Assessing fish assemblages similarity above and below a dam in a Neotropical reservoir with partial blockage

Araújo, FG.[*]*, Santos, ABI. and Albieri, RJ.*

Laboratório de Ecologia de Peixes, IB/DBA, Universidade Federal Rural do Rio de Janeiro, BR 465, km 7, 23890-000 Seropédica, RJ, Brazil

**e-mail: gerson@ufrrj.br*

Received July 16, 2012 - Accepted November 9, 2012 - Distributed November 29, 2013

(With 3 figures)

Abstract

Damming rivers disrupts the water flow and changes the ichthyofauna organisation. We investigated an impoundment with permanent connection and homogeneous environmental conditions between the zones above and below the dam. Temperature was comparatively higher during wet season irrespective of zone, and both zones had higher dissolved oxygen, conductivity and transparency in the dry season. A total of 1687 individuals comprising 27 species were collected in the downriver zone, while the reservoir had 879 individuals and 23 species. Each zone had different fish assemblage composition and structure, but assemblages were not explained by the examined environmental variables (r^2 = 0.08; p = 0.307). Migratory species such as *Pimelodus maculatus*, *Pimelodus fur*, *Leporinus copelandii* and *Prochilodus lineatus* were the most affected, and probably are prevented to perform upriver migrations. On the other hand, lentic adapted species such as *G. brasiliensis, Hoplias malabaricus* and *Hoplosternum littorale* successfully colonised the reservoir. Therefore we conclude that the presence of the lateral hydrological connectivity alone does not guarantee the ecological connectivity since fish assemblage similarity differed between the two zones. Fish passage facilities should be monitored and managed to evaluate and improve their functionality.

Keywords: reservoirs, ichthyofauna, fish migration, river connectivity, Paraíba do Sul River.

Avaliando a similaridade das assembléias de peixes acima e abaixo de uma barragem de um reservatório Neotropical com obliteração parcial

Resumo

O represamento de rios interrompe o fluxo de água e altera a organização da ictiofauna. Nós investigamos um represamento com conexão hidrológica permanente e homogêneas condições ambientais entre as zonas acima e abaixo da barragem. A temperatura foi comparativamente mais elevada na estação chuvosa independente da zona, e ambas as zonas apresentaram maior oxigênio dissolvido, condutividade e transparência na estação seca. Um total de 1687 indivíduos compreendendo 27 espécies foi coletado na zona de rio abaixo da barragem, enquanto 879 indivíduos e 23 espécies foram registrados no reservatório. Cada zona teve assembléias de peixes com diferente composição e estrutura, mas as assembléias não foram explicadas pelas variáveis ambientais examinadas (r^2 = 0.08; p = 0.307). Espécies de peixes migratórias, como *Pimelodus maculatus*, *Pimelodus fur* e *Prochilodus lineatus* foram as mais afetadas, e, provavelmente, são impedidas de realizar migrações rio acima. Por outro lado, espécies adaptadas a ambientes lênticos tais como *G. brasiliensis*, *Hoplias malabaricus* e *Hoplosternum littorale* colonizaram o reservatório com sucesso. Portanto, concluímos que a presença da conectividade hidrológica lateral sozinha não garante a conectividade ecológica já que a similaridade da assembleia de peixes diferiu entre as duas zonas. A passagem de peixes deve ser monitorada e gerenciada para avaliar e melhorar a sua funcionalidade.

Palavras-chave: reservatórios, ictiofauna, migração de peixes conectividade fluvial, Rio Paraíba do Sul.

1. Introduction

Hydrologic connectivity of riverine systems is crucially important to fish and other aquatic organisms. Nonetheless, these ecosystems are impaired by impoundments with different purposes (e.g. hydropower, water supply and flood control). Loss of connectivity is frequently linked to extinction of entire populations of freshwater fishes (Sheer and Steel, 2006; Olden et al., 2010), changes in hydrologic regimes (Graf, 1999), introduction of non-native piscivorous (Holmquist et al., 1998; Pelicice and Agostinho, 2009) and blocking of migratory routes (Roscoe and Hinch, 2010), thus contribut-

DOI: 10.1590/S1519-69842013000400007

ing to reduce the diversity and change the assemblage organisation.

Although the problems associated with impoundment have been addressed in a variety of reviews and scientific articles (Baxter, 1977; Cumming, 2004; Poff et al*.,* 2007), until now, the mitigation measures have been limited to fish passage facilities. Several types of fish passages (e.g., fish ladders, lifts, locks and trap-and-truck operations and "nature-like" fish ways; reviewed in Roscoe and Hinch, 2010) have been used to minimise the negative effects of the river fragmentation on fish assemblages. However, some mechanisms have been criticised for the low efficiency in facilitating two-way movements, high selectivity and inefficiency in allowing downriver return by adults, eggs, and larvae (Agostinho et al*.,* 2007; Godinho and Kynard, 2009, Pompeu et al., 2011).

In Brazil, there is a crescent investment on clean energy provided by hydropower, mostly because of its great water resources. Only in the main channel of Paraíba do Sul River there are four large dams, three low head dams (head height < 15 m), which vary in size, shape, function and operational routine. Although it is one of the most important Brazilian rivers, draining developed states in the country (São Paulo, Rio de Janeiro and Minas Gerais), little is known about the consequences of its regulation by dams (Bizerril, 1999; Polaz et al., 2011). Every dam has unique characteristics and, consequently, the scale and nature of the environmental changes are highly site-specific (McCartney, 2009). The traditional dams built for hydroelectric purposes blocks the entire river course, causing fragmentation of the river and storing a large volume of water. On the other hand, low-head dams are considered to have less environmental impact because maintain the fluvial connectivity, operating as "run-of-the-river" mode, not generating large reservoirs.

The effects of traditional dams i.e., those built for hydroelectric purposes, which block the entire river course and store a large volume of water, have been documented by a number of studies (Rosenberg et al., 2000; Poff and Hart, 2002; Agostinho et al., 2008; Pompeu et al., 2011). On the other hand, less research has been undertaken on the impacts of non-traditional dams. These particularities allow us to make investigations focusing on small scale and determine whether the connectivity between zones in a low-head dam (Santa Cecília Dam, Paraíba do Sul River) that have a side channel connecting permanently the reservoir and the downriver zone (partial blockage) is sufficient to ensure the maintenance of ichthyofauna structure. Unlike the traditional fish ways that facilitate upriver migrations, here we examine a fish passage which probably allows only downriver movements. We tested the hypothesis that similarity of the fish assemblages differ between these two zones (reservoir vs. downriver zone). The aim was to evaluate possible effects of this dam on fish fauna organisation, considering the spatial and temporal scales.

2. Materials and Methods

2.1. Study area

Santa Cecília Dam (22°28'5" S and 43°50'2" W; WGS84 map datum) was built in 1952 and is located in the middle stretch of the Paraíba do Sul River, Brazil (Figure 1), about 120 km below Funil Dam and 180 km above Ilha dos Pombos Dam. These reaches of the Paraíba do Sul River contain water of decreased quality due to indiscriminate land use (agricultural, industrial and urban) (Pfeiffer et al., 1986), and receive large amounts of untreated sewage and industrial effluents (Araújo et al., 2009). The substrate is unconsolidated to semi-consolidated sand, gravel, silt, and clay, with basalt outcroppings, low mountains, low-nutrient soils, fragments of semi-deciduous seasonal rain forest, and poor cropland areas (Pinto et al., 2006).

Santa Cecília impoundment forms a reservoir of about 2.7 km^2 in surface area, retention time < 1day and its main purpose is to divert water (~ 160 $m^3 s^{-1}$) to a Hydroelectric Complex. It is a low-head dam composed by eight floodgates that has a permanent lateral connection between the reservoir and downriver zones i.e., it operates as a run off for the river dam in order to keep a mini-

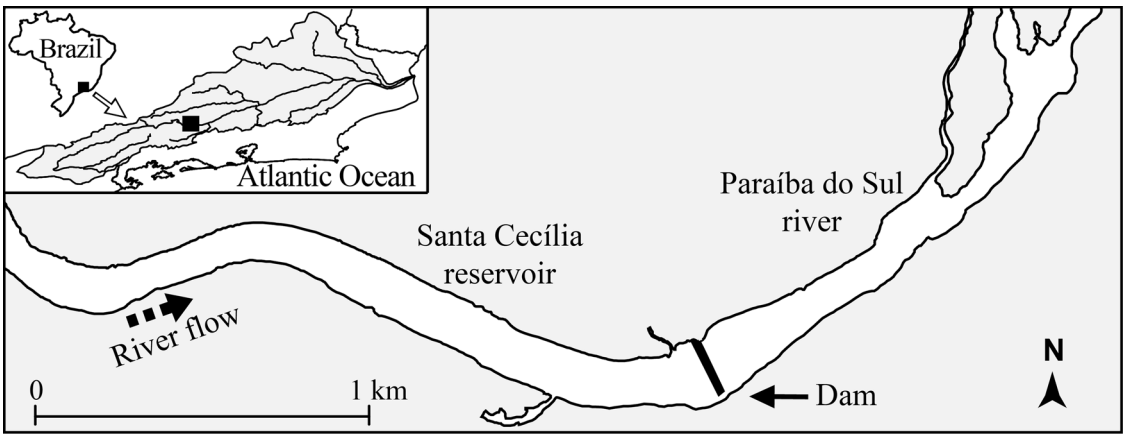

Figure 1 - Paraíba do Sul River Basin highlighting the studied area of Santa Cecília Dam.

mum flow release, defined by law, of 90 m^3 s^{-1}. The reservoir and the downriver zone have water levels that differ approximately by 2.5 m. Due to the narrowing of the river channel by the lateral connection, the water velocity is increased (~ 5 m s^{-1}) in the only 4 m wide x 5 m depth channel, and may be limiting upriver fish movements and facilitating the opposite route.

2.1. Data collection

A standardised fish sampling was conducted during 2010-2011 in both zones (reservoir and downriver), along a stretch of approximately 1.5 km from the dam. In each year, four fish collections were carried out during the wet (January and March) and dry seasons (July and September). Ten randomly chosen sites in each zone were sampled by three gillnets (25 x 2 m; stretched mesh 25, 50 and 75 mm) that were set up at sunset and retrieved in the following morning (~ 15 hours of operation). Thus, our sampling design had a total of 160 samples: 10 samples x 2 zones x 2 seasons x 4 fish collections. All collected fishes were identified up to the lowest taxonomic level possible, measured and weighed. Vouchers were fixed in formalin 10% for 48 hours, preserved in ethanol 70% and deposited in the reference collection of the Laboratório de Ecologia de Peixes, Universidade Federal Rural do Rio de Janeiro.

Environmental variables of temperature (°C), oxygen dissolved (mg L^{-1}), conductivity (μS cm^{-1}), pH and redox potential (mV) were taken using a multisensor Horiba W-21 (Horiba Trading Co., Shanghai). Water transparency (cm) was taken with a Secchi disk. These measurements occurred concurrently with the fish sampling at ten locations within each zone. Measurements were made during the morning, at a depth of 20 cm from the water surface and a distance of approximately 3 m from the margin of the river or reservoir.

2.3. Data analysis

Abiotic environmental variables were log-transformed to meet the requirements of parametric statistics and to minimise the difference between units of different variables. Patterns in the abiotic data were assessed by a principal components analysis (PCA) on the variance/covariance matrix of environmental variables. To avoid super factorisation, only factors with eigenvalues > 1.0 were considered. Component loadings > 0.7 from PCA were used to identify latent variables. This procedure was performed using the Statistica 7.0 package (Statsoft, Tulsa, OK, USA).

The raw data of species abundance was fourth-root transformed to reduce the contributions of highly-abundant species, and a Bray-Curtis dissimilarity matrix calculated for all pair-wise sample comparisons. We then used multidimensional scaling (MDS) to assess fish assemblage similarity/dissimilarity based on species abundances. The criterion for the number of dimensions was based on the goodness of fit with change of dimensionality; a stress < 0.20 is acceptable as good for discriminating the groups. This analysis was performed using PRIMER version 5 (Clarke and Warwick, 1994).

We used simple linear regression to determine whether a significant portion of fish assemblage organisation (represented by first axis of multidimensional scaling, MDS1) is explained by abiotic variables patterns (represented by the first axis of principal components analysis, PCA1). If the ichthyofauna is structured by limnological variables, we should observe significant relationships in the regression of MDS1 against PCA1.

Ultimately, the indicator species analysis was used to determine which species might be used as indicators, characterising different zones/seasons. This method, developed by Dufrêne and Legendre (1997), was applied using the software PCOrd (McCune and Mefford, 1997). Statistical significance of each species was assessed by a Monte Carlo permutation test, using 1000 sample permutations ($p < 0.05$).

3. Results

A total of 1687 individuals comprising 27 species were collected in the downriver zone, while the reservoir had 879 individuals and 23 species (Table 1). Only four fish species occurred in more than one-third of the samples: *Astyanax bimaculatus* (Linnaeus, 1758), *Oligosarcus hepsetus* (Curvier, 1829), *Rhamdia quelen* (Quoy and Gaimard, 1824) and *Hypostomus affinis* (Steindachner, 1877) with the former being present in 59.4% of all samples. A wide size range of the fish population was sampled, ranging from the smallest *A. bimaculatus* with 6.5 cm Total Length to the largest *Hoplias malabaricus* (Bloch, 1794) with 42.5 cm Total Length. Six species were recorded exclusively from the downriver zone, while only two species were exclusive from the reservoir. All the seven migratory species were recorded in the downriver section, but only five in the reservoir. Moreover, two non-native species were recorded in both zones and one more non-native species was exclusive of each zone.

Abiotic environmental values of the different sampling zones/seasons are summarised in Table 2. The temperature was comparatively higher during wet season irrespective of zone. Both zones had higher dissolved oxygen, conductivity and transparency in the dry season.

Principal component analysis on the abiotic data yielded two axes with eigenvalues greater than one, explaining 71.6% of the total variance (Table 3). Abiotic variables which most contributed to PC1 were temperature (positively associated to this axis), conductivity, pH and transparency (negative related). The most variation in the abiotic data (PC1 = 53.28%) was explained by seasonal patterns, discriminating wet and dry season samples (Figure 2). Dissolved oxygen was inversely associated to PC2 that explained only 18.3% of the total variance.

MDS analysis suggests that the spatial component is more relevant to determine the fish assemblage organisation than the seasonality, i.e. distinct fish assemblages

Table 1 - Absolute abundance, total number of specimens (ΣN), total length range (TL, in cm), and frequency of occurrence (%FO) of the sampled fishes in the Santa Cecília - Paraíba do Sul River. [a] non-native species, [b] migratory species.

Species	Reservoir (S = 23)		Downriver (S = 27)		ΣN	%N	TL	%FO
	Wet N	Dry N	Wet N	Dry N				
CHARACIFORMES								
Anastomidae								
Leporinus copelandii Steindachner, 1875[b]	5	3	32	11	51	2.0	12.5-38.2	19.4
Leporinus conirostris Steindachner, 1875[b]	1		3		4	0.2	13-33	2.5
Hypomasticus mormyrops (Steindachner, 1875)[b]	2		2	1	5	0.2	18.2-30	2.5
Characidae								
Astyanax bimaculatus (Linnaeus, 1758)	79	97	299	168	643	25.1	6.5-15.5	59.4
Astyanax parahybae (Eigenmann, 1908)	6	1	61	23	91	3.5	9-22	15.6
Astyanax scabripinnis (Jenyns, 1842)			15		15	0.6	9-17.5	1.3
Astyanax sp.	15	1	120	28	164	6.4	7.3-14	13.8
Oligosarcus hepsetus (Curvier, 1829)	86	101	34	63	284	11.1	11-30	48.1
Metynnis maculatus (Kner, 1858)[a]	1				1	0.0	13	0.6
Salminus brasiliensis (Curvier, 1816)[a, b]			1		1	0.0	34.2	0.6
Curimatidae								
Cyphocharax gilbert (Quoy & Gaimard, 1824)				2	2	0.1	13.2-44.6	1.3
Erythrinidae								
Hoplias malabaricus (Bloch, 1794)	15	37	8	10	70	2.7	13-42.5	26.9
Prochilodontidae								
Prochilodus lineatus (Valenciennes, 1837)[b]	2		49	10	61	2.4	20.5-42	18.8
SILURIFORMES								
Auchenipteridae								
Trachelyopterus striatulus (Steindachner, 1877)	1				1	0.0	22	0.6
Callichthyidae								
Hoplosternum littorale (Hancock, 1828)	148	41	8	16	213	8.3	11.6-24	30.0

Table 1 (cont.)

Species	Reservoir (S = 23)		Downriver (S = 27)		ΣN	%N	TL	%FO
	Wet N	Dry N	Wet N	Dry N				
Heptapteridae								
Pimelodella eigenmanni (Boulenger, 1891)	1		1	20	22	0.9	10.5-51	5.6
Rhamdia quelen (Quoy & Gaimard, 1824)	15	95	19	57	186	7.2	13.5-38.5	46.3
Loricariidae								
Hypostomus affinis (Steindachner, 1877)	25	20	35	29	109	4.2	11-36.5	36.3
Hypostomus auroguttatus Kner, 1854			2	5	7	0.3	14.5-24.2	3.1
Rineloricaria lima (Kner, 1853)	1	2	20	13	36	1.4	6-15.3	8.8
Pimelodidae								
Pimelodus fur (Lütken, 1874)[b]			127	109	236	9.2	11.5-28.5	31.9
Pimelodus maculatus La Cèpede, 1803[b]	18	8	37	38	101	3.9	13.5-37	31.3
GYMNOTIFORMES								
Gymnotidae								
Gymnotus carapo Linnaeus, 1758	19	6	7	2	34	1.3	17-40	15.0
Sternopygidae								
Eigenmannia virescens (Valenciennes, 1842)		1	17	1	19	0.7	20.5-38.8	6.3
PERCIFORMES								
Cichlidae								
Australoheros paraibae Ottoni & Costa 2008				2	2	0.1	14.5-15.5	1.3
Crenicichla lacustris (Castelnau, 1855)	1	3		4	8	0.3	12-30	4.4
Geophagus brasiliensis (Quoy & Gaimard, 1824)	3	11	6	31	51	2.0	11-28	21.9
Oreochromis niloticus (Linnaeus, 1758)[a]	1			2	3	0.1	28.2-30	1.9
Sciaenidae								
Plagioscion squamosissimus (Heckel, 1840)[a]	7		105	34	146	5.7	15.5-36	22.5
Total	452	427	1008	679	2566	100		

Table 2 - Abiotic data (mean ± s.d.) from Santa Cecília - Paraíba do Sul River

Zone/season	Temperature (°C)	Dissolved oxygen (mg L^{-1})	pH	Redox potential (mV)	Conductivity (μS cm^{-1})	Transparency (cm)
R/w	26.6 ± 0.4	6.5 ± 0.7	6.5 ± 0.4	240.7 ± 34.9	7.4 ± 0.7	50 ± 30
D/w	26.6 ± 0.6	7.1 ± 0.9	6.4 ± 0.5	259.3 ± 20.3	7.3 ± 0.5	70 ± 40
R/d	21.4 ± 0.8	7.3 ± 1.2	6.9 ± 0.1	228.8 ± 6.2	9.8 ± 0.3	130 ± 20
D/d	21.5 ± 0.7	7.5 ± 1.0	7.2 ± 0.2	221.9 ± 18.7	9.7 ± 0.2	150 ± 40

Codes: R = reservoir; D = downriver; w = wet; d = dry.

Table 3 - Factor loads from principal component analysis on abiotic data from Santa Cecília - Paraíba do Sul River

Abiotic variables	PC1	PC2
Tempetarature	**0.913**	-0.092
Redox potential	0.624	0.153
Dissolved oxygen	-0.252	**-0.921**
pH	**-0.776**	0.248
Conductivity	**-0.884**	-0.216
Transparency	**-0.726**	0.335
Eigenvalues	3.20	1.10
Percentage of explained variance	53.28%	18.33%

Values in bold highlight the most contributing scores to the observed variance.

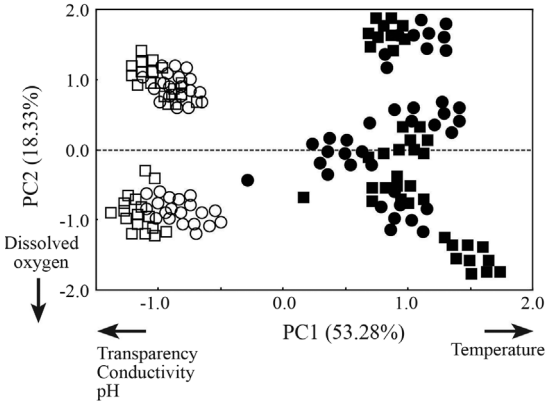

Figure 2 - Ordination diagram from the first two principal components on the abiotic variables measured from Santa Cecília - Paraíba do Sul River. Circles = reservoir; squares = river; filled symbols = wet season; open symbols = dry season.

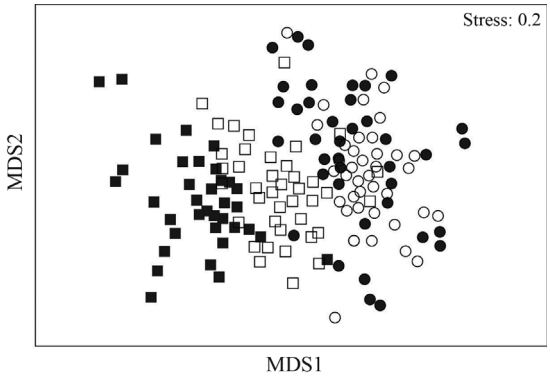

Figure 3 - Multidimensional scaling of fish data from Santa Cecília - Paraíba do Sul River. Circles = reservoir; squares = ; filled symbols = wet season; open symbols = dry season.

were found for each zone (Figure 3). Moreover, linear regression of fish assemblage (MDS1) against abiotic variables (PC1) was no significant ($r^2 = 0.08$; $p = 0.307$).

Thirteen species had significant indicator values according to the indicator species analysis (Table 4). The downriver zone had the greatest number of indicators species, among them three were rheophilics (*Leporinus copelandii, Prochilodus lineatus* and *Pimelodus fur*), with seven being indicators for the wet season and only one for the dry season. *Hoplias malabaricus*, *Geophagus brasiliensis* (Quoy & Gaimard, 1824) and *Rhamdia quelen* were indicators for the reservoir zone during the dry season, while *Hoplosternum littorale* (Hancock, 1828) was indicator for the reservoir zone during the wet season.

4. Discussion

A major change in the ichthyofauna organisation was detected in the spatial scale, i.e. the impoundment impacts on fish distribution, while seasonal variation between wet and dry seasons played a pivotal role in abiotic environmental patterns. Although some fish species were typical from wet or dry season, their distribution are probably more related to biological rhythm, foraging mode, and/or behavioural adaptations, than with limnological variability.

Abiotic variables had a strong influence in the seasonal patterns, explained by variation in temperature, transparency, pH and conductivity. High temperature values were directly related with the warm summer season, which coincides with rainy periods in rivers from Southeastern Brazil. Low water transparency found dur-

Table 4 - Significant values of the indicator species analysis for fish assemblages in the Santa Cecília - Paraíba do Sul River

Species	Indicator value	p	Zone/ season
Astyanax bimaculatus	29.1	0.034	D/w
Astyanax parahybae	21.8	0.002	D/w
Eigenmannia virescens	17.9	< 0.001	D/w
Plagioscion squamosissimus	36	< 0.001	D/w
Leporinus copelandii	23.5	< 0.001	D/w
Pimelodus fur	36.3	< 0.001	D/w
Prochilodus lineatus	38.2	< 0.001	D/w
Pimelodella eigenmanni	15.9	0.002	D/d
Gymnotus carapo	15.4	0.01	R/w
Hoplosternum littorale	33	< 0.001	R/w
Hoplias malabaricus	26.4	< 0.001	R/d
Geophagus brasiliensis	28.9	0.001	R/d
Rhamdia quelen	35.8	< 0.001	R/d

Codes: R = reservoir; D = downriver; w = wet; d = dry.

ing the wet season can be regarded a consequence of the increased sedimentary inputs from erosion, which is characteristic of the Paraíba do Sul River during flood periods (Pfeiffer et al., 1986). Water conductivities tend to be lower during wet season (Winemiller and Jepsen, 1998), and influenced byanthropogenic activities because of inputs of organic matter, and its later decomposition by heterotrophic organisms (Matthews, 1998; Guarino et al., 2005). The importance of abiotic factors in structuring fish assemblages is thoroughly recognised (Schlosser, 1982; Jackson et al., 2001; Oberdorff et al., 2001). However, in this study, similarly to the findings of Gubiani et al. (2010), the variation detected in abiotic variables was not very meaningful to define fish composition.

A more abundant and richer assemblage was found in the downriver compared with the reservoir zone, which is a widely documented consequence of dam construction (e.g., Gomes and Miranda, 2001; Oliveira et al., 2004; Santos et al., 2010). According to Williams et al. (1998), it is explained by large-scale changes in temperature, turbidity, flow, allochthonous nutrient inputs, and availability of food resources regimes. Considering the absence of relationships between fish assemblage and selected environmental variables, we suggest that regional changes caused by the impoundment is a main factor responsible for spatial fish distribution; increasing the aggregation of fishes below the dam due to the obstacle for upriver movements, and preventing the colonisation of species above the dam.

River impoundments generally exert negative effects on native fish species, especially on migratory species, disrupting longitudinal connectivity and obstructing migrations routes (Joy and Death, 2001; Fukushima et al., 2007). Furthermore, the accumulation of migratory fishes immediately below dams is well documented (Taylor et al., 2001; Gehrke et al., 2002) and were found in this study, since several species associated to downriver zone are migratory or rheophilic species - e.g., *Leporinus copelandii* Steindachner, 1875; *Pimelodus fur* (Lütken, 1874); and *Prochilodus lineatus* (Valenciennes, 1837). In addition, all these species were associated with wet season, probably due to reproductive purposes. It is widely reported that tropical migratory fishes need environmental stimuli (rain and floods) to trigger migrations and spawning (Lowe-McConnell, 1975; Vazzoler et al., 1997).

Prochilodus lineatus distribution is heavily impacted by successive impoundments in Paraíba do Sul River, which must be preventing reproductive migrations. Here, only two individuals were caught in the reservoir zone. It is a long-distance migratory species that depend on the flood pulse to complete the life cycle (Gubiani et al*.,* 2007). Early experimental studies revealed that *Prochilodus* species can migrate between 450 and 600 km y^{-1} (Bayley, 1973; Agostinho et al., 1993). According to Antonio et al. (2007), it is able to make two-way migrations, and tend to avoid the impounded regions in their reproductive period.

We found a decrease in abundance, especially large-sized migratory species in the reservoir zone, which are replaced by small-sized, generalist (in terms of habitat and food requirements) and opportunist fishes (Agostinho et al., 2007). Although the Paraíba do Sul River has lesser large-sized species compared with other larger Brazilian River Basins (Araújo et al., 1996), numbers of large-sized species could be underestimated because of the mesh size of nets that were at most 75 mm stretched mesh. Among the species inhabiting the reservoir zone, the following stand out as well suited to reservoir environment: *G. brasiliensis* which is a highly adapted to lentic environments (Bizerril, 1999) and has generalist feeding habits with great trophic plasticity to support changes in food resources availability (Meschiantti, 1995; Aguiaro and Caramashi, 1998); and *H. littorale* that is a typical fish of muddy habitats with physiological adaptations to breathe atmospheric oxygen and, consequently, to tolerate impacted environments (Chagas and Boccardo, 2006).

Another factor that contributes to decrease and/or displacement of native species is the predation pressure exerted by carnivorous fishes. Usually, in reservoirs, this guild is composed by non-native species, such as *Cichla kelberi* Kullander & Ferreira, 2006 and *Plagioscion squamosissimus* (Heckel, 1840) (Bennemann et al., 2006; Pelicice and Agostinho, 2009). Here, curiously, this group was dominated by two native species, H. malabaricus and *R. quelen*. The persistence of *H. malabaricus* in the reservoir zone is probably favoured by its prey-ambush foraging behaviour and strong territoriality during the reproductive season (Paiva, 1974). In turn, *R. quelen* is an omnivorous opportunist species, eating in-

sects, crustaceans, plant debris and small-sized fishes (Casatti and Castro, 2006; Oyakawa et al., 2006), and has nocturnal habits with preference by lentic and deep waters (Gomes et al., 2000). Therefore, both species showed adaptations to lead to new environmental conditions found in impounded areas.

Non-native fish predators, generally, have a higher abundance above than below large dams in tropical streams (Holmquist et al., 1998). Such a distribution pattern is well established for *P. squamosissimus* (see Oliveira et al., 2003; Agostinho et al., 2007; Terra et al., 2010). It is a top predator fish native from Amazon River basin responsible for the decrease of native fish population in many Brazilian reservoirs (Bennemann et al., 2006; Pelicice and Agostinho, 2009). In the studied system *P. squamosissimus* was an indicator species of downriver zone, contradicting known patterns of distribution. We believe that this bias can be related to the lateral connection between zones. According to Agostinho et al. (1999), this species produces small, pelagic and buoyant eggs spawned in several batches during the reproductive season, and use this strategy to colonise reservoirs. However, due to the run of the river characteristics of the studied system, this strategy should be ineffective in Santa Cecília Reservoir, where eggs and larvae drift downriver while they develop. Other factors, such as largest availability of preys and the better oxygenation of the water could explain the highest abundance of this species in downriver section.

In fact, this study illustrates the negative impact of river impoundment on fish assemblages, with fish assemblage organisation significantly different between reservoir and the downriver zone. Almost all changes detect in this non-traditional dam were similar those found in traditional ones, except for the *P. squamosissimus* distribution, the lack of non-native piscivorous in reservoir zone, and the independence between limnological and biotic variables. Most affected species were the rheophilic and migratory ones, such as *Pimelodus maculatus* La Cèpede, 1803, that is much more abundant in the downriver zone compared with the reservoir. Moreover, *Leporinus copelandii*, *Pimelodus fur* and *Prochilodus lineatus* are probably not able to perform their reproductive upriver migration due to dam blockage. Furthermore, our findings are in agreement with Matthews (1998) who pointed out that only those species with adaptations that fit the available habitats will successfully colonise a reservoir. We also found some evidences that the lateral hydrological connection has low ecological efficiency e.g., the absence of *P. fur*, as well as, the limited distribution of *P. lineatus* in the reservoir zone. In fact, strictly rheophylic species will probably never adapt in the reservoir habitat, even if it passes to the channel. Therefore, despite low-head dams being considered to have less impact on ichthyofauna, these dams produce semi-lentic environments with fish assemblage organisation significantly different from the fluvial system. In conclusion, we encourage biotelemetry or radio-acoustic count experiments to elucidate whether the lateral connection is able to promote fish transpositions, and to investigate the role of non-traditional dams in fish assemblage distribution.

Acknowledgments

This study was supported by the Brazilian National Council for Scientific and Technological Development, CT-Hydro Programme (Process 474875/2009-1 and 4556247/2009-4). The Rio de Janeiro Carlos Chagas Filho Research Support Agency also supplied financial support for this project (Process E-26/112.118/2008 and E-26/102.704/08). We thank Paulo César and Luciano Silva for field assistance. Two anonymous referees contributed significantly to improve this article.

References

AGOSTINHO, AA., GOMES, LC. and PELICICE, FM., 2007. *Ecologia e manejo de recursos pesqueiros em reservatórios do Brasil*. Maringá: EDUEM. 501 p.

AGOSTINHO, AA., MIRANDA LE., BINI, LM., GOMES, LC., THOMAZ, SM. and SUZUKI HI., 1999. Patterns of colonisation in neotropical reservoirs, and prognoses on aging. In TUNDISI, JG. and STRASKRABA, M. (Eds.). *Theoretical reservoir ecology and its applications*. Leiden: Backhuys Publishers. p. 227-265

AGOSTINHO, AA., PELICICE, FM. and GOMES, LC., 2008. Dams and the fish fauna of the Neotropical region: impacts and management related to diversity and fisheries. *Brazilian Journal of Biology*, vol. 68, no. 4, p. 1119-1132.

AGOSTINHO, AA., VAZZOLER, AEAM., GOMES, LC. and OKADA, EK., 1993. Estratificacion espacial y comportamiento de *Prochilodus scrofa* en distintas fases del ciclo de vida, en la planície de inundación del alto rio Paraná y embalse de Itaipu, Paraná, Brasil. *Revue d'Hydrobiologie Tropicale*, vol. 26, p.79-90.

AGUIARO, T. and CARAMASCHI, EP., 1998. Trophic guilds in fish assemblages is three coastal lagoons of Rio de Janeiro State (Brazil). *Verhandlungen des Internationalen Verein Limnologie*, vol. 26, p. 2166-2169.

ANTONIO, RR., AGOSTINHO, AA., PELICICE, FM., BAILLY, D. and DIAS, JHP., 2007. Blockage of migration routes by dam construction: can migratory fish find alternative routes? *Neotropical Ichthyology*, vol. 5, p. 177-184.

ARAUJO, FG., 1996. Composição e estrutura da comunidade de peixes do médio e baixo Rio Paraíba do Sul, RJ. *Revista Brasileira de Biologia*, vol. 56, p. 111-126.

ARAÚJO, FG., PEIXOTO, MG., PINTO, BCT. and TEIXEIRA TP., 2009. Distribution of guppies *Poecilia reticulatus* (Peters, 1860) and *Phalloceros caudimaculatus* (Hensel, 1868) along a polluted stretch of the Paraíba do Sul River, Brazil. *Brazilian Journal of Biology*, vol. 69, p. 41-48.

BAXTER, RM., 1977. Environmental effects of dams and impoundments. *Annual Reviews in Ecology and Systematics*, vol. 8, p. 255-283.

BAYLEY, PB., 1973. Studies on the Migratory characin, *Prochilodus platensis* Holmberg, 1889, (Pisces, Characoidei) in the River Pilcomayo, South America. *Journal of Fish Biology*, vol. 5, p. 25-40.

BENNEMANN, ST., CAPRA, LG., GALVES, W. and SHIBATTA, OA., 2006. Dinâmica trófica de *Plagioscion squamosissimus* (Perciformes, Sciaenidae) em trechos de influência da represa Capivara (rios Paranapanema e Tibagi). *Iheringia Série Zoologia*, vol. 96, p. 115-119.

BIZERRIL, CRSF., 1999. A ictiofauna da bacia do rio Paraíba do Sul: biodiversidade e padrões biogeográficos. *Brazilian Archives of Biology and Technology*, vol. 42, no. 2, p. 233-250.

CASATTI, L. and CASTRO, RMC., 2006. Testing the ecomorphological hy-pothesis in a headwater riffles fish assemblage of the rio São Francisco, southeastern Brazil. *Neotropical Ichthyology*, vol. 4, no. 2, p. 203-214.

CHAGAS, RJ. and BOCCARDO, L., 2006. The air-breathing cycle of *Hoplosternum littorale* (Hancock, 1828) (Siluriformes: Callichthyidae). *Neotropical Ichthyology*, vol. 4, p. 371-373.

CLARKE, KR. and WARWICK, RM., 1994. *Change in Marine Communities: An Approach to Statistical Analysis and Interpretation*. Plymouth: Plymouth Marine Laboratories. 144 p.

CUMMING, GS., 2004. The impact of low-head dams on fish species richness in Wisconsin, USA. *Ecological Applications*, vol. 14, p. 1495-1506.

DUFRÊNE, M. and LEGENDRE, P., 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs*, vol. 67, p. 345-366.

FUKUSHIMA, M., KAMEYAMA, S., KANEKO, M., NAKAO, K. and STEEL, EA., 2007. Modelling the effects of dams on freshwater fish distributions in Hokkaido, Japan. *Freshwater Biology*, vol. 52, p. 1511-1524.

GEHRKE, PC., GILLIGAN, DM. and BARWICK, M., 2002. Changes in fish communities of the Shoalhaven River 20 years after construction of Tallowa Dam, Australia. *River Research and Applications*, vol. 18, p. 265-286.

GODINHO AL. and KYNARD B., 2009. Migratory fishes of Brazil: life history and fish passage needs. *River Research and Applicattions*, vol. 25, p. 702-712.

GOMES, LC., GOLOMBIESKI, JI., GOMES, ARC. and BALDISSEROTTO, B., 2000. Biologia do jundiá *Rhamdia quelen* (Teleostei, Pimelodidae). *Ciência Rural*, vol. 30, no. 1, p. 179-185.

GOMES, LC. and MIRANDA, LE., 2001. Riverine characteristics dictate composition of fish assemblages and limit fisheries in reservoirs of the Upper Paraná River Basin. *Regulated Rivers: Research & Management*, vol. 17, p. 67-76.

GRAF, WL., 1999. Dam nation: A geographic census of American dams and their large-scale hydrologic impacts. *Water Resources Research*, vol. 35, p. 1305-1311.

GUARINO, AWS., BRANCO, CWC., DINIZ, GP. and ROCHA, R., 2005. Limnological characteristics of an old tropical reservoir (Ribeirão das Lajes Reservoir, RJ, Brazil). Acta Limnologica Brasiliensia, vol. 17, p. 129-141.

GUBIANI, EA., GOMES, LC., AGOSTINHO, AA. and BAUMGARTNER, G., 2010. Variations in fish assemblages in a tributary of the Upper Paraná River, Brazil: a comparison between pre and postclosure phases of dams. River Research and Application, vol. 26, p. 848-865.

GUBIANI, EA., GOMES LC., AGOSTINHO, AA. and OKADA, EK., 2007. Persistence of fish populations in the upper Paraná River: effects of water regulation by dams. *Ecology of Freshwater Fish*, vol. 16, p. 191-197.

HOLMQUIST, JG., SCHMIDT-GENGENBACH, JM. and YOSHIOKA, BB., 1998. High dams and marine-freshwater linkage: effects on native and introduced fauna in the Caribbean. *Conservation Biology*, vol. 12, p. 621-630.

JACKSON, DA., PERES-NETO, PR. and OLDEN, JD., 2001. What controls who is where in freshwater fish communities - the roles of biotic, abiotic, and spatial factors. *Canadian Journal of Fisheries and Aquatic Sciences*, vol. 58, p. 157-170.

JOY, MK. and DEATH, RG., 2001. Control of freshwater fish and crayfish community structure in Taranaki, New Zealand: dams, diadromy or habitat structure? *Freshwater Biology*, vol. 46, p. 417-429.

LOWE-MCCONNELL, RH., 1975. *Fish communities in tropical freshwaters: their distribution, ecology and evolution*. London: Longman. 337 p.

MATTHEWS, WJ., 1998. *Patterns in freshwater fish ecology*. New York: Chapman and Hall. 756 p.

MCCARTNEY M., 2009. Living with dams: managing the environmental impacts. *Water Policy*, vol. 11, p. 121-139.

MCCUNE, B. and MEFFORD, MJ., 1997. *Multivariate Analysis of Ecological Data*. Version 3.11. MjM Software: Gleneden Beach, Oregon, USA.

MESCHIATTI, AJ., 1995. Alimentação da comunidade de peixes de uma lagoa marginal do rio Mogi-Guaçu, SP. *Acta Limnologica Brasiliensia*, vol. 7, p. 115-137.

OBERDORFF, T., PONT, D., HUGUENY, B. and CHESSEL, D., 2001. A probabilistic model characterizing riverine fish communities of French rivers: a framework for environmental assessment. *Freshwater Biology*, vol. 46, p. 399-415.

OLDEN, JD., KENNARD, MJ., LEPRIEUR, F., TADESCO, PA., WINEMILLER, KO. and GARCÍA-BERTHOU, E., 2010. Conservation biogeography of freshwater fishes: recent progress and future challenges. *Diversity and Distributions*, vol. 16, p. 469-513.

OLIVEIRA, EF., GOULART, E. and MINTE-VERA, CV., 2003. Patterns of dominance and rarity of fish assemblage along spatial gradients in the Itaipu reservoir, Paraná, Brazil. *Acta Scientiarum Biological Sciences*, vol. 25, no. 1, p. 71-78.

OLIVEIRA, EF., GOULART, E. and MINTE-VERA, CV., 2004. Fish diversity along spatial gradients in the Itaipu Reservoir, Paraná, Brazil. *Brazilian Journal of Biology*, vol. 64, p. 447-458.

OYAKAWA, OT., AKAMA, A., MAUTARI, KC. and NOLASCO, JC., 2006. *Peixes de riachos da Mata Atlântica nas unidades de conservação do vale do rio Ribeira de Iguape no Estado de São Paulo*. São Paulo: Neotropica. 201 p.

PAIVA, MP., 1974. *Crescimento, reprodução e alimentação da traíra Hoplias malabaricus Bloch, no Nordeste Brasileiro*. Fortaleza: Imprensa Universitária da Universidade Federal do Ceará. 32 p.

PELICICE, FM. and AGOSTINHO, AA., 2009. Fish fauna destruction after the introduction of a non-native predator (*Cichla kelberi*) in a Neotropical reservoir. *Biological Invasions*, vol. 11, p. 1789-1801.

PFEIFFER, WC., FISZMAN, M., MALM, O. and AZCUE, JM., 1986. Monitoring heavy metals pollution by the critical pathway analysis in the Paraíba do Sul River. *The Science of the Total Environment*, vol. 58, p. 73-79.

PINTO, BCT., ARAÚJO, FG. and HUGHES, RM., 2006. Effects of landscape and riparian condition on a fish index of biotic integrity in a large southeastern Brazil river. *Hydrobiologia*, vol. 556, p. 69-83.

POFF, NL. and HART, DD., 2002. How dams vary and why it matters for the emerging science of dam removal. *BioScience*, vol. 52, p. 659-668.

POFF NL., OLDEN JD., MERRITT DM. and PEPIN DM., 2007. Homogenization of regional river dynamics by dams and global biodiversity implications. *Proceedings of*

the Natural Academy of Sciences of the United States of America, vol. 104, p. 5732-5737.

POLAZ, CNM., BATAUS YSL., DESBIEZ, A. and REIS ML., 2011. *Plano de ação nacional para a conservação das espécies aquáticas ameaçadas de extinção da Bacia do Rio Paraíba do Sul*. Brasília: ICMBio. 140 p. Série Espécies Ameaçadas, no. 16.

POMPEU, PS., AGOSTINHO, AA. and PELICICE, FM., 2011. Existing and future challenges: the concept of successful fish passage in South America. *River Research and Applications*, vol. 28, p. 504-512.

ROSCOE, DW. and HINCH, SG., 2010. Effectiveness monitoring of fish passage facilities: historical trends, geographic patterns and future directions. *Fish and Fisheries*, vol. 11, p. 12-33.

ROSENBERG, DM., MCCULLY, P. and PRINGLE, CM., 2000. Global-scale environmental effects of hydrological alterations: Introduction. *BioScience*, vol. 50, p. 746-751.

SANTOS, ABI., TERRA, BF. and ARAÚJO, FG., 2010. Fish assemblage in a dammed tropical river an analysis along the longitudinal and temporal gradients from river to reservoir. *Zoologia*, vol. 27, p. 732-740.

SCHLOSSER, IJ., 1982. Fish community structure and function along two habitat gradients in headwater stream. *Ecological Monographs*, vol. 52, p. 395-414.

SHEER, MB. and STEEL, EA., 2006. Lost watersheds: barriers, aquatic habitat connectivity, and salmon persistence in the Willamette and Lower Columbia River basins. *Transactions of the American Fisheries Society*, vol. 135, p. 1654-1669.

TAYLOR, CA., KNOUFT, JH. and HILAND, TM., 2001. Consequences of stream impoundment on fish communities in a small North American Drainage. *Regulated Rivers: Research and Management*, vol. 17, p. 687-698.

TERRA, BF., SANTOS, ABI. and ARAÚJO, FG., 2010. Fish assemblage in a dammed tropical river: an analysis along the longitudinal and temporal gradients from river to reservoir. *Neotropical Ichthyology*, vol. 8, p. 599-606.

VAZZOLER, AEAM., 1996. *Biologia da reprodução em peixes teleósteos: teoria e prática*. Maringá: EDUEM. 169p.

WILLIAMS, JD., WINEMILLER, KO., TAPHORN, DC. and BALBAS, L., 1998. Ecology and status of piscivores in Guri, an oligotrophic tropical reservoir. *North American Journal of Fisheries Management*, vol. 18, p. 274-285.

WINEMILLER, KO. and JEPSEN, DB., 1998. Effects of seasonality and fish movement on tropical river food webs. *Journal of Fish Biology*, vol. 53, p. 267-296.