



Importance of dam-free tributaries for conserving fish biodiversity in Neotropical reservoirs

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ABSTRACT

Dams change the hydrological dynamics, patterns of biological production and distribution of organisms in space and time. In contrast, tributary rivers can function as source areas in reservoirs, since they harbor spawning and early development grounds for native fish species. Here, we analyze a time series of the first 14 years after the impoundment of the Porto Primavera Reservoir, a large reservoir with free tributaries in southeastern Brazil. To evaluate the impact of damming on the fish assemblage, we evaluated the abundance (catch per unit effort, CPUE) and α (species richness and Shannon-Wiener index) and β (Sørensen dissimilarity and turnover) diversity of four sites distributed along the reservoir. Overall, there was no decreasing trend in the α diversity and no increasing trend in the β diversity relative to the initial year or among the sites over time. Despite the expected disturbance in the fish assemblage at the lacustrine site, the sites located near the tributary mouths presented resistant fish assemblages, compensating the results of the overall assessment. We attribute this unusual variation in the ecological attributes to source-sink demographic dynamics, with the undammed tributaries as the source and the reservoir as the sink for native species. We highlight that the presence of these rivers minimized the expected trend towards biotic homogenization, and the preservation of the tributaries is imperative since they contribute to diversity maintenance in areas that are already impacted by damming. The inclusion of this agenda in environmental management programs and new impoundment plans will allow a balance between the demand for electricity production and the conservation of fish diversity.

1. Introduction

The impoundment of rivers causes the homogenization of fluvial dynamics by decreasing the intensity of floods and droughts and the interannual variation of flow (Poff et al., 2007). Moreover, impoundments fragment habitats, decrease river connectivity (Nilsson et al., 2005), and reduce fish access to nursery and feeding grounds (Winemiller et al., 2016). This anthropic process represents one of the most drastic habitat changes (Agostinho et al., 2008; Agostinho et al., 2016), since it modifies the natural hydrological dynamics, limnological variables, biological productivity patterns and the distribution of organisms in space and time (Nilsson et al., 2005). Such effects dramatically change many aspects of the native fish fauna, resulting in consequences to the abundance and composition of native fish by the reduction of species richness (Agostinho et al., 2007; Agostinho et al.,

2008; Agostinho et al., 2016). This mainly affects migratory species, impeding them from being able to migrate and complete their life cycle (Agostinho et al., 2016; Winemiller et al., 2016). On the other hand, some opportunistic and sedentary species, with a short life cycle and generalist feeding habits, are favored under these conditions and can proliferate (Agostinho et al., 2008; Agostinho et al., 2016). Furthermore, impoundments increase the homogenization of aquatic biota (Rahel, 2002; Olden & Poff, 2004; Vitule et al., 2009; Petesse & Petreire Jr, 2012; Vitule et al., 2012). This results from the interaction of three processes: the introduction of nonnative species, the elimination of native species and habitat changes, which facilitates the two previously listed processes (Rahel, 2002).

Despite the impacts caused by human activities and the consequent loss of biological diversity (Magurran & Dornelas, 2010), there is a trend of natural variation over time to a greater or lesser extent

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(Magurran et al., 2010; Magurran & Dornelas, 2010; Magurran & Henderson, 2010). This natural variation is important for community diversity maintenance (Magurran & Henderson, 2010) and occurs according to the environmental conditions, which reflect ecological and evolutionary processes (Magurran & Dornelas, 2010). Although it is well known that all ecological communities experience temporal variations, there is still little information about how these changes occur over time (Magurran & Henderson, 2010). Therefore, the challenge is to distinguish changes caused by natural processes from the anthropic ones (Magurran et al., 2010).

In this sense, long-term monitoring is indispensable because it allows the understanding of temporal changes in biodiversity, thus enabling the detection and assessment of the anthropogenic impacts underlying these processes (Magurran et al., 2010). In impacted environments such as dammed rivers, long-term studies are necessary for the determination of the major factors that influence the faunal structure (Říha et al., 2009). These studies also can provide information about fish fauna responses to perturbations over time and are necessary for management conservation measures (Gido et al., 2000). Additionally, long-term data allow the verification of hypotheses related to ecological succession processes and diversity-stability relationships (Magurran et al., 2010; Mellin et al., 2014).

In metacommunity models, where a large number of migratory species occupy diversified habitats, structurally distinct communities could provide different responses to environmental variations, since negative fluctuations in one community could be compensated by positive fluctuations in another, increasing the resilience of the whole metacommunity (Mellin et al., 2014). A set of demographic dynamics in a source-sink model where populations living in spatially heterogeneous environments select habitats based on differences in the environmental quality (Pulliam, 1988) could accomplish this kind of process. In this way, recent studies have demonstrated that tributaries could function as source areas in reservoirs, since they harbor spawning and early development grounds for fish assemblages (da Silva et al., 2015; Nunes et al., 2015; Angulo-Valencia et al., 2016; Ferreira et al., 2016; Kruk et al., 2017), which is essential for ichthyofauna conservation.

The Upper Paraná is one of the most dammed basins in the world (Agostinho et al., 2004) and suffers from the cumulative effects of changes in land use, pollution and nonnative species (Agostinho et al., 2008). With at least 150 large dams (Stevaux et al., 2009), the Upper Paraná is the most impounded and studied basin in the Neotropical region (Agostinho et al., 2008). However, little is known about the long-term effects of damming on fish α and β diversity. Especially in reservoirs with nonregulated tributaries that can play the role of source areas (Nunes et al., 2015; Angulo-Valencia et al., 2016; Ferreira et al., 2016), such information is important because it can support management decisions in order to conserve those tributaries.

The goal of this study was to evaluate the long-term effects of damming on the ichthyofauna structure of a large reservoir with tributaries with little or no regulation by assessing the α and β diversity trends of its fish assemblages over a period of 14 years. We expected that, due the presence of preserved tributaries with natural flood regimes, the tendency for α diversity to decrease and for β diversity to increase would be reduced, possibly minimizing the impact of damming on the fish assemblages.

2. Materials and methods

2.1. Study area

The Paraná River is ranked 10th in water discharge in the world and

is the second largest drainage basin of South America (Stevaux et al., 1997). The Upper Paraná comprises the upper third of the basin (Abell et al., 2008), with an area of 891,000 km², 10.5% of the total area of Brazil (Agostinho et al., 2008). It represents the upstream stretch above Sete Quedas Falls, which was flooded during the filling of the Itaipu Reservoir in 1982. This event induced a massive invasion of fish species from the Lower Paraná River (Júlio Jr. et al., 2009), resulting in biotic homogenization (Vitule et al., 2012). The Porto Primavera Reservoir is located on an alluvial floodplain in the Upper Paraná River, southeastern Brazil (Fig. 1). It was built for hydroelectric power generation and became operational in March 1999. With a length of 10,186 m, it is the longest dam in Brazil. The dam has a pool-weir-orifice fish passage (Makrakis et al., 2007; Wagner et al., 2012). The reservoir was filled in two stages; the first (elevation of 253 m) was completed in December 1998, and the second (elevation of 257 m) was completed in March 2001. The power plant operates in a run-of-the-river system with very small variations in the water level (< 0.4 m) and a long-term average discharge of 6981 m³·s⁻¹, with an average water residence time of 33.9 days. Based on area, Porto Primavera is the largest reservoir in the Paraná basin, with a length of 270 km, a surface area of 2040 km² and an average depth of 6.8 m; in addition, it drains a basin of 572,480 km² (Shibatta & Dias, 2006).

There are four major tributaries with low-level or no regulation that flow into the reservoir (Fig. 1). The Verde River (draining a basin of 24,184 km²; average discharge of 222 m³·s⁻¹) and the Pardo River (39,419 km²; 359 m³·s⁻¹) are on the right bank, and the Aguapeí River (13,196 km²; 98 m³·s⁻¹) and the Peixe River are on the left bank (10,769 km²; 84 m³·s⁻¹).

2.2. Samplings and data analysis

Quarterly samplings were performed at four locations (Fig. 1) from 1999 to 2012 (the coordinates and description of each site are presented in Table S1). The data from 2002 and 2010 were not used due to a lack of sampling standardization. Fish were collected with gillnets (30-to-200 mm mesh, see Table S2 for a detailed description of the fishing gear) set for 24 h at each sampling site.

Based on the abundance matrix of the individuals collected by each sampling, the catch per unit effort (CPUE) was generated from the number of individuals captured per 1000 m² of gillnet set for 24 h. The CPUE data were log₁₀ transformed to meet the assumptions of the parametric tests. All statistical analyses were performed using R (R Development Core Team, 2016). From the CPUE matrix grouped annually, we calculated the Shannon-Wiener (H') diversity index according to Magurran (2004). To standardize efforts across samplings, we used the rarefy function from the vegan package (Oksanen et al., 2016) to calculate species richness.

To assess the temporal trend in α diversity (using the rarefied species richness and Shannon-Wiener index as measures), abundance (log₁₀ CPUE) and β diversity, we used ordinary least squares (OLS) regressions (Magurran et al., 2015). The β diversity assesses the homogenization process (Magurran et al., 2015) and was measured as the Sørensen dissimilarity and its turnover component (Baselga, 2010), which were both calculated in relation to the first year of impoundment (1999) using the beta.pair function in the betapart package (Baselga & Orme, 2012). Next, we used the beta.multi-function from the betapart package to compute, for each year, the Sørensen dissimilarity for all sites. To verify differences in the trends among sites, the regressions were performed for each sampling site. Furthermore, we analyzed the trends in α diversity for the native and nonnative species separately.

For the temporal and spatial variance of the rarefied species richness, Shannon-Wiener index and abundance (log₁₀ CPUE), we

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