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Fish assemblages in Neotropical reservoirs: Colonization patterns, impacts and management

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ABSTRACT

Brazil has more than 700 large reservoirs distributed in all of the major river basins of South America. Most dams were constructed to produce electricity. Although these reservoirs favor the development of local and regional economies, they seriously impact the aquatic biota. An unavoidable consequence is the change in the composition and abundance of species, with the proliferation of some and reduction or even local extinction of others. The intensity and nature of these changes are related to peculiarities of the local biota and the location, morphometric and hydrological characteristics of the reservoir, dam operation and interactions with other uses of the basin, including other reservoirs. These impacts exhibit substantial spatiotemporal variations. The filling phase is marked by abrupt and intense changes in the key attributes of aquatic habitats, followed by predominantly heterotrophic processes, with possible thermal stratification and anoxic conditions. Fish richness increases soon after filling and decreases in subsequent years. Trophic depletion is expected, and diversity gradients are intensified toward more lentic stretches, the average length of fish decreases, and the fish fauna becomes dominated by species with sedentary strategies and/or parental care. The virtual absence of species with pre-adaptations to inhabit lentic areas of large reservoirs leads to a concentration of biomass in shallow littoral areas. Long-distance migratory species are the most affected, which include larger fish with high market value. Migratory species require different biotopes to fulfill their life cycles and strongly depend on the seasonal flood regime, which is altered due to dam operation. In this study, we discuss the details of these trends as well as the mitigation measures and management actions that are practiced in Brazil. We conclude that these actions have not promoted the conservation of fish; on the contrary, some of them have generated additional impacts. As a consequence, the conservation of Neotropical fish and aquatic resources is severely threatened.

1. Introduction

Impoundments lead to extreme changes in fluvial habitats, transforming rivers into semi-lentic systems. Animals and plants for which these new conditions are restrictive will have their populations drastically reduced. However, species that can complete their life cycle in the new environment and take advantage of the available food resources will achieve their full potential for proliferation (Agostinho et al., 2007a). The nature of and intensity with which the fluvial biota is altered by impoundments are highly variable among reservoirs and must be studied case by case.

The literature demonstrates that even reservoirs arranged in series in the same river, with unidirectional interactions from upstream to downstream, show distinct peculiarities in relation to the colonization process and the organization of assemblages (Agostinho and Gomes, 1997; Petesse and Petrere, 2012). The degree of alteration in the structure and dynamics of the local biota depends on several local and regional factors, such as morphometry of the catchment, discharge, patterns of water circulation, depth, habitat structure, species pool, surface area, the design of the dam and its operational procedures. Thus, a detailed understanding of

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the context of a particular reservoir is paramount for effective mitigation measures and/or management actions for the conservation of fish populations (Weithman and Haas, 1982). A manager should, based on local and regional studies, identify any alterations in the structure of the local fish assemblage and take action to avoid irreversible losses of regional biological diversity and/or natural resources as a consequence of river damming.

In general, the fish species most affected by impoundments are large in size, migrate and have high longevity (*k*-strategist). In contrast, a massive proliferation of primarily small-sized sedentary species (i.e. those that do not migrate) occurs, which have a high reproductive potential and short longevity (*r*-strategists) and for which the availability of food resources is high (Agostinho et al., 1999, 2008a; Hoeinghaus et al., 2009). Yet, sedentary species are also affected by hydrological alterations and tend to redistribute along the river/reservoir gradient (Araújo et al., 2013). In the inner areas of large reservoirs, fish assemblages are profoundly altered and composed of a few species with pre-adaptations to live in semi-lentic environments (Gomes and Miranda, 2001; Agostinho et al., 2007a).

Reservoirs are present in the main river basins in Brazil, and the principal purpose is the production of electricity. Although reservoirs are widespread in the country, their distribution is not homogeneous, e.g. the Upper Paraná River has half of the total impounded area and is one of the most regulated rivers in the world (Agostinho et al., 2008a). Even considering the specificity of the response of the biota to the impacts generated by each reservoir, some patterns can be described based on studies of dozens of reservoirs in Brazil. Therefore, the objective of this paper is to review the patterns of fish fauna once a reservoir is formed. First, we described the variation in fish assemblages over time, from the filling of the reservoir to the periods in which environmental and biotic conditions are rearranged and more stable. We categorized these variations into phases (heterotrophic, post-heterotrophic and trophic equilibrium), considering predicted alterations in productivity. Then, considering the phases, we described broad trends in fish abundance, species richness, pre-adaptations to pelagic environments, and variations in size and reproductive strategies. Finally, we evaluated management measures presently implemented to mitigate impacts caused by reservoirs on the Neotropical fish fauna, and we discuss opportunities for improvement as well as the existing knowledge gaps. As the Upper Paraná River basin is the most dammed in South America as well as the most studied, we used it as a model to achieve our goals every time an example was necessary.

2. Reservoirs and fish diversity

It is estimated that the number of large reservoirs (dams higher than 15 m; World Commission on Dams, 2000) in South America is greater than one thousand, and around 50% of them are located within Brazilian territory (Fig. 1). Thirty-seven percent of these reservoirs produce electricity. Although hydroelectric production in dams started in Brazil at the end of the XIX century (Marmelos Dam; Paraíba do Sul River; 1889), most of the dams were constructed in the second half of the XX century. With regard to the area inundated by all reservoirs (>36,000 km^2), almost half of it (47%) is located in the Paraná River, followed by the São Francisco and Tocantins Rivers (Agostinho et al., 2007a). As potential areas for the installation of new dams in these basins are depleted, there is a motivation to extend the construction of dams to the Amazon basin, especially in the Madeira, Tapajós and Xingú Rivers (Castello et al., 2013), in addition to the Andean tributaries (Finer and Jenkins, 2012).

Ichthyofaunal monitoring surveys conducted in 77 reservoirs of the main river basins in Brazil (Agostinho et al., 2007a) showed that fish diversity in the impounded area is very low. This study showed that 85% of the reservoirs contain fewer than 40 fish species; reservoirs with more than 120 fish species are rare and usually young. Forty species can be considered very low if we consider that 80% of these reservoirs have areas greater than 10 km^2 and that a single floodplain lake of much smaller dimensions can harbor from 30 species (Paraná River basin; Oliveira et al., 2001) up to 99 species (Amazon River basin; Pouilly et al., 2004). In addition, streams and rivers in the Neotropical region usually present hundreds of species (Lowe-McConnell, 1999; Agostinho et al., 2007b), e.g. a stream less than 10 km long had 108 species (Cancela Stream; Cuiabá River basin; Mendes et al., 2008). However, species richness in reservoirs varies with their surface area, age and, primarily, the basin where they are located. Thus, reservoirs located in the Amazon basin with areas greater than 500 km^2 and less than 15 years old contain more species than other reservoirs of similar dimensions and age that are located in other Neotropical basins. For example, more than 200 fish species were found in the São Salvador Reservoir, Tocantins River (104 km^2; Amazon basin), in the first years after impoundment (Limnobios, 2014). In contrast, 34 species were recorded in Segredo Reservoir (85 km^2; Iguaçu River; Agostinho and Gomes, 1997) and 107 in Itaipu Reservoir (1350 km^2; Agostinho et al., 1992) in a similar time lag. Furthermore, in Capivara Reservoir (576 km^2; Paranapanema River; Orsi and Britton, 2014) and Salto Osório (63 km^2; Iguaçu River; Baumgartner et al., 2006), both impoundments are older than 30 years, were recorded 41 and 23 species, respectively. In fact, there is a consistent decrease in species richness over time (Mol et al., 2007; Orsi and Britton, 2014), i.e. the number of species averages 20 in Neotropical reservoirs older than 20 years (Agostinho et al., 2007a). This conspicuous decline in species richness is the result of environmental filters that gradually remove pre-existing fluvial species; the new assemblages are composed basically of species that present pre-adaptations to thrive in standing waters, with lower dependence on fluvial environments and habitat heterogeneity (Gomes and Miranda, 2001).

3. Variation in fish abundance

The large release of nutrients resulting from the decomposition of organic matter in the flooded area during a reservoir's early years and the subsequent reduction of nutrients result in wide fluctuations in production throughout a reservoir's history. The nutrient input increases the production of all trophic levels during a period known as the "trophic upsurge period" (Kimmel and Groeger, 1986; Kimmel et al., 1990). This heterotrophic period begins in the filling phase, which is marked by rapid and profound alterations in the water's physical and chemical characteristics. During the filling phase, vertical patterns resulting from the expansion of the water column, lentic characteristics and thermal stratification, which affect the sedimentation rate, nutrient cycling and the distribution of the biota, are added to the predominant transport vector of the river phase. The high concentration of nutrients initially due to the pulses of litter decomposition and the release of nutrients from the inundated soil, followed by the decomposition of the leaves of the inundated vegetation (Cunha-Santino et al., 2013), may lead to stressful conditions for the aquatic biota (e.g. low concentrations of dissolved oxygen, thermal stress, and low pH), especially near the bottom (Agostinho et al., 2008a).

For example, studies conducted in Corumbá Reservoir (located in the Upper Paraná River basin) showed a sharp increment in primary production after an initial period of increased water transparency (Secchi depth) due to sedimentation. Thus, the phytoplankton productivity that was below 0.17 mgO^2 l^{-1} in the first 10