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Fish in Brazilian reservoirs

Influence of limnological zones on the spatial distribution of fish assemblages in three Brazilian reservoirs

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ABSTRACT

Reservoirs can have both positive and negative effects on different fish species depending on the species concerned and reservoir morphology, flow regime, and basin location. We assessed the influence of limnological zones on the ichthyofauna of three large neotropical reservoirs in two different river basins. We sampled fish through use of gill nets set at 40 systematically selected sites on each reservoir. We used satellite images, algae, and suspended solids concentrations to classify those sites as lacustrine or riverine. We observed significant differences in assemblage composition between riverine and lacustrine zones of each reservoir. We tested if the same zone (lacustrine or riverine) showed the same patterns in different reservoirs. In São Simão, the riverine zone produced greater abundances of native species, long-distance migratory species, diversity, and richness, whereas the lacustrine zone

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supported greater total and non-native species abundances. Conversely, in Três Marias, the riverine zone supported greater total and non-native species abundances, whereas the others traits evaluated did not differ significantly between zones. Only lacustrine sites occurred in Volta Grande Reservoir. The same zones in the three reservoirs usually had significantly different patterns in the traits evaluated. The differences in spatial patterns observed between reservoirs could be explained partly by the differing morphologies (complex versus simple), the differential influence on tributaries of each reservoir and basin positions (presence or absence of upstream dams) of the reservoirs.

INTRODUCTION

Changes in community composition, including local species extinctions and introductions, can occur rapidly as a consequence of human activities (Clavero and Hermoso, 2010; Mejía-Mojica *et al.*, 2014). Large dams create major changes in rivers globally (Dynesius and Nilsson, 1994; Stanford *et al.*, 1996; Hughes *et al.*, 2005) and in Brazil, where there are more than 700 plants operating for power generation (Agostinho *et al.*, 2008). The reservoirs behind dams create discontinuous longitudinal gradients because of changes in hydrology and geomorphology and consequently on the chemical and physical features of rivers (Oliveira *et al.*, 2003; Britto and Carvalho, 2006; Terra *et al.*, 2010).

Damming establishes physical barriers that limit fish movement (upstream and downstream), contributing to population isolation and extirpation (Hughes *et al.*, 2005; Araújo *et al.*, 2008; Pompeu et al., 2012). Thus, loss of connectivity is another relevant issue related to river damming, and it is associated with degraded fish assemblage condition (Musil *et al.*, 2012). Dams disrupt migration routes (Hoeinghaus *et al.*, 2009) that are particularly important for fish species with long-distance migrations that depend on long river reaches for reproduction and growth. Many native species are not tolerant enough to become competitive in the new environment because lotic species are replaced by lentic species (Irz *et al.*, 2002; Hughes *et al.*, 2005; Sanches *et al.*, In Press). As a result, the fish assemblage that once inhabited the river is substantially modified.

The dominance of non-native species in the new environment is another concern (Hoeinghaus *et al.*, 2009) because reservoirs often shift from native-dominated stream fishes to non-native invasive-dominated fish assemblages (Clavero and Hermoso, 2010). This occurs because of intentional and accidental introductions of non-natives to support fisheries and to help control pest organisms, plus the greater environmental tolerances to anthropogenic



disturbance of the introduced species (Moyle and Light, 1996; Hughes et al., 2005; Terra et al., 2010).

These impoundments combine ecological and functional features of both rivers and lakes, so it is possible to find distinct habitats that are more lake-like or river-like in the same reservoir (Søballe and Kimmel, 1987; Terra et al., 2010; Sanches et al., In Press). Usually, the upper part of a reservoir tends to have riverine features, whereas the lower part has lacustrine characteristics (Irz et al., 2002; Terra et al., 2010; Sanches et al., In Press). However, the presence of tributaries along the reservoir can reset these patterns somewhat (Sanches et al., In Press). Freshwater fish species respond differently to these riverine/lacustrine zones because the differing habitat types control the spatial distribution of fish species and the resulting fish assemblages (Holmgren and Appelberg, 2000; Irz et al., 2002; Terra et al., 2010). For example, riverine zones tend to support more native species (Oliveira et al., 2005; Agostinho et al., 2007; Gao et al., 2010) and rare species (Oliveira et al., 2003), whereas lacustrine zones tend to support fewer species (Oliveira et al. 2004; Agostinho et al., 2007)). If reservoir riverine and lacustrine zones support markedly different fish assemblages, it would be wise to manage them differently if managers desire to conserve or rehabilitate native fish assemblages and control invasive non-native species. For example, zones supporting healthy populations of native fish species or relatively large numbers of rare fish species could be designated as conservation or protection areas with improvements or actions focused at those locales (Hughes et al. 2005; Wang et al. 2006). On the other hand, zones or entire reservoirs supporting few native fish species or mostly tolerant or non-native fish species could be designated as rehabilitation areas and targeted for improvement projects at local and catchment scales (Hughes et al. 2005; Mueller et al. 2005; Valdez and Muth 2005; Wang et al. 2006).

We sought to verify if distinct reservoir zones affected the fish assemblages of three large neotropical reservoirs in two differentbasins. We tested the hypotheses that i) spatial distribution of fish assemblages is influenced by reservoir zone; ii) fish species abundance and richness are greater in riverine zones; iii) the same zones from different reservoirs show similar patterns in the traits evaluated.

METHODS

Study area

The study region comprised the upper portion of two large neotropical Brazilian river basins: the Paraná and São Francisco. We sampled one reservoir in the São Francisco Basin:



Três Marias (TM), and two reservoirs in the Paraná Basin: São Simão (SS) and Volta Grande (VG).

The Paraná River is 3965 km long, from its source in the Mantiqueira Range, to the La Plata River in Buenos Aires (Stevaux *et al.*, 2009). It is the second longest river in South America, and is formed by the junction of the Grande and Paranaíba Rivers (Agostinho *et al.*, 2008; Stevaux *et al.*, 2009). The Upper Paraná River Basin is located upstream of the old Sete Quedas waterfalls (now flooded by Itaipu Reservoir) (Langeani *et al.*, 2007). This region has the greatest number of large reservoirs in Brazil (over 145) with only 230 km of freely flowing reaches between Porto Primavera and Itaipu Reservoirs (Agostinho *et al.*, 2008). São Simão reservoir (geographical coordinates in UTM: 22K 551969E 7896233S) has a storage volume of 5.5 billion m³ of water and its maximum depth is 127 m. It began operations in 1978 (CEMIG, 2014). Volta Grande reservoir (22K 789414E 7782805S) has a storage volume of 268 million m³ of water and is the only run-of-river reservoir sampled in this study. This kind of reservoir has a reduced flood area and does not accumulate water, showing no significant changes in water level. It is the smallest reservoir that we studied and its operation began in 1974.

The São Francisco River is 2900 km long and flows through 6 Brazilian states and three biomes: Mata Atlantica (Atlantic forest), Cerrado (Savannah), and Caatinga (xeric shrubland). Approximately 6250 km² was flooded by three large hydroelectric reservoirs. Três Marias, finished in 1960, currently is the only dam built in the Upper São Francisco Basin. The reservoir is 150 km long (Godinho and Godinho, 2003), has a storage volume of 15.2 billion m³, and is over 60 m deep in its lower reaches. The reservoir locations, the locations of their samplings stations and their classifications into lacustrine and riverine zones are illustrated in Fig. 1.

Division of reservoirs into lacustrine and riverine zones

We initially classified Landsat 5 TM images taken during the respective sampling periods of each reservoir to visually distinguish riverine and lacustrine zones. After acquisition and image geo-referencing, we performed atmospheric correction by the dark object subtraction method (Chavez Jr., 1988). Areas influenced by rivers have higher concentrations of suspended solids and algae (Wetzel, 2001). We used three spectral bands: green (0.52 to 0.60 mm), red (from 0.63 to 0.69 mm), and near infrared spectral bands (0.76 to 0.90 mm) to detect those two zones (Jensen, 2006). First, we used an algorithm of automatic unsupervised classification, to discriminate the areas that have distinct spectral





response. We used the algorithm "Iterative Self-Organizing Data Analysis Technique" (ISODATA; Ball and Hall, 1965), one of most commonly used automated methods in multispectral image classification. The algorithm identifies patterns in spectral response and creates arbitrary classes. After that classification, we identified the areas that were visually distinct, considering that riverine areas have a markedly different reflectance than the lacustrine areas because of greater levels of suspended sediment (Fig. 2). To corroborate this classification, we assessed the significance of differences in measurements of turbidity and algae (measured by pheophytin *a*) between lacustrine and riverine sites. For this purpose, we employed a Mann-Whitney test corrected by Bonferroni criteria (Zar, 2009). Our limnological data and the methodology used for the separation of the areas did not enable us to separate a transition zone clearly. For the Volta Grande Reservoir just the lacustrine area was identified.

Some authors have classified sites near the dam as lacustrine and those more distant as riverine (Petesse *et al.*, 2007; Dabrowski *et al.*, 2013). However, like Sanches et al. (2014) we observed riverine zones near the dam and lacustrine zones distant from the dam because of the relative influence of tributaries or deep flooded canyons, respectively. Therefore we used limnological characteristics to refine our initial remote sensing classifications to classify sites as riverine or lacustrine relative to their position to the dam as well as the relative influence of large tributaries near the dam and flooded canyons far from the dam. Such a refined classification reflects both the riverscape concept (Fausch *et al.*, 2002) and the river wave concept (Humphries *et al.*, 2014), both of which reflect the pulsed nature of river-lake ecosystems, even in systems as large as the Laurentian Great Lakes (Regier *et al.*, 2013).

Fish sampling

We collected fish between April and May in 2011 (Três Marias), 2012 (Volta Grande) and 2013 (São Simão). We sampled each reservoir at 40 littoral zone sites uniformly spread along its perimeter with a random start point. At each site, we set 10 gill nets, each 20-m long and with mesh size varying from 3 to 16 cm (between opposing knots). Five pairs of nets were set in series at an angle of approximately 45° from the shore and with the smaller mesh nets nearest the shore. A distance of 40 m was maintained between each pair of nets, so the total site length was 200 m. The nets were set in the evening and retrieved in the morning for a soak time of 15 h.

The collected specimens were euthanized in clove oil solution with ethanol, following the guidelines of the CONCEA euthanasia practice (Brazilian National Council for Animal Experiments Control), fixed in 10% formalin, and identified in the laboratory through use of



taxonomic keys (Britski *et al.*, 1988; Graça and Pavanelli, 2007). We considered as nonnative those species that did not originally belong to the Upper Paraná or São Francisco Basins. We deposited voucher specimens in the ichthyological collections of the Museu de Ciências Naturais da Pontifícia Universidade Católica and Universidade Estadual do Paraná.

Data analyses

Abundance was determined by the sum of the number of collected fish per 100 m² of gillnets, employed in 15 hours of operation. This procedure standardized catches and allowed quantitative catch comparisons. Data normality was verified through application of a Kolmogorov-Smirnoff test. The assemblage traits used to assess differences between lacustrine and riverine zones in the same reservoir were: total abundance, abundance of long-distance migratory and non-native and native individuals, total species richness, and Shannon diversity (H') as stated in Magurran (2011). For the comparisons between the same zones in different reservoirs, we tested: % of migratory individuals, % of migratory species, % of native individuals, % of native species, evenness (Pielou's J'), total abundance, total species richness, and Shannon Diversity index (H'). To verify whether these differences were significant, we performed a Mann-Whitney test on non-parametric data (Zar, 2009). Because Volta Grande Reservoir was all lacustrine, only one zone could be evaluated.

Assemblage differences among reservoirs and between reservoirs zones were evaluated through use of nonmetric multidimensional scaling (NMDS) procedure from a Bray-Curtis similarity matrix using 9999 iterations. For this analysis, species that occurred at < 5% of the sites were excluded to reduce analytical noise. After that, species abundance data were transformed by log (x+1) (Legendre and Legendre, 1998; McCune *et al.*, 2002). To validate the analysis, only stress values near 0.2 (Legendre and Legendre, 1998) were admitted. To test the significance of zonal clusters and reservoir assemblage differences, we performed PERMANOVA analyses (Bain *et al.*, 1988; Manly, 1997).

A Mantel test was used to verify whether there was spatial autocorrelation on abundance data (Mantel, 1967). In that step we determined the correlation between a Bray Curtis similarity matrix constructed with abundance data and a Euclidean distance matrix constructed with geographic coordinates.

To determine the level of irregularity of the margins of each reservoir, we calculated its Shoreline Development Index (SDI) (Hutchinson, 1957) through use of the following equation:



where

SL, shoreline length;

sqrt, square root;

Ao, length of the circumference of a circle of area equal to that of the lake.

All the statistical analyses were conducted in Primer (Clarke and Gorley, 2006), Anderson *et al.*, 2008; R (R Core Team, 2012) and Statistica 8.0 (StatSoft, Inc. 2007) softwares.

RESULTS

*Fish sampling*We collected a total of 84 fish species, belonging to 19 families and 4 orders, in the three reservoirs (Supplementary Tab 1). Sixteen species were considered long-distance migratory and twelve were non-natives. São Simão had greater species richness (48 total, 11 migratory, 11 non-native), followed by Três Marias (37 total, 6 migratory, 3 non-native) and Volta Grande (30 total, 4 migratory, 7 non-native). However, Três Marias Reservoir yielded many more individuals (3843) than São Simão Reservoir (2842) or Volta Grande Reservoir (1489).

Non-native species were important in all three reservoirs. In Três Marias, 2 non-native piscivorous species (*Cichla* cf. *piquiti* and *Cichla kelberi*) represented 20% of total abundance, mostly in the riverine zone. In São Simão, 3 non-native piscivorous species (*Plagioscion squamosissimus, C. piquiti* and *Raphiodon vulpinus*) were among the most abundant accounting for 32% of the individuals captured. In this reservoir the 11 non-native species captured occurred most frequently in the lacustrine zone. Of these, *Geophagus proximus* accounted for 33% of the total catch and *P. squamosissimus* and *C. piquiti* accounted for 27% of the total catch. Most of the catch and 8 of the species in Volta Grande consisted of non-native individuals; *P. squamosissimus, Satanoperca* cf. *pappaterra, Metynnis* gr. *lippincottianus, C. piquiti*, and *C. kelberi*, comprised 72% of the individuals collected (Supplementary Tab. 1).

Effect of reservoir zone on fish assemblage abundance and richness

We detected total abundance differences between reservoir zones in Três Marias and São Simão (Tab. 1). The riverine zone of São Simão yielded significantly more native individuals, migratory species individuals, species richness, and diversity than did the



lacustrine zone. But only total and non-native abundances were significantly greater in the Três Marias lacustrine zone.

Effect of reservoir zone on fish assemblage composition

Ordination revealed differentiation among the fish assemblages in the different reservoir zones and river basins (Figs. 2 and 3). The fish assemblages captured in the lacustrine and riverine zones of São Simão are clearly distinguished (Fig. 2A) On the other hand, the fish assemblages in Três Marias are only weakly distinguished (Fig. 2B). The fish assemblages in São Simão and Volta Grande Reservoirs are more similar to each other (left side of Figure 3) than to those in Três Marias because they are in the same river basin (Upper Paraná), whereas the Três Marias fish assemblages are in the São Francisco Basin. (Fig. 3b). Nonetheless, PERMANOVA results indicated significant differences in fish assemblage structure between riverine and lacustrine zones in both reservoirs (Três Marias: t=1.81, P=0.003; São Simão: t=1.99, P=0.001). NMDS plots (Fig. 4) and PERMANOVA results also indicate significant differences in fish assemblage structure among the three reservoirs (t=2.77; P=0.001).

Fish assemblage pattern similarity among different reservoirs

When comparing the same zones among reservoirs, Três Marias and São Simão had non-significant differences in total abundance for both lacustrine (U=112.5, P=0.1304) and riverine (U=239, P=0.9811) zones because of the wide abundance ranges among sites (Fig. 5a). Both reservoirs had significantly fewer lacustrine zone individuals than Volta Grande (VG x TM: U=167, P=0.0002; VG x SS: U=75, P<0.0001; SS x TM:, U=112.5, P=0.1305). The three reservoirs differed significantly in lacustrine zone species richness (VG x TM: U=10, P<0.0001; VG x SS: U=118.5, P<0.0001; SS x TM: U=19, P<0.0001) and diversity (VG x TM: U=189, P<0.0001; VG x SS: U=171.5, P=0.0070; SS x TM: U=15, P<0.0001), with the greatest richness and diversity in Três Marias (Fig. 5b,c). São Simão had significantly lower lacustrine evenness than Três Marias and Volta Grande (VG x SS: P=0.0044, U=163; TM x SS: P<0.0001, U=30; Fig 5d).

The lacustrine and riverine zones of Três Marias produced significantly greater percent of native species (lacustrine: VG x TM: U=1, P<0.0001; SS x TM: U=0, P<0.0001; riverine: SS x TM: U=65, P<0.0001; Fig.5e) and percent of native individuals (lacustrine: VG x TM: U=183, P=0.0006; VG x SS: U=152, P=0.0023; SS x TM: U=9, P<0.0001; riverine: SS x TM: U=65, p<0.0001; Fig 5f). The percent of migratory species individuals

was significantly greater in São Simão lacustrine (VG x SS: U=385, P=0.0281; TM x SS: U=53, P<0.0001) and riverine (TM x SS: U=53, P=0.0006) zones (Fig. 5g). We found the same pattern for thepercentage of migratory species (lacustrine: VG x SS: U=123, P=0.0002; TM x SS: P=0.0007, U= 54.5; riverine: TM x SS: P=0.0118, U= 133.5; Fig. 5h). There was insignificant correlation between the similarity matrix constructed from the abundance data and the dissimilarity matrix based on geographic coordinates (São Simão: R= -0.03, P=0.51; Três Marias: R= -0.08, P=0.81 and Volta Grande: R= 0.08, P=0.06). The Shoreline Development Index (SDI) calculated for the three reservoirs showed that Três Marias was the most dendritic by far (SDI=1915), versus 968 for São Simão and 340 for Volta Grande.

DISCUSSION

Fish sampling

We found significant differences in the fish assemblages among the three reservoirs, although the assemblages in Volta Grande and São Simão Reservoirs are more similar to each other than to Três Marias (Fig. 4). This results from the fact that those two reservoirs are located in the same basin, and consequently, have several species in common (Supplementary Tab. 1). To better understand assemblage responses to differences in reservoir morphology, flow regime, and basin or ecoregion location it is necessary to implement more rigorous study designs of populations of reservoirs such as have been conducted by the U.S. Environmental Protection Agency in its National Lake Survey (Kaufmann *et al.*, 2014a, 2014b).

Effect of reservoir zone on fish assemblage abundance & richness

The combination of spatial gradients and biological interactions can influence the distribution of different species with different ecological requirements and adaptability to one or more habitats (Gido *et al.*, 2002; Field *et al.*, 2009; Mouchet *et al.*, 2013). The Três Marias riverine zone had greater total abundance of fishes than its lacustrine zone, which has been reported in other reservoir studies (Britto and Carvalho, 2006; Juza *et al.*, 2009). Once these lakes are built, their fishes are likely to seek habitats that are most similar to their natural habitats, like tributary mouths (Fernando and Holčík, 1991; Sanches *et al.* 2014). Furthermore, the greater density of fishes in the riverine zone may reflect greater availability of resources there, compared with the lacustrine zone (Lind *et al.*, 1993).

In São Simão Reservoir, however, the lacustrine zone supported more individuals than the riverine zone. One of the explanations for this is the high abundance of piscivorous species in this reservoir, which also was observed by Delariva *et al.* (2013) at Salto Caxias



Reservoir. Visual predators are well adapted to lacustrine habitats with high transparency (Guthrie and Muntz, 1993). In addition to the high abundance of piscivores, the most frequently captured species in this reservoir (*Geophagus proximus*) was usually found in the lacustrine zone. Santos et al. (2010) found that a *Geophagus* species was also among the most abundant species in Funil Reservoir, southeastern Brazil. It exhibited restricted distribution to lacustrine sites, to which *Geophagus* species are well adapted. The success of this genus in reservoirs is partly explained by its detritivorous-iliophagous and omnivorous feeding habitats (Meschiatti, 1995), guilds that are often identified as prevalent in reservoirs (Agostinho et al., 2007).

Effect of reservoir zone on fish assemblage composition

We found that fish assemblage composition was affected by limnological zones in Três Marias and São Simão Reservoirs (Fig. 3), but there was only one zone in Volta Grande. This zonal influence was clear in São Simão, but less so in Três Marias Reservoir. Nevertheless the PERMANOVA analysis showed that fish assemblages in reservoir riverine zones differed significantly from those in their lacustrine zones in both reservoirs.

Areas influenced by tributaries have more organic matter and suspended solids, providing temporary habitat for migratory species that use reservoirs as feeding areas (Pagioro and Thomaz, 2002; Oliveira *et al.*, 2005; Miranda and Bettoli, 2010). That may explain the greater abundance of long-distance migratory individuals in the São Simão riverine zone. Okada *et al.* (2005) also found more migratory individuals in the Itaipu Reservoir riverine zone, as did Sanches *et. al* (2014) (in press) in Nova Ponte Reservoir.

The fish fauna of a freely flowing river constitutes the initial assemblage of the newly formed reservoir. Therefore, the remaining species are often concentrated in tributary mouths, which are more similar to the original habitat than other parts of the reservoir, where their ability to compete and survive is lower (Irz *et al.*, 2002; Oliveira *et al.*, 2004). We observed this pattern in São Simão, where the riverine zone had more native species than the lacustrine zone. Likewise, the lacustrine zone of this reservoir yielded more non-native individuals, mainly *G. proximus* and three piscivorous species.

Environmental disruptions, such as reservoir construction, can contribute to the establishment of non-native species (Johnson *et al.*, 2008; Daga and Gubiani 2012; Erős *et al.* 2012). Disturbed environments may compromise the competitive and survival abilities of native species, making them more vulnerable to invasive non-native species that are more tolerant of those altered environments (Moyle and Light, 1996). This pattern was observed by

Sanches *et. al.* (2014) in Volta Grande Reservoir, where few native species were associated with abundant non-native piscivores (also see Supplementary Tab. 1).

Piscivorous species were the most abundant among non-native species in Três Marias Reservoir. However, they were more abundant at riverine sites, where the total fish abundance was also higher. In Três Marias, increased prey density at riverine zone may have compensated the visual foraging constraints for the distribution of non-native predators, as observed by Jacobsen *et al.* (2014). According to this researcher, although predators be successful in high-visibility environments, predation rates may also be higher in places with lower visibility, but with high abundance of prey.

Similar to São Simão, greater species richness has been reported in the riverine zone of other Brazilian reservoirs (Oliveira *et al.*, 2004; Gubiani *et al.*, 2010; Terra *et al.*, 2010) as well as in reservoirs of other countries (Gido *et al.*, 2002; Prchalová *et al.*, 2009; Freedman *et al.*, 2013). The riverine zone can be considered a quasi ecotone, because of the overlap of fluctuating riverine and lacustrine conditions (Terra *et al.*, 2010). These environments have a wide range of exploitable microhabitats and high rates of primary productivity, which contribute to greater species richness and fish diversity than in other areas (Eadie and Keast, 1984; Cecílio *et al.*, 1997; Irz *et al.*, 2004; Oliveira *et al.*, 2004). Furthermore, lacustrine zones often have chemical or thermal stratification creating microhabitats that are severe environmental filters for many species (Oliveira *et al.*, 2003; Agostinho *et al.*, 2008). Oliveira *et al.* (2004) found low richness in such microhabitats. Thus, environments that resemble the original riverine characteristics or those with greater habitat heterogeneity, such as tributary mouths, support more species with different ecological needs than other sites (Agostinho *et al.*, 2007).

There were no significant differences between lacustrine and riverine zones for some metrics in Três Marias. One factor that could explain those different patterns between reservoirs is their differing morphologies, because morphology influences water and sediment process dynamics, which also affect biological communities (Tundisi and Tundisi, 2008). Três Marias Reservoir has a pronounced dendritic pattern and complex morphology, which creates complex patterns in water circulation and accumulation of organic material and sediment (Tundisi and Tundisi, 2008) relative to São Simão and Volta Grande Reservoirs, which have simpler morphologies. Another difference between Três Marias, São Simão and Volta Grande Reservoirs is their locations. The latter two reservoirs are located in the Upper Paraná Basin, which has the highest dam concentration in Brazil (Agostinho *et al.*, 2008). The cascade of reservoirs constitutes sediment and nutrients traps, reducing the concentrations of





these elements in downstream reservoirs (Agostinho *et al.*, 1995). Três Marias, on the other hand, is the only reservoir in the Upper São Francisco Basin; therefore, its sediment and nutrient deliveries are not influenced by upstream reservoirs and may be less limiting than in São Simão and Volta Grande.

Fish assemblage pattern similarity among different reservoirs

When comparing the same zones among different reservoirs, number of individuals was the only trait that did not differ significantly between São Simão and Três Marias, lacustrine or riverine zones. Differences in physical characteristics and location of these reservoirs are factors that may have influenced the lack of patterns of the evaluated traits, although among-site abundance is a highly variable indicator as seen in Fig. 5a. Volta Grande, however, showed the lowest total abundance and richness. The low spatial heterogeneity in the lacustrine zone and the absence of a riverine zone may explain the low fish catch from this reservoir (Oliveira *et al.*, 2003). Another possible explanation for the lower number of individuals and richness in Volta Grande is the *P. squamosissimus* dominance, a piscivorous species representing 44% of total captures in the reservoir (Sanches *et al.*, 2014; Supplementary Tab. 1). This introduced species is well established in Volta Grande Reservoir, which lacks large tributaries and, therefore, lacks a riverine zone that can serve as a shelter for sensitive species. Predation by introduced piscivores is a well-established mechanism to limit or extirpate native prey (Miller *et al.*, 1989; Moyle and Light 1996; Cucherousset and Olden 2011; Hughes and Herlihy 2012).

Três Marias and São Simão riverine zones had similar richness, diversity and evenness. Although they are in unconnected basins, the number of species and fish dominance patterns had the same response at sites with riverine influences. The same cannot be assumed for their lacustrine zones, because Três Marias had greater values than São Simão except for evenness. As discussed previously, São Simão is part of a series of reservoirs built on the Paranaíba River, which likely constitutes greater environmental pressure on fish assemblages than Três Marias, which is the uppermost reservoir of the São Francisco River.

The composition of migratory and native species differed among the three assemblages. Três Marias Reservoir supported the greatest percentage of native species and individuals, both in lacustrine and riverine zones, which is contrasted with the greater abundance and richness of non-native species collected in the other two reservoirs. Sanches *et al.* (2014) reported that in Três Marias 20% of the total catch was non-native species, versus 78% in São Simão and 73% in Volta Grande (Supplementary Tab. 1).



Despite belonging to the same basin as São Simão, Volta Grande had similar percentages of migratory individuals and species as Três Marias. Sanches *et al.*, (2014) also found that Nova Ponte Reservoir had low migratory abundance and richness compared with São Simão. These differences are associated with the differential influence of tributaries in the three reservoirs evaluated, which provide temporary habitat for migratory species and can serve as a shelter for sensitive species.

Because of their differing effects on fish assemblages, we recommend that riverine and lacustrine zones of large reservoirs be managed differently if managers desire to conserve or rehabilitate native fish assemblages and control invasive non-native species. Keys to this management include normalizing flow regimes in riverine zones, limiting introductions and dispersal of non-native species, and limiting the number of other large dams and reservoirs in the river basin to the degree possible given other reservoir management objectives (Hughes *et al.*, 2005)

CONCLUSIONS

Results confirmed our hypothesis that the composition of reservoir fish assemblages are affected by reservoir zonation. The lacustrine and riverine zones are occupied differentially depending on the ecological needs of fish species. However, we failed to confirm our hypotheses that fish species abundance, richness, diversity, and life history guilds are consistently greater in riverine zones or that the same zones from different reservoirs have similar responses for the traits evaluated. Depending on reservoir complexity and materials delivery, riverine zones may be refuges for remaining native and migratory species, reinforcing the importance of riverine habitats for conserving fish species in intensively dammed rivers. The river basins and morphologies of each reservoir also affected the evaluated traits, sometimes having greater influences on the assemblages than zonation. The effects of zonation patterns and tributary influences on fish assemblages could be assessed more effectively if sets of reservoirs with similar morphology, flow regime, and basin position were studied. This is true especially for those that are not located in a cascade of dams and which have stronger riverine characteristics (like Três Marias). Few studies consider reservoirs with such features; however, such research designs are essential for elucidating how fish assemblages behave in reservoirs with different and similar local and basin characteristics.



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	São Simão Reservoir (Upper Paraná Basin)						Três Marias Reservoir (Upper San Francisco Basin)				
	~	Р	U	Rank sum lacustrine	Rank sum riverine	Zone with highest rank sum	Р	U	Rank sum Lacustrine	Rank sum Riverine	Zone with highest rank sum
Q	T ₂ al no. Individuals	<u>0.009</u>	<u>98.5</u>	421.5	398.5	Lacustrine	0.003	92.0	302.0	518.0	Riverine
	INO. non-native	<u>0.002</u>	83.0	437.0	383.0	Lacustrine	0.013	109.0	319.0	501.0	Riverine
	N. native individuals	<u>0.015</u>	103.5	239.5	580.5	Riverine	0.069	133.0	343.0	477.0	-
	No. migratory	<u>0.041</u>	118.0	254.0	566.0	Riverine	0.1516	147.0	357.0	463.0	-
	Shannon diversity	0.000	35.0	171.0	649.0	Riverine	0.4488	172.0	382.0	438.0	-
	Species richness	<u>0.009</u>	97.5	233.5	586.5	Riverine	0.093	138.0	348.0	472.0	-

Tab. 1. Results of Mann-Whitney tests on fish assemblage traits between lacustrine and riverine zones.

Underlined values indicate significant P-values (P<0.05).

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Fig. 1. Reservoir site locations and classifications into lacustrine and riverine zones (all Volta Grande sites were lacustrine).



Fig. 2. Division of reservoirs into lacustrine and riverine zones using Landsat and the ISODATA algorithm.



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Fig 3. NMDS ordinations of fish species abundance data in a) São Simão and b) Três Marias Reservoirs by lacustrine and riverine zones.





Fig. 4. NMDS ordinations depicting fish assemblage differences among São Simão (S), Três Marias (T), and Volta Grande (V) Reservoirs.





Fig. 5. Trait comparisons between the same zones of São Simão, Três Marias and Volta Grande Reservoirs. Boxes are: 25th and 75th percentiles, whiskers are non-outlier ranges, and dots are medians. Letter differences mean statistically significant differences among reservoirs.



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