



Structure of fish assemblages in seven tropical reservoirs in southeastern Brazil during the rainy season; what matters: physico-chemical or hydrological connectivity influences?

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Summary

Closely connected reservoirs were hypothesized to have more similar fish compositions than do spatially isolated reservoirs, and that environmental variables play an important role in shaping assemblage structure on a local scale. Fish assemblages and environmental variables were sampled in seven reservoirs constructed to generate hydroelectricity, with most inflowing water coming directly or via transposition of the Paraíba do Sul River, in Southeastern Brazil. Using gill nets and environmental measurement variables, fish collections were carried out between January and February 2008 (wet season), when increases in temperature and rainfall increase hydrological connectivity, facilitating fish movements throughout the river-reservoir system. Mean fish density, biomass and the number of species did not differ significantly among the seven reservoirs. On the other hand, the assemblage structure differed among almost all pairs of reservoirs. Of the reservoirs connected in series, only two (Santana and Vigário) showed a similar assemblage structure, suggesting that hydrological connectivity plays a minor role. Physico-chemical variables changed among reservoirs and seemed to play an important role in determining the assemblage structure, with higher conductivity (average = $108 \mu\text{S cm}^{-1}$) and TDS – total dissolved solid (0.07 g L^{-1}), and low pH (5.8) in the Pereira Passos Reservoir associated with a high number of the Siluriformes *Loricariichthys castaneus*, and with the opposite conditions in Tocos (conductivity = $27 \mu\text{S cm}^{-1}$; TDS = 0.02 g L^{-1} ; pH = 7) that were associated with a high number of the carnivorous Characiformes *Oligosarcus hepsetus* and *Hoplias malabaricus*. A direct relationship was found between abundance of the catfishes *Pimelodus fur* and *Glanidium albescens* and high turbidity (90.4 NTU) and low temperature (25.3°C) and transparency (0.1 m) in the Ilha dos Pombos Reservoir. Moreover, a close relationship was found between high abundance of the cichlid *Cichla kelberi* and the high temperature and transparency of Lajes (28.3°C ; 2.2 m) and Santa Branca (27.1°C ; 2.6 m) reservoirs. These findings support the hypothesis that physico-chemical variables structure fish assemblages in reservoirs, but that hydrological connectivity seems to play a minor role in shaping assemblage structure. However, other unmeasured variables (e.g. physical habitat characteristics and biotic interactions) and other seasons need to be evaluated in further studies.

Introduction

Programs for hydroelectric generation in Brazil developed within the past century were based on river impoundments for reservoir construction (Straskraba and Tundisi, 1999; Agostinho et al., 2007). More than 600 dams were constructed throughout the country, occupying an area of approximately $40\,000 \text{ km}^2$ for a volume of circa $6.5 \times 10^{11} \text{ m}^3$, with generating hydroelectric power being the main goal (Agostinho et al., 2005; Barletta et al., 2010). Reservoirs are thus a major part of the landscape and contribute to the economy over a wide territory and are a ‘compulsory’ part of Brazil’s development. In spite of their negative impact on the ichthyofauna, hydroelectric power plants are sources of ‘clean’ power because of the broad availability of river basins spread throughout Brazil. Studies assessing the impacts of these hydroelectric plants are thus needed to help environmental managers to formulate policies for quality restoration of the environment.

Reservoirs form physical barriers to fish passage, limiting species distribution and contributing to the change in assemblage structure. The most obvious impact caused by river damming is the drastic changes in rivers – from flowing to still waters – within a short time period, with the fish having to adapt to the newly-formed environmental conditions (Castro and Arcifa, 1987; Maitland and Morgan, 1997). Such alteration have been directly associated with loss of fish populations and even species extinction on a local scale (Baigún et al., 2007), since the reproductive potential of a population is reduced (Penczak et al., 1998; Mérona et al., 2005). The damming of rivers can also favor some fish species, but have deleterious effects on others (Castro and Arcifa, 1987; Nilsson et al., 2005). Species able to adapt to the lentic environment created by the dam can benefit from the change, becoming abundant or even dominant in these environments.

Hydrological connectivity between reservoirs favors genetic interchange and results in similar fish assemblages when compared with spatially isolated reservoirs that tend to have different assemblage structures (Lorenz et al., 1997). Connectivity among river-reservoir systems is considered essential for the functioning and integrity of ecosystems (Fullerton et al., 2010; Larsen et al., 2012). During the rainy season, increases in flow favor hydrological connectivity by increasing habitat availability. Some studies have focused on the

influence of physicochemical variables, such as oxygen, pH, conductivity and temperature, as the main variables structuring fish assemblages (Matthews et al., 1992; Mol and Ouboter, 2004). Therefore, it is expected that different environmental conditions determine different fish assemblage structures.

Seven reservoirs that were constructed either for the generation of hydroelectricity or for diverting water for hydroelectric generation in the Paraíba do Sul River (PSR) were researched for fish and environmental variables in the wet season of 2008. The aim was to compare fish assemblage structures among reservoirs and to assess whether the environmental variables or the hydrological connectivity influenced the assemblage structures. We anticipated that closely connected reservoirs would have similar fish assemblages than those spatially isolated reservoirs. We also expected that physico-chemical variables would play an important role in structuring the fish assemblages.

Materials and methods

Studied reservoirs

The seven studied reservoirs were: (1) Santa Branca, (2) Lajes, (3) Tocos, (4) Santana, (5) Vigário, (6) Pereira Passos, and (7) Ilha dos Pombos (Fig. 1; Table 1). Tocos Reservoir is an impoundment in the upper reaches of the Pirai River, a tributary of the Paraíba do Sul River, which was constructed to divert waters to the Lajes Reservoir. Both the Tocos and Lajes reservoirs were assumed to have similar fish assemblages, although they differ significantly in area and water volume (see below for description details of each reservoir). Santa Branca and Ilha dos Pombos are direct impoundments of the Paraíba do Sul River and are supposed to have similar ichthyofauna because they block the main river and receive the most water inflow from PSR, although they are approximately 400 km apart. Santana, Vigário and Pereira Passos are formed mainly by water abstraction from the Paraíba do Sul River basin (ca. $160 \text{ m}^3 \text{ s}^{-1}$) and form a closely connected serial system, also purportedly with a similar fish assemblage.

Santa Branca Reservoir ($23^{\circ}18' - 23^{\circ}29'S$; $45^{\circ}45' - 45^{\circ}53'W$) is located in the upper stretches of the Paraíba do Sul River, but lacks floodplain areas to facilitate lateral connections between the river and marginal lagoons. Construction was in the late 1950s for flow control, but the hydroelectric plant became operational only in 1997. The dam blocks the entire river course, completely restraining fish movements from

Fig. 1. Study area indicating seven studied reservoirs, summer 2008, and the Paraíba do Sul River basin. Reservoir codes: 1, Santa Branca; 2, Lajes; 3, Tocos; 4, Santana; 5, Vigário; 6, Pereira Passos; 7, Ilha dos Pombos

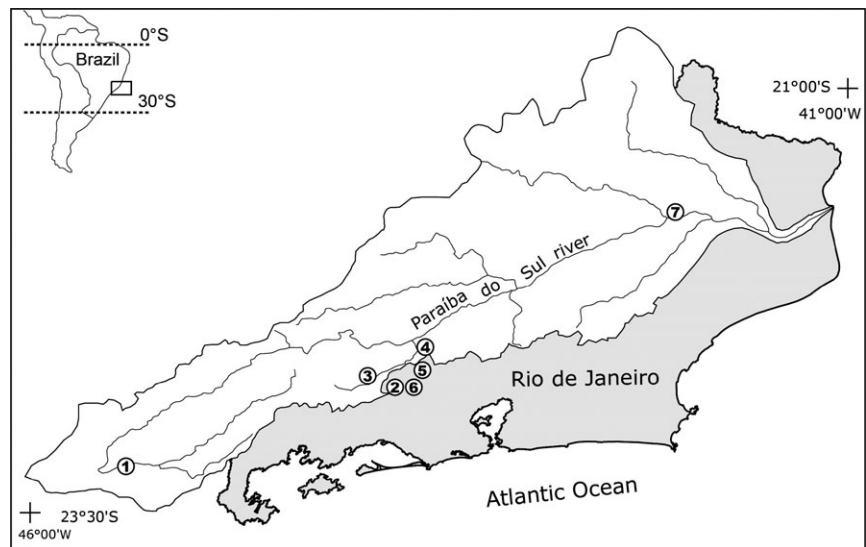


Table 1
Key environmental features of the seven studied reservoirs

Reservoirs	<i>Santa Branca</i>	<i>Lajes</i>	<i>Tocos</i>	<i>Santana</i>	<i>Vigário</i>	<i>Pereira Passos</i>	<i>Ilha dos Pombos</i>
Start operation	1959	1908	1913	1952	1952	1962	1924
MW	58	132	–	–	380	100	164
Area (km ²)	27.2	30.7	1.2	5.9	3.8	1.4	4.3
Volume (hm ³)	307	450.4	1.9	6.1	11.7	4.1	6.7
Change in water level	Seasonal	Seasonal	Seasonal	Daily	Daily	Daily	Daily/seasonal
Retention time (days)	62.7	300.7	1.6	1.0	2.0	1.2	0.2
Trophic state	Mesotrophic	Mesotrophic	Mesotrophic	Hipertrophic	Eutrophic	Eutrophic	Eutrophic
River affluence	Yes	No	Yes	Yes	No	No	Yes
Volume afluente (m ³ s ⁻¹)	90	18	13	160	160	180	700

Source: <http://www.lightenergia.com.br/parque-gerador/complexo-de-lajes/subsistema-lajes/>

up- to downriver and vice-versa. Seasonal rainfall peaks dictate the dynamics of the reservoir water level. The reservoir has a retention time of 62.7 days, and a wide water-level oscillation that contributes to marginal erosion and sedimentation.

Lajes Reservoir (22°43'–22°46'S; 44°30'–44°60'W) was built in 1908 to generate hydroelectric power. The hydroelectric plant has a power generation of 612 MW (CEIVAP, 2001) and is located among the hills of the Sea Mountains at 415 m a.s.l. in a relatively undisturbed area mostly surrounded by rain forest, with a few cattle farms. The littoral zone is poorly developed, since the slopes of the surrounding hills are abrupt, probably caused by variations in the water level. Due to its long retention time (297 days), it has been considered highly subject to eutrophication. Most of the incoming waters of the reservoir ($12 \text{ m}^3 \text{ s}^{-1}$) come from the Tocos Reservoir, the smallest reservoir with only 1.2 km^2 that blocks the Pirai River; it was built to divert water for the Lajes Reservoir and to begin operation in 1913.

In 1945, parts of the Paraíba do Sul waters were diverted to the Santana Reservoir, an impoundment of the Pirai River near its confluence with the Paraíba do Sul River. The Santana Reservoir was thereby formed, receiving not only waters pumped from the Paraíba do Sul River but also from the remnant Pirai River. Waters from the Santana Reservoir are diverted to form another reservoir (Vigário Reservoir) used in a hydroelectric power plant and discharged in the Pereira Passos Reservoir. Deforested areas used for ranching predominate the surrounding area. Pereira Passos Reservoir is the most downriver reservoir in this series that receives diverted waters from Paraíba do Sul River, following the Santana and Vigário reservoirs. Pereira Passos Reservoir has more diverse habitat, formed in part by rocky substrate and trees and shrubs along the shoreline (F. G. Araújo, personal observation).

Ilha dos Pombos Reservoir (21°51'11.6"S; 42°36'24.6"W) is located approximately 190 km from the river estuary that flows into the Atlantic Ocean. The upriver habitat is a run-of-the-river reservoir with a 12 m average depth. The marginal vegetation is patchy, surrounded by pasture and sand mining, with some areas of grass, bushes and trees. It is the only dam in the middle stretch of the basin with a fish-passage mechanism (Araújo et al., 2005). However, the fish ladder (12 m high \times 2 m width) is operational only during the wet season.

Fish sampling

Fish collections were carried out between January and February 2008 (wet season), when peaks of rainfall increase the water level, facilitating hydrological connectivity and fish movements among reservoirs and rivers stretches. A standardized sampling effort was applied on each occasion. The sample unit was defined as three gillnets (25 m \times 2 m) of different mesh sizes (25, 50 and 75 mm stretched mesh) encompassing ca. 150 m^2 . The nets were set up at sunset and retrieved the following morning, remaining for ca. 15 h. In all reservoirs we sampled shallow littoral areas of islands, bays and banks, and covering habitats with logs, submerged trees and aquatic plants. A total of 102 samples was taken,

distributed proportionally to the reservoir area and site accessibility: 18 samples from the largest reservoir or from the intermediate reservoir having an easy access (Santa Branca, Lajes, Pereira Passos and Ilha dos Pombos); 12 samples in intermediate reservoirs with difficult access (Santana and Vigário); and six samples from the smallest reservoir (Tocos).

All collected fishes were identified to the lowest taxonomic level and measured for total length (in mm) and weighed (in g). Voucher specimens were fixed in 10% formalin for 48 h then transferred to 70% ethanol and deposited in the Reference Collection of the Laboratorio de Ecologia de Peixes of the Universidade Federal Rural do Rio de Janeiro. Environmental variables of temperature ($^{\circ}\text{C}$), oxygen dissolved (mg L^{-1}), pH, conductivity ($\mu\text{S cm}^{-1}$) and total dissolved solid – TDS (g L^{-1}) were measured using a multiprobe HoribaW-21 (Horiba Trading Co., Shanghai, China). Turbidity (as Nephelometric Turbidity Units) was measured using a Policontrol Turbidimeter model AP2000, and transparency was measured with a Secchi Disk. Measurements were taken in the mornings at depths of 20 cm from the water surface and at a distance of ca. 3 m from the margins.

The guilds of each fish species were defined as detritivore (detritus/sediment predominant), herbivore (plant items such as leaf fragments and seed/fruit predominated), omnivore (when the amounts of plants and other food animal categories were similar), and piscivore (when fish predominated). Species guilds were defined based on inspection of stomach contents of some individuals and after consulting the literature (e.g. Hahn et al., 1998; Froese and Pauly, 2015).

Data analysis

Abundance and biomass were estimated through standardized Capture per Unit Effort (CPUE), defined as the sum of the total number ($\text{CPUE}_{\text{number}}$) or total weight ($\text{CPUE}_{\text{biomass}}$) of captured fish per 100 m^2 per 12 h. This procedure allowed quantitative comparisons of individuals and species among zones. Data were log-transformed [$\text{Log}_{10}(x + 1)$] to stabilize variance, and to offset the effect of highly abundant species. Comparisons of CPUE (number and biomass), species richness and environmental variables among reservoirs were carried out using one-way analysis of variance (ANOVA) followed by *a posteriori* Tukey HSD tests at a significance level of 95%, to test for significant differences among the reservoirs.

Assemblage structure was compared among the reservoirs using Analysis of Similarity – ANOSIM; fish species that contributed more to within-group similarity were detected using the Similarity Percentage – SIMPER procedures in the PRIMER software package (Clarke and Warwick, 2001). Statistical significances of these analyses were assessed by a Monte Carlo permutation test, using 1000 samples permutations.

Relationships between fish species abundance and abiotic variables were investigated for those species that contributed more than 1% of total abundance using a non-parametric Spearman coefficient correlation. A canonical correspondence analysis (CCA) was also performed to assess the relationship between fish and environmental variables. This later analysis

was performed using the software CANOCO for Windows version 4.5.

Results

Environmental variables

All environmental variables differed significantly ($P < 0.05$) among the reservoirs (Table 2). Higher temperatures and transparency were found for Santa Branca and Lajes reservoirs, and were lower for the Tocos Reservoir (ANOVA, $P < 0.05$); the remaining reservoirs had intermediate values for these variables. Conductivity and TDS had similar trends, with lower values in Santa Branca, Lajes and Tocos reservoirs and higher values in the remaining reservoirs.

The Pereira Passos reservoir differed from the others by having the lowest pH, whereas Ilha dos Pombos Reservoir had the highest dissolved oxygen, followed by the Lajes and Tocos reservoirs.

The first axis from the principal components analysis was positively correlated ($P < 0.05$) with temperature and transparency and negatively with turbidity, TDS and conductivity (Fig. 2). The second axis had a positive correlation with conductivity and TDS and was negative to dissolved oxygen and pH.

The ordination diagram from PCA separated along the first axis of the Santa Branca and Lajes reservoirs in opposition to the Santana, Vigário and Ilha dos Pombos reservoirs, with the former being associated with highest transparencies and temperatures; the latter were associated with the highest TDS, turbidity and conductivity (Fig. 2). The second axis discriminates the Pereira Passos Reservoir with the highest conductivity and TDS from the Tocos and Ilha dos Pombos reservoirs with the highest dissolved oxygen and pH (Fig. 2).

Fish composition

We collected a total of 3150 individuals weighing a total of 301 320 grams shared by 36 species, 16 families and 4 orders in the seven reservoirs. No significant differences ($P > 0.05$) were found in the number of individuals, the total biomass, or the number of species among the seven reservoirs. The highest number of species (Table 3) was recorded in Santana (21 species), followed by Ilha dos Pombos (20); the lower number was recorded for Tocos (7).

The highest mean densities were recorded in Santana ($65.2 \text{ ind} \times 100 \text{ m}^{-2}$) and Pereira Passos ($52.0 \text{ ind} \times 100 \text{ m}^{-2}$) and the lowest in Vigário ($19.9 \text{ ind} \times 100 \text{ m}^{-2}$). Fish density ($F_{6,95} = 1.17$, $P = 0.33$), biomass ($F_{6,95} = 0.53$, $P = 0.78$) and the mean number of species ($F_{6,95} = 0.85$, $P = 0.53$) did not differ significantly among the seven reservoirs.

Considering all pooled reservoirs, *Astyanax* aff. *bimaculatus* (Linnaeus, 1758), *Loricariichthys castaneus* (Castelnau, 1855) and *Astyanax paraybae* (Eigenmann, 1908) were the most numerically abundant species, accounting for 54% of the total number of collected fishes. *Oligosarcus hepsetus* (Cuvier, 1817) was the only species found in all reservoirs, whereas *Glanidium albescens* (Lütken, 1874) occurred in only two reservoirs (Pereira Passos and Ilha dos Pombos), being the second most abundant species in the Ilha dos Pombos

Table 2
Physico-chemical information of seven studied reservoirs, January–February 1998

Environmental variables	Reservoirs							F-values
	Santa Branca n = 18	Lajes n = 18	Tocos n = 6	Santana n = 12	Vigário n = 12	Pereira Passos n = 18	Ilha dos Pombos n = 18	
Temperature, °C	28.3 (4) ^c [24.3–29.3]	27.1 (5) ^c [24.2–30.7]	22.2 (5.6) ^a [21.4–24.6]	25.0 (1.1) ^b [25.0–25.7]	24.6 (0.2) ^b [24.6–24.7]	24.9 (0.7) ^b [24.6–25.1]	25.3 (0.7) ^b [25.2–25.9]	87.4 ^{**}
Dissolved oxygen, mg L ⁻¹	7.9 (2) ^{bc} [7.5–8.2]	8.0 (11) ^c [7.5–11.4]	8.2 (6) ^c [7.8–9.0]	6.9 (4) ^a [6.4–7.1]	7.0 (4) ^{ab} [6.9–7.5]	7.5 (2) ^b [7.1–7.7]	8.8 (3) ^d [8.6–9.5]	51.9 ^{**}
pH	7.5 (5) ^b [7.2–8.7]	7.3 (7) ^b [6.4–8.0]	7.0 (11) ^b [6.4–8.0]	6.9 (7) ^b [6.7–8.0]	7.1 (9) ^b [6.8–8.6]	5.8 (11) ^a [5.4–8.1]	7.6 (2) ^b [7.5–8.1]	25.7 ^{**}
Conductivity, $\mu\text{S cm}^{-1}$	38.0 (8) ^b [30–42]	33 (10) ^b [28–42]	27 (8) ^a [24–30]	87 (1) ^c [87–89]	83 (2) ^c [82–86]	108 (38) ^c [105–301]	59 (3) ^d [57–64]	220.4 ^{**}
Turbidity, NTU	3.6 (41) ^b [1.6–8.2]	1.8 (119) ^a [0.1–14.3]	16.8 (19) ^{cd} [12.4–19.7]	67.6 (13) ^f [61.9–84.6]	44.2 (5) ^e [39.9–46.2]	19.6 (13) ^d [15.7–25.4]	90.4 (2) ^f [87.1–95.2]	282.9 ^{**}
Transparency, m	2.2 (31) ^{cd} [0.8–2.6]	2.6 (40) ^d [0.3–3.8]	0.9 (9) ^c [0.8–1.0]	0.3 (15) ^{ab} [0.2–0.5]	0.4 (13) ^b [0.3–0.5]	0.5 (29) ^{bc} [0.4–0.8]	0.1 (10) ^a [0.09–0.1]	82.1 ^{**}
Total dissolved solid, g L ⁻¹	0.02 (20) ^a [0.01–0.03]	0.02 (15) ^a [0.01–0.03]	0.02 (1) ^a [0.01–0.02]	0.06 (1) ^c [0.05–0.06]	0.05 (8) ^c [0.04–0.06]	0.07 (23) ^d [0.07–0.14]	0.04 (1) ^b [0.04–0.04]	125.1 ^{**}

Values expressed as median (coefficient of variation) and [min–max]. F-values and significance from ANOVA also indicated. n, sample size. ** $P < 0.01$; Superscripts letters = significant differences/similarities among reservoirs.

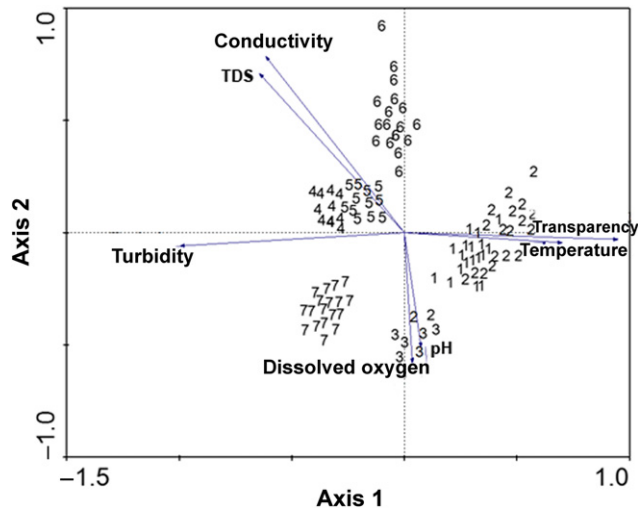


Fig. 2. Ordination diagram from principal component analysis on environmental variables of seven studied reservoirs, summer 2008: 1. Santa Branca (n = 18); 2. Lajes (n = 18); 3. Tocos (n = 6); 4. Santana (n = 12); 5. Vigário (n = 12); 6. Pereira Passos (n = 18); 7. Ilha dos Pombos (n = 18). n, sample size

Reservoir. *Astyanax paraybae* and *L. castaneus* together accounted for approximately half the total number of fishes in the Lajes Reservoir and were also the most abundant species in Vigário Reservoir. The non-native *Metynnis maculatus* (Kner, 1858) ranked among the most abundant species in Santana and Lajes reservoirs (Table 3).

The fish assemblage structure differed between all pairs of reservoir, as indicated by high *R*-values of ANOSIM (Table 4), with only two reservoirs (Santana and Vigário) showing low (0.29) *R*-values, suggesting low dissimilarity between their ichthyofaunas.

Different fish assemblages associated with the different physico-chemical environmental condition were detected for different reservoirs according to CCA (Fig. 3). A more conspicuous difference was found between Tocos and Pereira Passos reservoirs, with ichthyofauna from Tocos being positively associated with high pH values, whereas fishes from Pereira Passos were directly associated with high conductivity and TDS. Species from Ilha dos Pombos also differed clearly from the other reservoirs, which was directly associated with high turbidity and dissolved oxygen. Fishes from Santa Branca and Lajes reservoirs were directly associated with high temperatures and transparency (Fig. 3).

A significant relationship was found between the abundance of the 12 most numerous fish species that accounted for more than 1% of the total number of fishes and the examined environmental variables, according to the non-parametric Spearman correlation coefficient (Table 5). The transparency had a significantly positive correlation with abundances of *L. castaneus*, *Cichla kelberi* (Kullander & Ferreira, 2006) and *Geophagus brasiliensis* (Quoy & Gaimard, 1824), and a negative correlation with *G. albescens* and *P. fur*. The temperature had a significantly positive correlation with abundances of *Hypostomus affinnis* (Steindachner, 1877), *C. kelberi*, and *G. brasiliensis* but was negative with

Table 3 Mean density (number × 100 m⁻²) ± standard deviation for 12 most abundant fish in the seven studied reservoirs

Species	Reservoirs							Pereira Passos	Ilha dos Pombos	F-ANOVA	P-values	Trophic guild
	Santa Branca	Lajes	Tocos	Santana	Vigário	Pereira Passos	Ilha dos Pombos					
<i>Astyanax aff. bimaculatus</i>	4.4 ± 4.9 ^b	5.0 ± 6.4 ^{ab}	0 ± 0 ^b	7.8 ± 10.4^a	0.8 ± 1.3 ^b	5.9 ± 5.9 ^{ab}	4.7 ± 4 ^b	0.0190	Omnivore			
<i>Axyanax paraybae</i>	4.9 ± 7.91 ^b	9.5 ± 17.4 ^{ab}	0 ± 0 ^b	18.2 ± 23.4^a	2.8 ± 4.7 ^b	3.7 ± 4.9 ^b	2.5 ± 5 ^b	4.264	Omnivore			
<i>Oligosarcus hepsetus</i>	4.9 ± 4.5 ^{ab}	0.4 ± 0.9 ^b	9.6 ± 7.11^a	1.6 ± 1.73 ^b	0.75 ± 0.8 ^b	0.3 ± 0.6 ^b	4.8 ± 5.3 ^{ab}	15.322	Piscivore			
<i>Metynnis maculatus</i>	0 ± 0 ^b	7.2 ± 14.6 ^{ab}	0 ± 0 ^b	17.3 ± 38.0^a	1 ± 1.2 ^b	0.1 ± 0.5 ^b	0 ± 0 ^b	11.132	Herbivore			
<i>Hoplias malabaricus</i>	0.6 ± 0.9 ^b	0 ± 0 ^b	4 ± 3.6^a	0.6 ± 0.9 ^b	0.4 ± 0.5 ^b	0 ± 0 ^b	0 ± 0 ^b	13.709	Piscivore			
<i>Hypostomus affinnis</i>	0.3 ± 0.6	0.8 ± 1.1	0.5 ± 0.5	0.1 ± 0.3	0.4 ± 0.5 ^b	0.4 ± 0.7	0.7 ± 0.8	2.4663	Detritivore			
<i>Loricariichthys castaneus</i>	0 ± 0	8.5 ± 14.3^{ab}	0 ± 0	0.8 ± 1.4	3.6 ± 4.9^{bc}	21.3 ± 22.3^a	0 ± 0	20.592	Omnivore			
<i>Pimelodus fur</i>	0 ± 0 ^b	0 ± 0 ^b	0 ± 0 ^b	0.3 ± 0.6 ^b	0 ± 0 ^b	1.7 ± 3.1 ^{ab}	0 ± 0	6.6055	Omnivore			
<i>Pimelodus maculatus</i>	2.6 ± 5.2^a	0 ± 0 ^b	0 ± 0 ^b	0.2 ± 0.6 ^b	1.3 ± 1.5 ^{ab}	0 ± 0 ^b	0 ± 0 ^b	7.6346	Omnivore			
<i>Glanidium albescens</i>	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	2.4 ± 5.0 ^{ab}	0 ± 0 ^b	7.4918	Omnivore			
<i>Cichla kelberi</i>	3.6 ± 6.6^a	0.7 ± 1.1	0 ± 0	0 ± 0	0.2 ± 0.4	0.3 ± 0.6	0.1 ± 0.2	5.5034	Piscivore			
<i>Geophagus brasiliensis</i>	2.1 ± 2.4^a	1.8 ± 1.8 ^{ab}	0 ± 0	0.1 ± 0.3	0 ± 0	0 ± 0	1.9 ± 8.2^a	7.9037	Omnivore			
Fish density (ind × 100 m ⁻²)	32.9	48.3	24.0	65.2	19.9	52.0	39.0					
Number of species	17	14	7	21	17	18	20					

Boldface = significantly highest density compared to other reservoirs. Superscripts letters = significant differences/similarities among reservoirs.

Table 4
Results of ANOSIM (*R*) for comparisons of fish assemblages structure among seven studied reservoirs

Grupos	<i>R</i> statistic (0.63)	Significance level (%)
Santa Branca vs Lajes	0.65	0.1
Santa Branca vs Tocos	0.71	0.1
Santa Branca vs Santana	0.58	0.1
Santa Branca vs Vigário	0.60	0.1
Santa Branca vs Pereira Passos	0.73	0.1
Santa Branca vs Ilha dos Pombos	0.49	0.1
Lajes vs Tocos	0.99	0.1
Lajes vs Santana	0.47	0.1
Lajes vs Vigário	0.47	0.1
Lajes vs Pereira Passos	0.44	0.1
Lajes vs Ilha dos Pombos	0.78	0.1
Tocos vs Santana	0.89	0.1
Tocos vs Vigário	0.74	0.1
Tocos vs Pereira Passos	0.91	0.1
Tocos vs Ilha dos Pombos	0.82	0.1
Santana vs Vigário	0.29	0.1
Santana vs Pereira Passos	0.55	0.1
Santana vs Ilha dos Pombos	0.65	0.1
Vigário vs Pereira Passos	0.54	0.1
Vigário vs Ilha dos Pombos	0.79	0.1
Pereira Passos vs Ilha dos Pombos	0.63	0.1

H. malabaricus (Quoy & Gaimard, 1824). The pH had a positive correlation with abundances of *O. hepsetus*, *Pimelodus maculatus* (Lacépède, 1803) and *G. brasiliensis*, while the conductivity was significantly correlated with abundances of *L. castaneus*, *G. albescens*, *Pimelodus fur* (Lütken, 1874) and negative with *O. hepsetus*, *H. malabaricus*, *C. kelberi* and *G. brasiliensis*. The dissolved oxygen had a positive correlation with *O. hepsetus*, *H. affinnis*, *G. albescens*, *P. fur*, and *G. brasiliensis* and was negative with *A. paraybae*, *M. maculatus* and *L. castaneus*. The turbidity had a significantly positive correlation with *O. hepsetus*, *G. albescens* and *P. fur* and was negative with *L. castaneus*, *C. kelberi* and *G. brasiliensis*; the TDS had a positive correlation with *L. castaneus*, *G. albescens* and *P. fur* and was negative with *O. hepsetus*, *H. malabaricus*, *C. kelberi* and *G. brasiliensis*.

Discussion

The seven studied reservoirs differed in fish communities, as indicated by ANOSIM comparisons and densities of the most abundant species, probably associated with their different physico-chemical characteristics that determine differentiated assemblage structures. Transparency, turbidity and temperature were the main environmental factors discriminating the reservoirs, namely Santa Branca and Lajes (highest transparencies and temperature; lowest turbidity) compared to the remaining reservoirs. The longest retention time in Santa Branca and Lajes reservoirs contributed to their increased temperature during the summer, when stratification is favored in tropical reservoirs (Esteves, 2011). High transparencies in Lajes and Santa Branca reservoirs were also expected because of their high retention times.

According to ANOSIM, the Tocos Reservoir was the unique assemblage structure compared to the other reser-

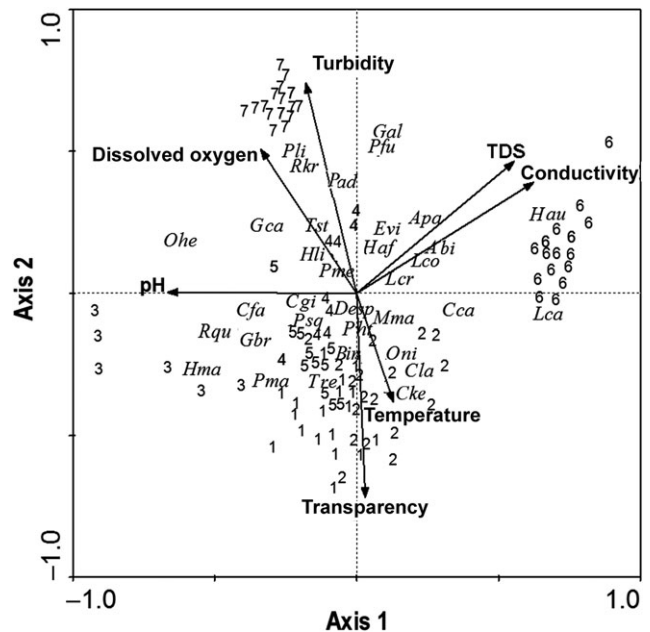


Fig. 3. Ordination diagram of canonical correspondence analysis of fish and environmental variables in the seven studied reservoirs (codes as in Fig. 1). Fish species: *Abi*, *Astyanax aff. bimaculatus*; *Apa*, *Astyanax paraybae*; *Bin*, *Brycon insignis*; *Cca*, *Callichthys callichthys*; *Cfa*, *Cichlasoma facetus*; *Cgi*, *Cyphocharax gilberti*; *Cla*, *Crenicichla lacustris*; *Cke*, *Cichla kelberi*; *Desp*, *Deuterodon* sp.; *Evi*, *Eigenmania virens*; *Gbr*, *Geophagus brasiliensis*; *Gal*, *Glanidium albescens*; *Gca*, *Gymnotus carapo*; *Hli*, *Hoplosternum littorale*; *Hma*, *Hoplias malabaricus*; *Haf*, *Hypostomus affinis*; *Hau*, *Hypostomus auroguttatus*; *Lca*, *Loricariichthys castaneus*; *Lco*, *Leporinus copelandii*; *Lcr*, *Leporinus cornirostris*; *Mma*, *Metymnis maculatus*; *Ohe*, *Oligosarcus hepsetus*; *Oni*, *Oreochromis niloticus*; *Pad*, *Pachyurus adspersus*; *Pfu*, *Pimelodus fur*; *Pma*, *Pimelodus maculatus*; *Pme*, *Pimelodella eigenmanni*; *Psq*, *Plagioscion squamosissimus*; *Pli*, *Prochilodus lineatus*; *Pht*, *Probolodus heterostomus*; *Rqu*, *Rhamdia quelen*; *Rkr*, *Rineloricaria kronei*; *Tst*, *Trahcheolypterus striatulus*; *Tre*, *Tilapia rendalli*

voirs. We recorded a predominance of piscivorous species in Tocos and a low abundance of forage species. *Oligosarcus hepsetus* was the most numerous abundant species in this reservoir, which could be associated to trophic plasticity to adapt and compete with opportunist species that feed on fishes and insects (Araújo and Santos, 2001; Araújo et al., 2005). *Hoplias malabaricus* was the second most abundant species, being well adapted to reservoirs and other lentic systems. *Rhamdia quelen* (Quoy and Gaimard, 1824) was also abundant in Tocos Reservoir and with omnivorous habits and a tendency to piscivory (Araújo et al., 2005). Although forage species are common in most reservoirs of southeastern Brazil (Pelicice et al., 2003; Agostinho et al., 2007), top-down mechanisms associated with abundant carnivores in Tocos Reservoir keep forage species at very low levels of abundance.

The smallest water surface, the Tocos Reservoir, is associated with the lowest number of recorded species in this system. According to Pelicice et al. (2003), small areas provide comparatively fewer habitats for the forage fish undergoing high pressure from predators (Castro and Arcifa, 1987;

	Transp	Temp	pH	Conductivity	DO	Turb	TDS
<i>Astyanax</i> aff. <i>bimaculatus</i>	-0.05	0.15	0.01	0.19	0.04	0.03	0.16
<i>Astyanax parahybae</i>	-0.04	0.07	-0.04	0.17	-0.20	0.05	0.15
<i>Oligosarcus hepsetus</i>	-0.02	-0.01	0.25	-0.32	0.33	0.20	-0.30
<i>Metynnix maculatus</i>	0.08	0.08	-0.07	-0.02	-0.26	-0.11	-0.01
<i>Hoplias malabaricus</i>	0.02	-0.27	0.06	-0.20	-0.09	-0.04	-0.21
<i>Hypostomus affinis</i>	0.05	0.21	0.08	-0.13	0.33	-0.04	-0.12
<i>Loricariichthys castaneus</i>	0.23	-0.05	-0.41	0.27	-0.28	-0.29	0.29
<i>Glanidium albescens</i>	-0.36	-0.06	0.04	0.27	0.25	0.36	0.27
<i>Pimelodus fur</i>	-0.45	-0.10	-0.06	0.22	0.24	0.46	0.23
<i>Pimelodus maculatus</i>	0.02	-0.02	0.22	-0.06	-0.16	0.09	-0.10
<i>Cichla kelberi</i>	0.38	0.29	0.08	-0.21	0.05	-0.37	-0.26
<i>Geophagus brasiliensis</i>	0.29	0.53	0.32	-0.46	0.37	-0.30	-0.48

Table 5
Spearman correlation coefficient among 12 most abundant fish species and environmental variables

Transp, transparency; Temp, temperature; DO, dissolved oxygen; Turb, turbidity; TDS, total dissolved solid.

Bold = significant correlation ($P < 0.05$).

Pelicice et al., 2003). This situation is likely to occur in the Tocos Reservoir. Pelicice et al. (2003) found a negative relationship between biomass of piscivorous species and prey biomass as indicative of a top down mechanism controlling prey biomass. Some reservoirs with a high biomass of piscivorous had a low prey biomass because of the the high turnover of individuals/biomass of dominant forage species (Pellicice et al., 2003). Low fisheries productivity in reservoirs from the Paraná State have been reported by Gomes et al. (2002), attributing to short trophic webs the low numbers of piscivorous fish which are controlled by nutrient availability (Krebs, 1994). Low prey biomass found in small reservoirs are associated with large numbers of small-sized species and short life cycles (small Characiformes), or with piscivorous species adapted to lentic systems that are successful in small sized reservoirs with a high shoreline-pelagic zone relationship (Gerking, 1994; Agostinho and Zalewski, 1995). Thus, it is possible that there are top down mechanisms of fish assemblage controls in Tocos, but further studies are necessary to elucidate this pattern.

Highest abundances of the Siluriformes *L. castaneus* and *Hypostomus auroguttatus* (Kner, 1858) in the Pereira Passos Reservoir can be associated with the highest conductivity (average = $108 \mu\text{S cm}^{-1}$) and TDS (0.07 g L^{-1}) and lowest pH (5.8). Environmental variables such as pH and conductivity have been reported as determining fish assemblage structures in impacted rivers (Fialho et al., 2008). *Hypostomus auroguttatus* is a detritivorous species that was recorded in high abundance in Pereira Passos Reservoir; this reservoir appears to have a great habitat diversity, with a substrate composed of stones, gravel, sand and mud (F. G. Araújo, pers. obs.), which favor the presence of these two Loricariidae species. Moreover, these two species are likely dividing the feeding and spatial niches, with *H. auroguttatus* using preferably fast flowing sites (Garavello and Garavello, 2004), while the *L. castaneus* prefer calmer waters (Gomes et al., 2008).

Due to the importance of species-habitat relationships, life strategies and the effect of movement patterns, it is suggested that migrations should be considered as ecological and evolutionary phenomena that allow connectivity between habitats

and promote renewal of demographic groups (Barletta et al., 2010). However, hydrological connectivity seems to play a minor role in the fish assemblage structure in the studied reservoirs. Hydrologically connected aquatic systems have similar ichthyofauna due to genetic interchange and similar environmental variables. Vigário and Santana are two reservoirs connected in a series that receives water diverted from the Paraíba do Sul River and have more similar fish assemblages. *Astyanax parahybae*, *A. aff. bimaculatus*, *O. hepsetus* and *M. maculatus* are typical of both reservoirs, confirming the proximity of the two ichthyofaunas. Moreover, Pereira Passos Reservoir, the third reservoir connected in the series in this system, was expected to have an ichthyofauna closely related to the Vigário and Santana reservoirs. However, the predominance of the Siluriformes *Loricariichthys castaneus* and *H. auroguttatus* in the Pereira Passos Reservoir contributed to differences in ichthyofauna structure, suggesting a more marked influence by the local habitat and environmental variables than the hydrological connectivity. According to Pianka (1994), structurally complex systems tend to offer a variety of habitats than do simplified systems, which is likely the case with the Pereira Passos Reservoir that offers a habitat variety to ichthyofauna.

A high similarity in ichthyofauna was also expected between Lajes and Tocos reservoirs, since most of the Tocos water is diverted to the Lajes Reservoir. However, the higher number of carnivores in Tocos did not occur in the Lajes Reservoir, which could be associated with a differentiated area between these two systems such as a low shoreline-pelagic zone relationship in Lajes Reservoir, and an opposite pattern in Tocos Reservoir. Several other uncontrolled factors could be influencing the fish structure and composition, such as primary production, habitat structure, and resource availability (Taylor et al., 1996; Matthews, 1998), resulting in distinct assemblage structures.

Non-native species could also be influencing the ichthyofauna structures in reservoirs. Introduction of non-native species can cause species extirpation, increase predation, and favor competitive exclusion and thereby causing serious ichthyofauna problems. Over the past decades, the introduction of non-native species is common in Brazil reservoirs

(Agostinho et al., 2007), affecting native populations and causing the reduction or even disappearance of some native species (Godinho et al., 1994). The non-native *C. kelberi* and *Metynnis maculatus* are common in both Santa Branca and Lajes reservoirs, with the former being native to the Amazon basin and introduced in large numbers in the 1960s to south-eastern reservoirs for sport fishery and to control high tilapias densities (Araújo, 1996). Moreover, high transparency of the water in reservoirs favors the success of *C. kelberi* (Agostinho et al., 2007). *Metynnis maculatus* is the second most abundant species in Santana Reservoir that takes advantage by using unoccupied niches. Lake-type reservoirs with long retention times seem to favor the establishment of those two species.

Overall, hydrological connectivity played a minor role in the structure of fish assemblages in the studied reservoirs; differences in fish assemblages seem to be better explained by the differing physico-chemical environmental variables. We have sampled fish only during the rainy season, when increases in temperature and peaks in rainfall increase the hydrological connectivity through increasing the water flow, thus facilitating fish movements throughout the river-reservoir system. Although it was also desirable to sample in the dry season, we believe that our findings are valid for other years and periods, when conditions for hydrological connectivity are less likely. Our findings support the hypothesis that local physico-chemical variables, rather than hydrological connectivity among the reservoirs, play an important role in structuring fish assemblages. Moreover, other unmeasured/uncontrolled environmental variables (e.g. local habitat constraints, species interactions) could also influence fish assemblage structure, but further studies on this subject are necessary.

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