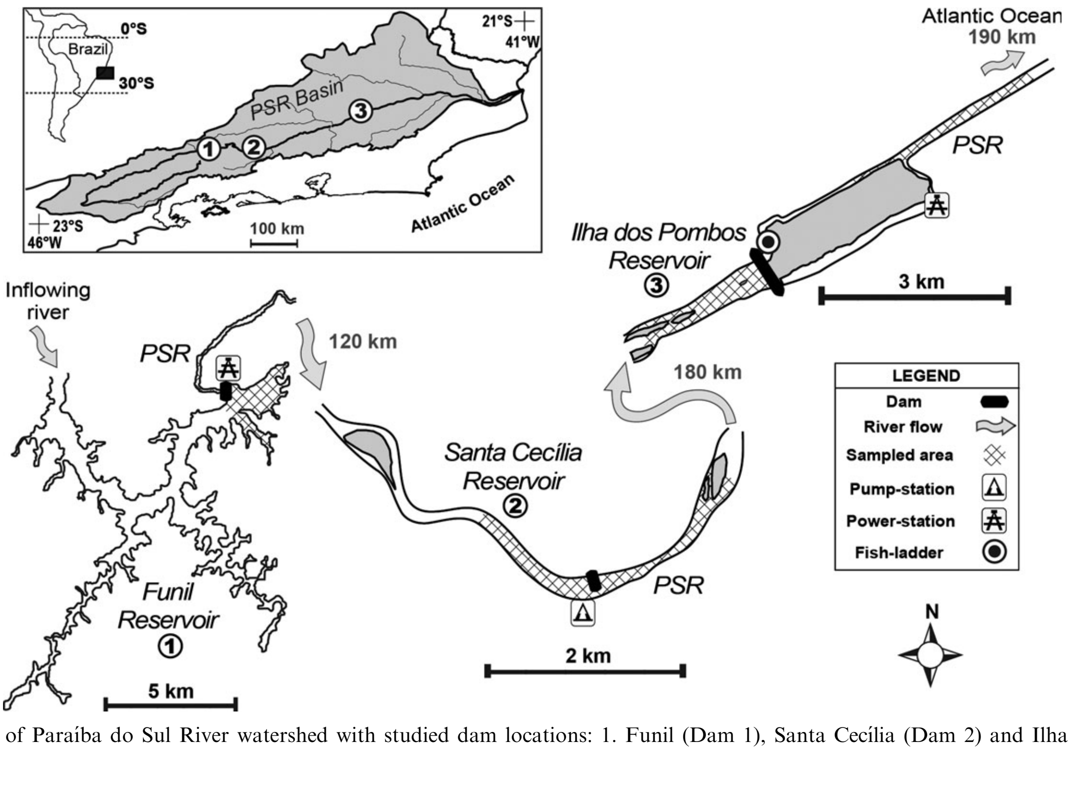


Fig. 1. Map of Paraíba do Sul River watershed with studied dam locations: 1. Funil (Dam 1), Santa Cecília (Dam 2) and Ilha dos Pombos (Dam 3)

downriver zones of each dam, along a ca. 2 km stretch from the dam (Fig. 1). Three gillnets of different mesh sizes (25, 50 and 75 mm stretched mesh) encompassing ca. 150 m^2 performed one sample unit. The nets were set up at sunset and retrieved the following morning, remaining for ca. 15 h. The sampling design thus had a total of 240 samples, i.e. 10 sites × 3 dams × 2 zones per dam (reservoir and downriver) × 2 wet seasons × 2 visits per season.

All collected fishes were identified up to the lowest taxonomic level, measured (mm) and weighed (g). Vouchers were fixed in 10% formalin for 48 h and subsequently transferred to 70% ethanol and deposited in the reference collection of the Laboratório de Ecologia de Peixes of the Universidade Federal Rural do Rio de Janeiro.

Environmental variables of temperature (°C), oxygen dissolved (mg L^{-1}), pH, conductivity (μS cm^{-1}) and redox potential (mV) were measured using a multisensor Horiba W-21 (Horiba Trading Co., Shanghai). Turbidity (NTU) was measured using a Policontrol model AP2000. These measurements were taken in the mornings at depths of 20 cm from the water surface and a distance of ca. 3 m from the margins.

Data analysis

Species richness was compared between the reservoir and the downriver stretch of the dam during each wet season. Species richness was estimated by using rarefaction of individuals, and species diversity in each zone was measured using the Shannon index (*H'*). The individual-based rarefaction curves representing the means of repeated re-sampling of all pooled individuals were computed by the software EstimateS 8.0 (Colwell, 2006).

The Indicator Species Analysis was used to determine which species might be used as indicators characterizing the different systems/zones. Developed by Dufrêne and Legendre (1997), this method was applied using the software PC-ORD (Mccune and Mefford, 1997). The resulting analysis gives a value from 0 to 100% to each species, 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. Statistical significance of each species was assessed by a Monte Carlo permutation test, using 1000 sample permutations ($P < 0.01$). Aiming to remove the influence of species with restricted distributions, only those species occurring in at least five of the six possible zones were considered.

Raw data of species abundance was square-root transformed to meet the assumptions of multivariate normality and to moderate influences of extreme values. The transformed data were then used to create a Bray–Curtis dissimilarity matrix calculated for all pair-wise sample comparisons. Then an ANOSIM procedure was performed to compare fish structure between the reservoir and downriver sections. A non-metric multidimensional scaling (nMDS) was used to identify groupings of samples and a SIMPER procedure was used to identify the species that most contributed to the within-group similarity (Clarke and Warwick, 1994). These analyses were performed with the software package PRIMER (Plymouth Routines Multivariate Ecological Research; Clarke and Warwick, 2001). This procedure has the advantage of quantifying and ranking the species that on average contribute strongly to assemblage structuring, without taking into account the rare species.

Abiotic variables were log-transformed to meet the requirements of parametric statistics and to minimize the differences between units of different variables. Spatial comparisons in abiotic variables (reservoir vs downriver) were tested by a Student *t*-test ($P < 0.05$).

Results

Environmental variables of temperature, redox potential, dissolved oxygen, pH, conductivity and turbidity did not differ significantly between the reservoir and the downriver zones in any of the three dams (Table 2). Such variables were also very similar among the dams, with the exception of turbidity that was higher in dams 2 and 3 compared to Dam 1.

A total of 4911 specimens distributed among six orders, 16 families, 37 genera and 43 species were collected, including eight non-native and two marine species (Table 3). The greatest number of species (35) and individuals (2541) were recorded in the Dam 1, Funil (reservoir and downriver zones); followed by Dam 3, Ilha dos Pombos (33 species, 891 individuals); and Dam 2, Santa Cecília (29 species, 1479 individuals). A higher richness was found in the downriver zone compared to the reservoir in all three systems.

The expected species richness estimated by the rarefaction curves revealed that the downriver zone had a comparatively higher richness than the reservoirs of Dam 1 and Dam 3, but an inverse pattern was found for Dam 2. The highest richness was estimated for downriver of Dam 3 (>40 species), while the remaining downriver zones had an expected

Table 2
Means ± SD of environmental variables in three reservoir (*R*) and downriver (*D*) zones. Between-zones comparisons according to Student's *t*-test

Reservoirs	Zone	Temperature (°C)	Redox potential (mV)	Dissolved oxygen (mg L^{-1})	pH	Conductivity (μ cm^{-1})	Turbidity (NTU)
Dam 1	Reservoir	29.0 ± 0.7	247.3 ± .26.8	6.5 ± 1.5	6.5 ± 0.4	73 ± 2	23.5 ± 11
	Downriver	25.9 ± 1.3	276.7 ± 46.8	6.3 ± 0.0	6.3 ± 0.3	70 ± 5	56.2 ± 17.7
Student's *t*-test	R vs D	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Dam 2	Reservoir	27.3 ± 1.2	238.7 ± 49.7	7.6 ± 0.9	6.7 ± 0.3	65 ± 5	162.6 ± 111.2
	Downriver	27.7 ± 1.1	235.1 ± 54.6	7.7 ± 0.8	6.9 ± 0.4	62 ± 5	204.7 ± 112.4
Student's *t*-test	R vs D	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Dam 3	Reservoir	26.6 ± 0.4	240.7 ± 34.9	6.5 ± 0.7	6.5 ± 0.4	74 ± 7	222.6 ± 181.9
	Downriver	26.0 ± 0.6	259.3 ± 20.3	7.1 ± 0.9	6.4 ± 0.5	73 ± 5	93.2 ± 35.4
Student's *t*-test	R vs D	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

Table 3
Total number (N), standard length range (SL, mm) and frequency of occurrence (% FO) of fishes collected in the reservoir (res) and downriver (down) zones of Funil (Dam 1), Santa Cecília (Dam 2) and Ilha dos Pombos (Dam 3)

	Dam 1		Dam 2		Dam 3				
Species	Res S = 21	Down S = 31	Res S = 21	Down S = 23	Res S = 26	Down S = 29	N	SL	%FO
Characiformes									
Anostomidae									
Leporinus copelandii Steindachner, 1875		56	6	31	8	16	117	115–490	28.3
Leporinus conirostris Steindachner, 1875	1	8	2	10	4	2	27	130–365	6.3
Leporinus mormyrops Steindachner, 1875		7		2			9	130–300	1.7
Characidae									
Astyanax cf. *bimaculatus* (Linnaeus, 1758)	481	242	72	303	158	41	1297	45–170	68.3
Astyanax parahybae (Eigenmann, 1908)		235	5	62	11	2	315	80–180	20.8
Astyanax intermedius Eigenmann, 1908		54		19			73	90–175	3.3
Astyanax spp.		116	1	122		13	252	80–160	13.3
Metynnis maculatus (Kner, 1858)[1]	8	1	2		2	1	14	70–153	4.6
Oligosarcus hepsetus (Curvier, 1829)	2	81	82	37	38	13	253	110–297	36.3
Piaractus mesopotamicus (Holmberg, 1887)[1]	1						1	700	0.4
Probolodus heterostomus Eigenmann, 1911		5					5	118–135	0.8
Salminus brasiliensis (Curvier, 1816)[1]		4		3	2	1	10	342–465	3.3
Crenuchidae									
Characidium lauroi Travassos, 1949	6						6	110–128	2.1
Curimatidae									
Cyphocarax gilbert (Quoy & Gaimard, 1824)					39	2	41	110–245	5.8
Erythrinidae									
Hoplias malabaricus (Bloch, 1794)	9	5	19	13	54	4	104	125–430	23.3
Prochilodontidae									
Prochilodus lineatus (Valenciennes, 1837)	1	30	2	54	32	17	136	135–570	33.8
Siluriformes									
Callichthyidae									
Callichthys callichthys (Linnaeus, 1758)		1					1	165	0.4
Hoplosternum littorale (Hancock, 1828)	66	7	145	8	23	11	260	90–330	32.5
Loricariidae									
Hypostomus affinis (Steindachner, 1877)		22	27	44	13	3	109	110–438	26.3
Hypostomus auroguttatus Kner, 1854	1	6		2		6	15	110–315	5.8
Harttia loricariformes Steindachner, 1877						1	1	60	0.4
Loricariichthys castaneus (Castelnau, 1855)						4	4	280–358	1.7
Rhinelepis aspera Spix & Agassiz, 1829[1]		33					33	200–380	2.9
Rineloricaria lima (Kner, 1853)	1	13	2	21	2	17	56	60–173	14.2
Pimelodidae									
Pimelodus fur (Lütken, 1874)	5	217		108	10	11	351	115–285	30.0
Pimelodus maculatus Lacépède, 1803	70	200	18	34	1	1	324	118–370	34.2
Pimelodella eigenmanni (Boulenger, 1891)		1	1	3	4	9	18	105–198	5.8
Rhamdia quelen (Quoy & Gaimard, 1824)		12	17	22	51	6	108	135–400	25.8
Auchenipteridae									

(continued)

Table 3
(continued)

	Dam 1		Dam 2		Dam 3				
Species	Res S = 21	Down S = 31	Res S = 21	Down S = 23	Res S = 26	Down S = 29	N	SL	%FO
Glanidium albescens Lütken, 1874						1	1	110	0.4
Trachelyopterus striatulus (Steindachner, 1877)		1	1		15	33	50	140–265	12.5
Gymnotiformes									
Gymnotidae									
Gymnotus carapo Linnaeus, 1758	3	11	20	11	31	24	100	150–400	28.8
Sternopygidae									
Eigenmannia virescens (Valenciennes, 1842)		37		26	25	40	128	121–405	25.0
Synbranchiformes									
Synbranchidae									
Synbranchus marmoratus Bloch, 1975	1						1	430	0.4
Mugiliformes									
Mugilidae									
Mugil curema Valenciennes, 1836[2]						1	1	375	0.4
Perciformes									
Sciaenidae									
Pachyurus adspersus Steindachner, 1879	55	7			1	14	77	125–305	14.6
Plagioscion squamosissimus (Heckel, 1840)[1]	258	64	7	97	35	28	489	60–450	51.3
Centropomidae									
Centropomus parallelus Poey, 1860[2]						3	3	410	1.3
Cichlidae									
Australoheros facetus (Jenyns, 1842)					2		2	90–185	0.4
Cichla kelberi Kullander & Ferreira, 2006[1]	64	1					65	90–405	9.6
Crenicichla lacustris (Castelnau, 1855)	6	4	1		3		14	130–305	5.4
Geophagus brasiliensis (Quoy & Gaimard, 1824)	17	2	7	8	1		35	110–265	12.9
Oreochromis niloticus (Linnaeus, 1758)[1]			2		1		3	282–300	1.3
Tilapia rendalii (Boulenger, 1897)[1]	2						2	100–110	0.4
Total	1058	1483	439	1040	566	325	4911		

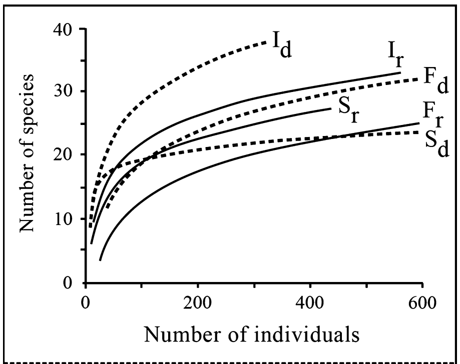
S, Number of species.
[1]Non-native species.
[2]Marine species.

number of species ranging from 20 to 35 in a sample of 600 individuals (Fig. 2).

The 13 most abundant species, i.e. those with >100 in number and >20% frequency of occurrence of the total samples, occurred in all three river stretches, encompassing four orders: six Characiformes (*A. bimaculatus, A. paraybae, H. malabaricus, L. copelandii, O. hepsetus* and *P. lineatus*); five Siluriformes (*H. affinis, H littorale, P. maculatus, P fur* and *R. quelen*); one Gymnotiformes (*E. virescens*); and one Perciforme (*P. squamosissimus*). Only five species (including two marine species) were exclusive to the Ilha dos Pombos downriver zone, namely one marine diadromus Perciformes (*C. parallelus*), one marine euryhaline Mugiliforme (*M. curema*), and three Siluriformes (*G. albescens, H. loricariformes* and *L. castaneus*). Nine species were restricted to the Funil system, with four species found only in the downriver zone (the Characiformes *C. lauroi* and *P. mesopotamicus,* the Synbranchiformes *S. marmoratus*, and the Perciformes *T. rendalii*), and four occurring only in the reservoir zone (the Characiformes *B. insignis* and *P. heterostomus,* and the Siluriformes *C. callichthys* and *R. aspera*), with one species, the non-native Perciformes *C. kilberi*, present in both zones.

Astyanax bimaculatus was the most abundant and widely distributed species in this study. Although some species were widely distributed in all river reaches, the catches of some species were greater in certain zones. For example, *A. parahybae, P. maculatus, L. conirostris, L copelandii* and *P. fur* were recorded mainly in the downriver zone of Dam 1, *P. squamosissimus* and *A. bimaculatus* in the reservoir; and *H littorale* and *R. quelen* mainly in the reservoir of Dam 2.

Nine species had significant indicator values according to the Indicator Species Analysis (Table 4). Dam 1 had the greatest number of indicators species: two for the reservoir zone (*A. bimaculatus* and *P. squamosissimus*), and four for the downriver zone (*A. parahybae*, *L. copelandii*, *P. maculatus* and *P. fur*). *Hoplosternum littorale* (reservoir) and



	F_r	F_d	S_r	S_d	I_r	I_d
J1	27.8	35.9	24.9	23	30.9	35.9
J2	33.6	35.1	23.2	21.2	31.9	40.9
H'	1.65	2.39	1.98	2.38	2.40	2.70

Fig. 2. Individually based rarefaction curves for species richness in reservoirs (r) and downriver (d) zones. Shannon index (H') and first (J1) and second (J2) order Jackknife estimates of species richness also indicated. F_r, Funil reservoir; F_d, Funil downriver; S_r, Santa Cecília reservoir; S_d, Santa Cecília downriver; I_r, Ilha dos Pombos reservoir; I_d, Ilha dos Pombos downriver

Table 4
Significant values of indicator species analysis for fish assemblages, reservoir and downriver zones in Funil (Dam 1), Santa Cecília (Dam 2) and Ilha dos Pombos (Dam 3)

Species	Indicator value	*P*	System/zone
Astyanax bimaculatus	33.4	0.000	Funil/reservoir
Plagioscion squamosissimus	44.8	0.000	Funil/reservoir
Astyanax parahybae	39.2	0.000	Funil/downriver
Pimelodus maculatus	46.3	0.000	Funil/downriver
Pimelodus fur	31.0	0.001	Funil/downriver
Leporinus copelandii	28.7	0.000	Funil/downriver
Hoplosternum littorale	29.3	0.000	Santa Cecília/ reservoir
Hypostomus affinis	19.2	0.00	Santa Cecília/ downriver
Prochilodus lineatus	22.8	0.000	Santa Cecília/ downriver
Eigenmannia virescens	16.4	0.007	Ilha dos Pombos/ downriver

H. affinis and *P. lineatus* (downriver) were indicators for Dam 2. Dam 3 had only *E. virescens* as a significant downriver indicator species.

The fish community structure changed between the reservoir and the downriver stretch from the dam according to ANOSIM, with the most significant difference recorded at Dam 1 ($R = 0.56$, $P < 0.01$), followed by Dam 2 ($R = 0.33$, $P < 0.01$) and Dam 3 ($R = 0.16$, $P < 0.01$). Plots of nMDS confirm such differences with higher significance for Dam 1 (Fig. 3). The analyses of similarities percentage (SIMPER) indicated that variability of the community structure was more pronounced in the Dam 2 reservoir zone (average similarity = 18.3%), in contrast to the Dam 1 reservoir zone that had the greatest within average similarity (40.2%). Moreover, SIMPER analysis also revealed a large dissimilarity between zones within a given system (Table 5). Dam 2 had the highest dissimilarity (88.9%) between the reservoir and the downriver stretch, compared to Dam 3 (81.9%) and Dam 1 (80.9%).

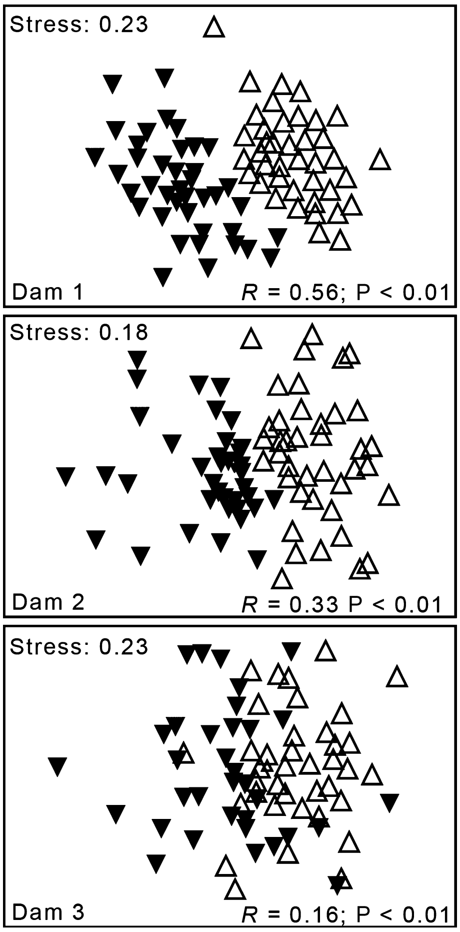


Fig. 3. Ordination diagram of fish assemblages from non-Metric Multidimensional Scaling (nMDS), with samples coded by reservoir (△) and downriver (▼) zones for Funil (Dam 1), Santa Cecília (Dam 2) and Ilha dos Pombos (Dam 3)

Table 5
Species most contributing to similarity (%) within zones (Reservoir = Res; Downriver = Down) in Funil (Dam 1), Santa Cecília (Dam 2) and Ilha dos Pombos (Dam 3), according to SIMPER analysis

	Dam 1		Dam 2		Dam 3	
Species	Res	Down	Res	Down	Res	Down
Average similarity (%)	40.2	23.2	18.3	24.2	26.2	21.8
Astyanax bimaculatus	47.6	30	15.7	29.8	42.7	15.4
Astyanax parahybae		10.5				
Pimelodus fur				16.1		
Plagioscion squamosissimus	28.7			12.5		13.8
Pimelodus maculatus		20.4	9.8			
Hoplosternum littorale			24.7			
Oligosarcus hepsetus			19.2			
Prochilodus lineatus					10.6	
Eigenmannia virescens						15
Gymnotus carapo						10
Average dissimilarity (%)	Reservoir vs downriver 80.9		Reservoir vs downriver 88.9		Reservoir vs downriver 81.8	

The species contributing the most to within-group similarity in the Dam 1 reservoir were *A. bimaculatus* and *P. squamosissimus*; in the downriver zone these were *A. bimaculatus*, *A. parahybae* and *P. maculatus*. Dam 2 had *A. bimaculatus, P. maculatus, H. littorale* and *O. hepsetus* contributing significantly to within average similarity in the reservoir, and *A. bimaculatus, P. squamosissimus* and *P. fur* in the downriver zone. Dam 3 had *A. bimaculatus* and *P. lineatus* (reservoir) and *A. bimaculatus, P. squamosissimus, G. carapo* and *E. virescens* as typical species downriver.

Discussion

The fish community has been impacted by the three dams under study in the Paraíba do Sul River, with significant differences in assemblage structure between the reservoirs and the downriver zones. Overall, most fishes recorded in a reservoir also occur in the downriver section, but their contributions to the assemblages differ significantly. Fish assemblages in reservoirs (and downriver sections) are the result of a restructuring of those communities that previously occupied the river before it was dammed (Kubecka, 1993; Poddubny and Galat, 1995; Agostinho et al., 1999) and a subsequent introduction of non-native fish species into these reservoirs (Martinez et al., 1994).

The fragmentation caused by Dam 1 had the strongest effect on the fish community, as indicated by the larger difference in the fish assemblage structure between the reservoir and the downriver zone. This is within expectations, since the total blockage of the system impairs fish passage from the reservoir to the downriver section and vice-versa. Additionally, Dam 1 has a reservoir with a retention time (10–55 days) and storage volume (890 m^3) greater than locations 2 and 3 (<1 day retention time; storage volume 4.35 m^3 and 7.87 m^3, respectively). The greatest hydraulic residence time (HRT) in Dam 1 can potentially influence, among other factors, the development of planktonic assemblages and processes and the transport of biota through the reservoir to downstream reaches (Kalff, 2002), leading to notable differences in the fish assemblage between the up- and downriver sections.

The moderate fragmentation of Dam 2 (partial blockage) results in surprising differences in the fish fauna between the reservoir and downriver, as indicated by the statistical analyses and the highest values of dissimilarity between these two zones according to SIMPER analysis. Since Dam 2 has a hydrologic connection between the two zones, it is supposed that differences in fish assemblage would not be as pronounced. Probably such a water connection provided by the lateral channel does not mean a habitat connection for most species, since the water reaches high velocities (5 m s^{-1}) because of the narrow channel width, preventing movement of fish from the downriver section to the reservoir. High water velocity (e.g. $5 \times$ Total Length $\times\ s^{-1}$) blocks upstream fish movement, and functions as a one-way barrier (Clay, 1995; Santos et al., 2008). Although the water velocity can be an explanation for the differences in fish assemblage structure between the reservoir and downriver zones in Dam 2, further studies are needed to confirm this hypothesis.

Fish assemblage differences between the reservoir and downriver zone in Dam 3 were less evident, but still present. This can be partially explained by the operation of the fish ladder. According to results, one can infer that *Prochilodus lineatus* successfully ascend the fish ladder. *P. lineatus* is a long-distance migratory species that depends on the flood pulse to complete its life cycle (Agostinho et al., 2004). The upriver migration inferred in this study is consistent with previous studies that describe the rheophilic characteristic of *P. lineatus* (e.g. Agostinho et al., 2003; Capeleti and Petrere, 2006). However, the efficiency of fish ladders for migration of neotropical fish species is a very controversial subject that has raised concerns about fish passage from the reservoir to the downriver zone (Pompeu and Martinez, 2007). Such information is necessary in order to expand scientific and technical knowledge on the mechanisms of the fish-passage.

The migratory species *P. maculatus* and *P. fur* occur mainly in the downriver zone of Dam 1 and Dam 2, which suggests that they are impaired in their migration upriver by these two dams, and thus are concentrated in the downriver stretches. Blockage of migration routes is a likely explanation for the high occurrence of these species in the downriver zone, although migratory behavior of the *Pimelodus* genus is not clearly defined. The status of *P. maculatus* as a migratory species is questionable because of its high abundance in reservoir cascades without large tributaries, such as those on the Tietê and Rio Grande rivers (Freitas and Petrere, 2001; Braga and Andrade, 2005). According to Agostinho et al. (2003), *P. maculatus* is a migratory species that needs fewer free stretches of river to spawn than other neotropical migrants. Migratory behavior of this species was described by Bonetto (1963) and Godoy (1967), who estimated movements greater than 1000 km. The present results agree with Agostinho et al. (2003), since this species is well established in Paraiba do Sul River, a highly fragmented system.

Overall, a higher number of individuals (Dam 1 and Dam 2) and species (Dam 1 and Dam 3) were detected in downriver zones in comparison to reservoirs. Moreover, migratory species were typical for downriver zones, as in *P maculatus, P. fur* and *L copelandii* for Dam 1, and *P. lineatus* for Dam 3. These species need to perform upriver migration during the reproductive seasons (Agostinho et al., 2004; Capeleti and Petrere, 2006; Godinho and Kynard, 2009) and are likely to be the most impacted by the dams. The large number of species and individuals in downriver zones from the dam can also be attributed to the tailwater effect of attracting fish species, as noted by Poff et al. (1997).

The highest expected richness was found in Dam 3, probably associated with the comparatively high and diverse habitat complexity in this most downriver stretch where the flow and transversal section of the Paraíba do Sul River is increased. According to Oliveira et al. (2004), species richness is constrained in lentic zones, being highly affected by the hydroelectric operations. Furthermore, it is accepted that reservoirs typically support fewer fish species than their associated rivers, often as a result of large-scale changes in temperature, turbidity, flow, allochthonous nutrient input, and availability of food resources (Williams et al., 1998). In the present study, the examined environmental variables seemed not to play an important role when comparing the reservoir with the downriver sections, since no significant differences were found for any environmental variable. Previous studies along the river–reservoir longitudinal gradient reported a comparatively lower richness in the reservoir (or lacustrine) zone compared with the riverine zone of neotropical impoundments (Gomes and Miranda, 2001; Oliveira et al., 2004; Santos et al., 2010).

As previously mentioned, predictions were not fully matched. However, this paper is just an initial assessment of the effects of different types of dams in a tropical river. Future research during other seasons is necessary to better support the predictions raised herein. Additionally, partial blockage and the absence of turbines (i.e. Dam 2, Santa Cecília) is not a guarantee that species and genetic flux will be interchanged, since the water velocity could be a constraint to upriver fish migration, as well as the fish ladder a constraint to downriver fish migration. Despite all information that a fish passage is not a better solution for preservation of fish in dammed environments (Pompeu and Martinez, 2007; Pelicice and Agostinho, 2008), Dam 3 with a fish ladder was the system that showed a less impacted icthyofauna structure. Finding a balance between the economic (power generation) and ecological demands (movement of fish) is necessary to achieve the sustainable development of impoundments.

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