



# 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.

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## 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

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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

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

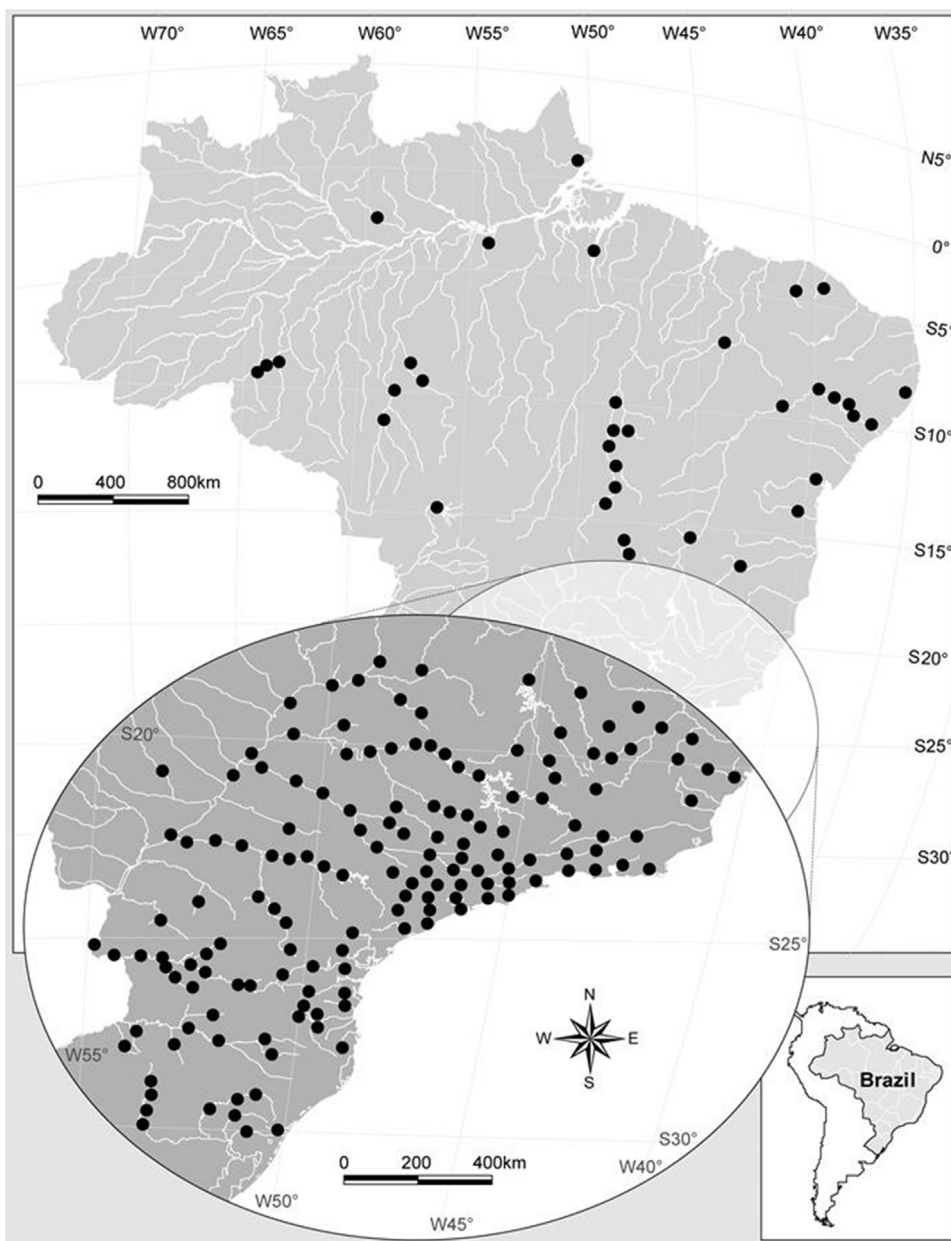
It is estimated that the number of large reservoirs (dams higher than 15 m; World Commission on Dams, 2000) in South America is greater than one thousand, and around 50% of them are located within Brazilian territory (Fig. 1). Thirty-seven percent of these reservoirs produce electricity. Although hydroelectric 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<sup>2</sup>), 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<sup>2</sup> 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<sup>2</sup> 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<sup>2</sup>; Amazon basin), in the first years after impoundment (Limnobiós, 2014). In contrast, 34 species were recorded in Segredo Reservoir (85 km<sup>2</sup>; Iguazu River; Agostinho and Gomes, 1997) and 107 in Itaipu Reservoir (1350 km<sup>2</sup>; Agostinho et al., 1992) in a similar time lag. Furthermore, in Capivara Reservoir (576 km<sup>2</sup>; Paranapanema River; Orsi and Britton, 2014) and Salto Osório (63 km<sup>2</sup>; Iguazu 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<sub>2</sub> l<sup>-1</sup> in the first 10



**Fig. 1.** Map showing the distribution of hydroelectric reservoirs in the main river basins of Brazil (Paraná River basin is highlighted due to the high number of dams).

days after the reservoir began filling, reached  $0.89 \text{ mgO}_2 \text{ l}^{-1}$  after 39 days (Agostinho et al., 1999). Therefore, due to this increase in primary productivity, it is common a marked increase in the fish abundance in the inner areas of the reservoir (Fig. 2). The increase in nutrient concentration is also responsible for the intense proliferation of floating macrophytes, as verified in Tucuruí Reservoir, located in the Tocantins River basin (Tundisi, 1994). The presence of an anoxic layer during filling is also an event common to tropical reservoirs and can last for months or even years. However, after filling, a reduction in fertility due to the loss of organic matter by oxidation, sedimentation, biological assimilation and exportation is common (Cunha-Santino et al., 2013); this period is known as the “post-heterotrophic” or “depression” period (Fig. 2).

Once the phase of high productivity is over, fish species begin to adjust to the new environment (Petrere, 1996). The high fish abundance verified during this phase tends to decrease in the reservoir over time (Fig. 2). This decrease will continue until the reservoir reaches a certain trophic equilibrium (at an unknown time), after

which the abundance of fish tends to be less variable but usually higher than in the river before the dam was constructed.

To exemplify this decrease in productivity over time, we used sample data collected in the Itaipu Reservoir (Paraná River basin) from 1983 (one year after filling in 1982) to 1997 (15 years after filling). In this reservoir, there was a clear temporal decrease in fish abundance in number (catch per unit effort, CPUE—number of individuals) and in weight (CPUE—kg), especially in the more internal areas (lacustrine zone). Note that the decreased abundance was from two- to four-fold in number and weight, respectively (Fig. 3). A clear decrease in fish abundance was noted for all zones (it was less noticeable in the transitional zone), but a sharper decrease was observed in the inner areas (lacustrine zone) of the reservoir. Fish biomass showed the same trends (Fig. 3). These results demonstrate that the degree of the impact of the impoundment on fish abundance or biomass has a longitudinal gradient. Orsi and Britton (2014) also reported a sharp decline in native fish abundance 40 years after the formation of Capivara Reservoir, which involved

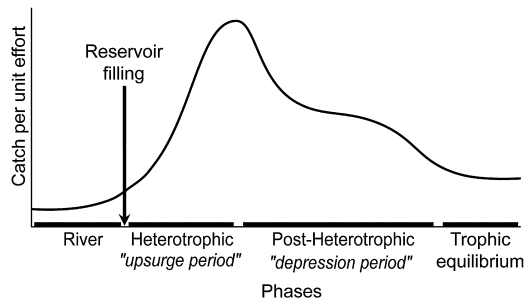


Fig. 2. Trends in fish abundance (catch per unit of effort—CPUE) over time in Neotropical reservoirs (modified from Petrere, 1996; Agostinho et al., 2007a).

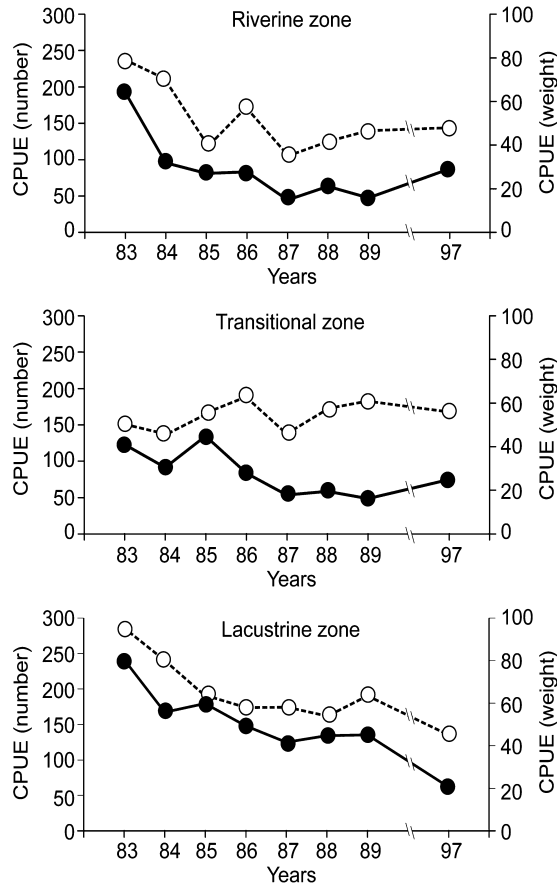


Fig. 3. Variations in the catch per unit effort (CPUE; individuals and weight for 1000 m<sup>2</sup> of gillnet in 24 h) in the longitudinal gradient of the Itaipu Reservoir from 1983 (one year after the impoundment) to 1997 (white circles: CPUE in numbers; black circles: CPUE in weight).

the loss of 27 species; at present, non-native opportunistic species dominate the assemblage in Capivara.

#### 4. Fish colonization during the filling phase

During reservoir filling, the patterns of vertical colonization of fish are associated with thermal stratification, an increase in depth and a sharp decrease or even the virtual absence of dissolved oxygen. All these factors impose changes on fish distribution patterns. The increase in water volume and the reduction in water flow lead to an increase in the area available for colonization (Agostinho et al., 2008a; Wang et al., 2013). The lack of oxygen in the deeper strata (in the bathypelagic zone) may lead species to disperse in vertical and horizontal directions or even upstream, far from the lacustrine

environment. Therefore, the changes in the physical and chemical characteristics of the water due to the beginning of reservoir filling may act as environmental filters, selecting for ecological traits such as trophic guilds, reproductive strategies and an alteration of the affinity for habitats (fidelity), which determine the success of colonization by a particular species. Species that successfully colonize a reservoir have the ability to search for adequate environments, such as lotic tributaries or even the littoral areas (Agostinho et al., 2007a), as well as those that develop strategies different from those exhibited in the previous lotic environment (Kubečka, 1993). Species with pre-adaptations to live in lacustrine environments are obviously selected to compose the new assemblages (Fernando and Holcik, 1991; Gomes and Miranda, 2001).

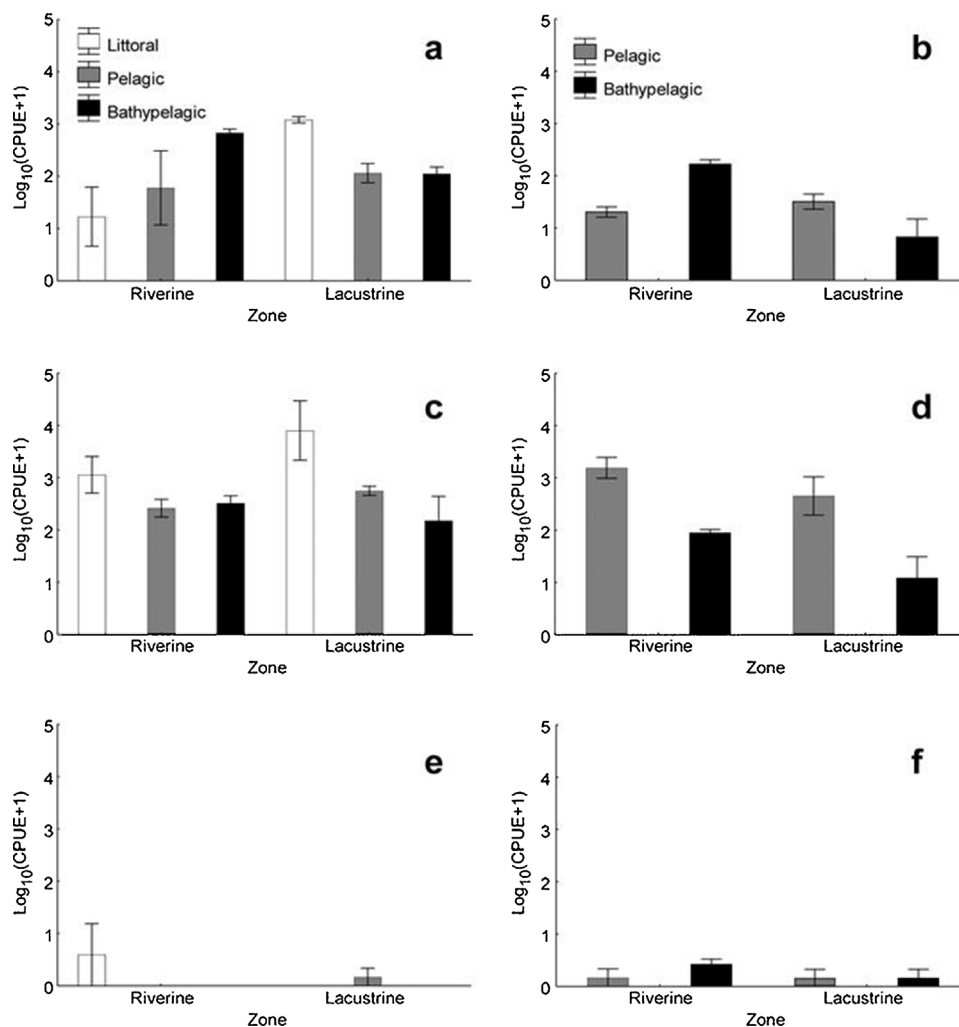
Colonization during the filling of the Salto Caxias (Iguaçu River Basin) and Corumbá (upper Paraná River Basin) reservoirs exemplifies the patterns of occupation of the new floodable area. To study this phenomenon, we categorized the fish species according to habitat preference (benthonic, benthopelagic and pelagic) and capture location in relation to the longitudinal gradient (riverine and lacustrine zones) and habitat (littoral, pelagic or bathypelagic). During the filling phase of these reservoirs, a greater abundance of benthonic species was observed in the littoral (Salto Caxias Reservoir—two-way ANOVA; Interaction, Zones × Habitat Type;  $F_{2,6} = 5.99$ ,  $p = 0.037$ ; Fig. 4a) and pelagic habitats (Corumbá—two-way ANOVA; Interaction Zones × Habitat Type;  $F_{1,8} = 7.90$ ,  $p = 0.023$ ; Fig. 4b), respectively. In the riverine zone, as expected, we found the opposite pattern, with benthonic species occupying deeper strata. A similar pattern was observed for benthopelagic fish, with a greater capture rate in the littoral ( $F_{2,6} = 5.98$ ,  $p = 0.037$ ; Fig. 4c) and pelagic ( $F_{1,8} = 14.00$ ,  $p = 0.006$ ; Fig. 4d) areas. In contrast, pelagic species were captured in very low abundance in both reservoirs and did not show any differences in abundance according to the zone and habitat type (all possible results with  $p > 0.05$ ). This result is due to the existence of few pelagic species in the Neotropical region (Gomes and Miranda, 2001; Araújo et al., 2013).

The results presented for Salto Caxias and Corumbá reveal low habitat fidelity for benthonic species in the inner part of the reservoirs during the filling phase. In fact, fish use a habitat according to physiological convenience, which depends primarily on the concentration of dissolved oxygen and water temperature (Prchalová et al., 2009); their vertical distribution is apparently driven by restrictions related to thermal and dissolved oxygen stratification in the reservoir. This stratification, during the first year after impoundment, can lead to a chaotic pattern of species occupying habitats in which they were previously not abundant (e.g. benthonic species abundant in the littoral or pelagic zones of reservoirs). Yet, the reassembly of fish species following changes in environmental conditions may occur within the first years after impoundment, creating new diversity patterns along the reservoir (Araújo et al., 2013).

After the filling of the reservoir and the beginning of dam operation, critical conditions of dissolved oxygen may persist, depending on the extension of the anoxic layer and the vertical position of the water intake for turbines and spillway. These conditions may lead to a narrow oxygenated layer, resulting in instability due to wind and temperature changes, which can culminate in fish mortality concentrated near the margins or the surface (Agostinho et al., 1999).

#### 5. Heterotrophic and trophic equilibrium phases

There is evidence from several Neotropical reservoirs that the species richness increases immediately after the filling phase (Fig. 5a and b). This increase in species richness is followed by an



**Fig. 4.** Mean catch per unit of effort (CPUE;  $\log_{10}x+1$  transformed; vertical lines are the standard errors) for the species categorized as benthonic (a and b), benthopelagic (c and d) and pelagic (e and f) among the distinct reservoir zones (riverine and lacustrine) and types of habitats (littoral, pelagic and bathypelagic). (a), (c) and (e) Filling phase of the Salto Caxias Reservoir (1998); (b), (d) and (f) Filling phase of the Corumbá Reservoir (1996). Note that in Corumbá, samples were taken only from the pelagic and bathypelagic regions.

increase in the abundance of fish (Fig. 5c), which is common during the trophic upsurge period. However, the magnitude of the increase in abundance varies among species in a new reservoir, and the dominance of certain species with regard to abundance (low evenness) causes a continuous decreasing in the species diversity measured by the Shannon index (Fig. 5a).

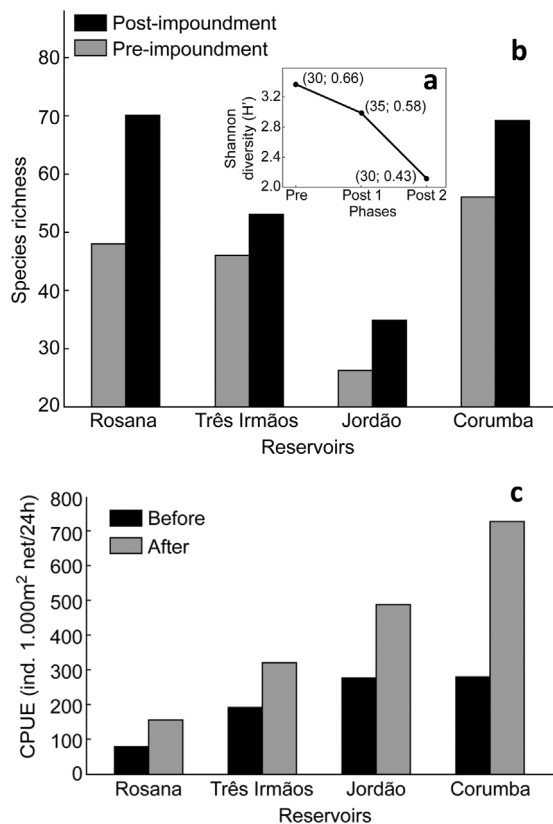
An increase in species richness is expected during filling because different biotopes, such as wetlands, isolated lakes, lakes permanently or seasonally connected to the river channel and adjacent tributaries (river, streams and creeks), are incorporated into the new environment. Species associated with these habitats are incorporated into the fish fauna of the reservoir, which consequently increases species richness. The number of species present in a recent reservoir should not be much lower than the sum of the previously existing species in the flooded habitats. However, this tendency for high richness does not last long (Fig. 5a). The reasons for its decrease have been previously discussed and appear to be related to environmental filters, species sorting and the accommodation of the fish fauna to the new environment, in addition to trophic depletion and the absence of truly lacustrine species (Agostinho et al., 2007a). Theoretically, the drop in species richness results from the movement of fish out of the reservoir (upstream or tributaries) in search of better conditions to complete their life

cycle (Lowe-McConnell, 1999; Agostinho et al., 2007b; Araújo et al., 2013; Franssen and Tobler, 2013).

Abundance follows a similar trend. Upon filling of a reservoir, fish abundance increases (Fig. 5c) due to the high input of terrestrial organic matter, which leads to increased food availability in the entire reservoir, especially for omnivorous, herbivorous and insectivorous species. The proliferation of these species causes an increase in food availability for piscivores. However, at the end of the heterotrophic phase (see Fig. 2), the abundance of fish decreases following the decrease in primary production (see Section 3).

## 6. Constraints and pre-adaptations

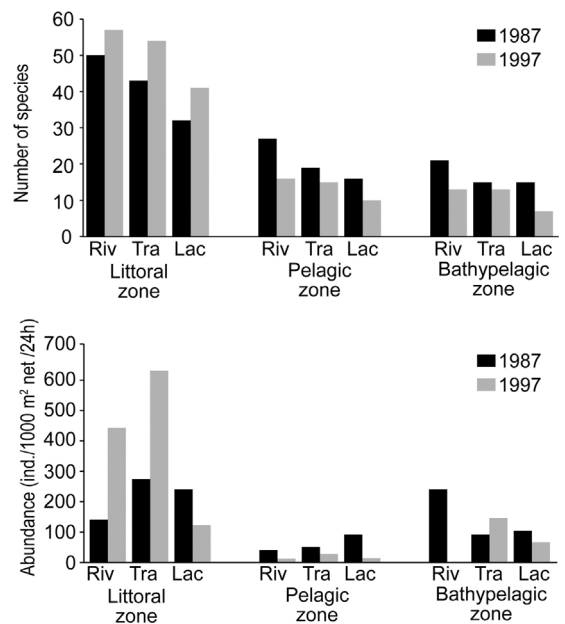
The virtual absence of natural lakes in Brazil (excepting those associated with fluvial corridors) and the consequent scarcity of species with pre-adaptations to occupy open areas of reservoirs, allied with the longitudinal gradients related to the processes of transport and deposition (e.g. transparency and nutrient loads), leads to a heterogeneous pattern of the occupation of the new environment. The most important characteristics of truly pelagic species are their short food chains, high fecundity, pelagic adaptations, and short life cycle, as exhibited by the Clupeiformes *Stolothrissa tanganicae* (in Africa) and *Dorosoma cepedianum* (in



**Fig. 5.** Variations in the Shannon diversity index ((a) before and two periods after the formation of Jordão Reservoir; numbers in brackets are species richness and evenness), species richness ((b) before and two periods after the formation of four reservoirs in the Upper Paraná River basin) and abundance ((c) catch per unit effort—CPUE ind. 1000 m<sup>2</sup> gillnet in 24 h before and after the formation of four reservoirs in the Upper Paraná River basin). Modified from Agostinho et al., (2007a).

North America) (Gomes and Miranda, 2001). Thus, in reservoirs, the colonization success of the species depends on their pre-adaptations. In the Upper Paraná River, Gomes and Miranda (2001) described that, among the 220 species they analyzed, only approximately 5% were considered as lacustrine adapted (i.e. *Plagioscion squamosissimus*, *Hypophthalmus edentatus*).

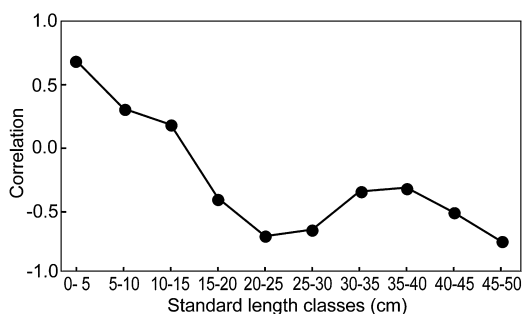
In general, the pelagic areas of the Upper Paraná Reservoirs are inhabited by few fish species, such as the piscivores *P. squamosissimus* (a sciaenid introduced from the Amazon basin) and *Rhaphiodon vulpinus*, and the planktivores *H. edentatus* and *Hemiodus orthonops* (the latter was recently introduced through the fish passage at Itaipu Dam; Julio et al., 2009; Agostinho et al., 2015). For example, the success of *P. squamosissimus* may be attributed to its reproductive strategy (Agostinho et al., 1999). This species produces small, pelagic (Fontenele and Peixoto, 1978), and buoyant eggs, spawned in several batches early in the reproductive period (matching with food availability), and the larvae are also pelagic (Nakatani et al., 1993). Other important characteristics are morphological and related to diet and food capture (Mérona and Vigouroux, 2012). Therefore, the low number and uneven distribution of large and deep natural lakes in the Neotropical region led to the complete absence of a truly pelagic and deep bottom-dwelling species that are pre-adapted to occupy open areas of large reservoirs. In general, species that successfully colonize reservoirs are those that inhabit shallow floodplain lakes, which usually occupy the littoral region of reservoirs (Casatti et al., 2003; Pelicice et al., 2005; Agostinho et al., 2007a). Thus, the greatest abundance of fish species and diversity are found in the littoral region.



**Fig. 6.** Spatial (longitudinal, lateral and vertical gradients) and temporal gradients in species richness and abundance of fish in the Itaipu Reservoir (Riv = Riverine; Tra = Transitional; Lac = Lacustrine Source: Agostinho et al., 1999).

This pattern can be verified in the Itaipu Reservoir five (1987) and 15 (1997) years after its formation (Fig. 6). Species richness and the abundance of fish were considerably higher in the littoral zone, and this pattern tended to increase over time. After 15 years, 64 out of the 67 species captured in gillnets in the Itaipu were in the littoral zone, whereas in the pelagic and bathypelagic zones, this number was 22 and 20, respectively (Fig. 6). The proportions of abundance among the zones were 19.4: 1.1: 1.0, respectively (Fig. 6). Moreover, the riverine zone, in which the processes of transport predominate over the depositional processes, has higher species richness but is not the most productive zone (Kimmel et al., 1990; Agostinho et al., 2007a). The upper third of the Itaipu Reservoir harbors all of the species recorded in the two more internal thirds in addition to those typical to the lotic stretch upstream (the river). The higher similarities in flow with the original river, the lower depth, the input of allochthonous matter, and predator attraction due the higher abundance of prey species in relation to the upstream stretch may explain this pattern (Agostinho et al., 2007a; Araújo et al., 2013).

Reproduction, due to its more conservative nature, imposes limitations on the occupation of a new reservoir by the river fish fauna; it is probably the main constraint limiting fish fauna reassembly. In reservoirs, it is expected that species with higher plasticity in the selection of spawning sites have more success in the colonization of these environments. Species that demand particular habitats (e.g. tributaries) or environmental triggers (e.g. hydrological variation) may not complete the reproductive process, mainly during the years following the impoundment. Medeiros et al. (2014) reported failed reproduction for Hemiodontidae after the formation of Lajeado Reservoir, Tocantins River, an event that changed energy allocation patterns for these species. However, most of the species that inhabit reservoirs search for lateral tributaries, upstream stretches or other lotic areas for spawning, indicating the dependence on riverine habitats to complete their life cycles. In the first years after the formation of a reservoir, internal fecundation appears to be a successful strategy. However, in older reservoirs, species with more elaborate reproductive strategies (usually cichlids with complex mating choice, nest-building and parental care) have greater occupation success, along with small-sized



**Fig. 7.** Pearson correlation coefficient between fish abundance in several size classes and the age of the Itaipu Reservoir (1983–1997) (Source: Agostinho et al., 1999).

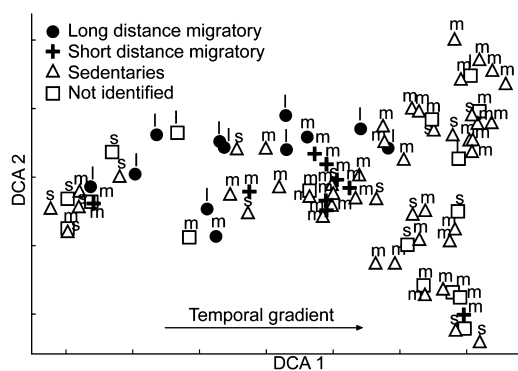
opportunistic characids that colonize shallow shores (Agostinho et al., 2007a).

A clear consequence of the species sorting process is the reduction in the mean size of the individuals comprising a fish assemblage that occupies a reservoir in relation to those that originally comprised the original river. This trend is important because of its implications concerning the profitability of fisheries (Agostinho et al., 2008a), and it is clearly seen in the size distribution of the fish captured in experimental fisheries in the Itaipu Reservoir from 1983 to 1997 (Fig. 7). The Pearson correlation between the number of fish in several size classes and the reservoir age decreased (or was negative) in the greater size classes, with high positive values for smaller fish. The main reasons for these findings are: (i) long-distance migratory species, usually large-sized, move out of the reservoir; (ii) small-sized species (usually *r*-strategists) are the tolerant species or those with pre-adaptations to thrive in the lentic environment, especially in the littoral zone, where they are abundant (Agostinho et al., 1999; Hoeinghaus et al., 2009). As a consequence, the new fish fauna is essentially composed of species with small body sizes that occupy shallow littoral areas of the reservoir.

## 7. Fish assemblage stabilization

The time span after reservoir closure that the fish community structure requires for a certain degree of stability varies widely, and no consensus concerning this time span exists in the literature (Petere, 1996). There are evidences of stabilization of the fish abundance and species richness between 15 and 40 years after a reservoir is formed (Mol et al., 2007; Orsi and Britton, 2014). Several factors may influence this time, such as latitude, hydraulic retention time, morphometry, fish fauna composition before damming, catchment area, position in the basin, the presence of large tributaries, and the design and operation of the dam (Agostinho et al., 2007a).

Patterns of dam operation and fluctuations in the water level of the reservoir may cause a constant perturbation, decreasing the potential for the fish community to reach stability. These constant perturbations induce oscillations in the abundance of *r*-strategist species. As noted above, periodic/seasonal species such as long-distance migratory species abandon the reservoir area. Therefore, the fish fauna of these reservoirs, over time, will be dominated by opportunistic (*r*-strategist) sedentary species and/or the ones that develop parental care (*k*-strategist). A detrended correspondence analysis (DCA) applied to summarize the data on fish life strategies in the Itaipu Reservoir (Agostinho et al., 1999) serves as an example. In the ordination (Fig. 8), long-distance migratory and large-sized species (standard length— $L_s > 50$  cm) were registered in the reservoir in the first years after impoundment. The opposite trend was verified for sedentary and small-sized species ( $L_s = 20$  to 50 cm),



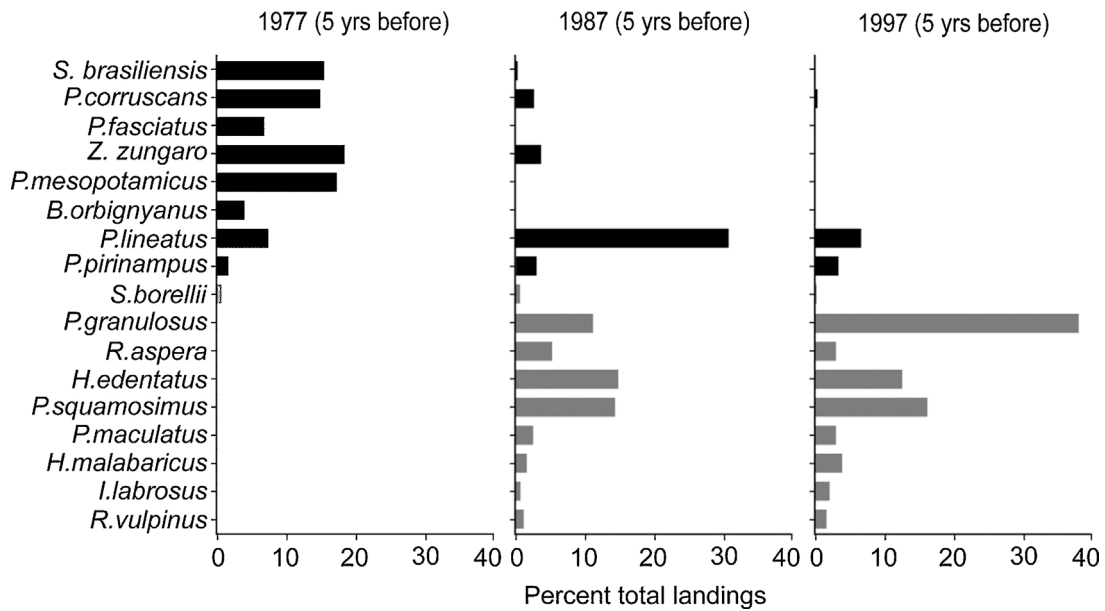
**Fig. 8.** Ordination from the detrended correspondence analysis (DCA; Axis 1 and 2—DCA1 and DCA2) applied to summarize the data on fish life strategies collected in the Itaipu Reservoir ( $S$  = small-sized species,  $L_s = 20$  cm;  $m$  = median-sized species,  $L_s = 20$ –50 cm;  $l$  = large-sized species,  $L_s > 50$  cm; adapted from Agostinho et al., 1999).

which were the only group of species captured at the end of the study (Fig. 8).

Changes in the mean size of the fish fauna after reservoir formation, as noted above, are mainly a result of the evasion of migratory species. These species are generally large-sized carnivorous or herbivorous fish and are the most preferable for human consumption, therefore demanding a higher market value. Monitoring of the artisanal (commercial) fishery conducted in the Itaipu Reservoir revealed the changes in the composition of landed fish with reservoir aging (Hoeinghaus et al., 2009). Before the construction of the Itaipu Dam, most captured species were large, migratory fish (Fig. 9). Five years after the reservoir formation, only one migratory species captured prior to the dam construction presented high abundance, but this species was a detritivore (*Curimba*, *Prochilodus lineatus*). Fifteen years after the reservoir formation, the artisanal fishery was essentially maintained by non-migratory or non-native species with low market values. A lotic environment and the blockage of migration routes are critical aspects for the maintenance of migratory species stocks in reservoirs, and the replacement of migratory species by coarse fish and usually less valuable causes substantial losses to the fishing industry. These changes clearly illustrate the aging process of the reservoir, in which the river system develops into a new and different stable state after impoundment, with different productivity levels, species composition, distribution, biomass and services for society. Future research must investigate the time span to reach this new state, and the factors responsible for oscillations and stabilization in the structure of the fish fauna.

## 8. Management and impact mitigation

The search for measures to mitigate impacts caused by dams and associated reservoirs on fish diversity and fish stocks in Brazil began with the construction of the first hydroelectric reservoirs. The first action taken was the construction of the fish ladder in the Itaipava Dam (Pardo River, Upper Paraná River basin) at the beginning of the last century. After that initiative, the history of management in Brazil encompassed several phases, with emphasis on fish stocking, fish farming in cages (in the reservoirs), and fishery control. The results obtained after a century of management were insignificant, leaving key questions unanswered and generating great controversy regarding the effects of the fisheries management strategies. However, these results and the controversy are due to (i) the still incipient knowledge about the Neotropical fish fauna, which is characterized by high diversity level in different scales; (ii) the absence or inadequate monitoring of the results of



**Fig. 9.** Decade tendencies of the dominant species in the landings of the artisanal fishery conducted in the Paraná River before and after the formation of the Itaipu Reservoir. The years presented are five years before the reservoir was formed and five and 15 years after the formation of the reservoir (adapted from Agostinho et al., 2007a).

the implemented actions; (iii) the eminently political nature of the management decisions, which should be essentially technical; (iv) insufficient knowledge about the problems to be solved, which led to a lack of clarity in the objectives of management actions; and (v) the naïve belief that impacts caused by impoundments can be reversed or minimized with simple management actions or copied from other part of the world.

Concerns with impoundment impacts on migratory species populations led to the recommendation to construct fish passages in the dams. This action attempted to facilitate the transit of fish to their spawning or feeding sites or the dispersal of juvenile fish to downstream stretches of the basin. The installation of these passages was mandatory for decades (Decree 4390 of 1928), and it is still mandatory in some Brazilian states. However, the construction requirements and the use of standardized protocols to install fish passages, whose performance depends on the interaction between their technical characteristics and the nature of the local ichthyofauna, were at high risk of failure, wasting financial resources, effort and opportunity (Agostinho et al., 2002; Pelicice and Agostinho, 2008; Pompeu et al., 2012). In fact, some fish passages were built immediately upstream of natural barriers that fish historically did not cross (Charlier, 1957). Other passages were highly selective, allowing the passage of large numbers of sedentary species and restricting the passage of the migratory species (Agostinho et al., 2007b; Makrakis et al., 2007a). In addition, invasive species previously limited by natural barriers have been reported to be greatly dispersed along river channels, as the case of the Itaipu Dam in the Paraná River, where the Piracema Canal is located (Julio et al., 2009; Makrakis et al., 2007b; Agostinho et al., 2015). In this case, the Itaipu Reservoir, filled in 1982, covered the Sete Quedas Falls, which was the limit for the distribution of several species, separating two distinct ichthyofauna provinces, the upper and the middle Paraná (Bonetto, 1986). After the Itaipu Reservoir was completely filled, several species were able to reach the upper part of the basin (Julio et al., 2009). Some of these species became abundant and replaced native congeneric species (Agostinho, 2003; Alexandre et al., 2004). During the following 20 years, approximately 17 species remained restricted to the stretch downstream from the Itaipu Dam. However, after the Canal de Piracema (a natural-like fish passage) started operation, other species were able

to reach the reservoir and dispersed to the upstream stretches of the watershed (Makrakis et al., 2007a; Julio et al., 2009; Vitule et al., 2012). An emblematic example was *H. orthonops*, absent from the upper Paraná River Basin. The invasion of this species was noteworthy for both its fast colonization of the new environment and for its abundance, reaching approximately 8% of the total catch at the upstream plain, in less than five years (Agostinho et al., 2015).

However, effective monitoring of the performance of these passages began only in the 2000s; even though fishways have been installed for a century. Yet, most of the current studies are restricted to monitoring species in the fish passage (fish ladders and fish elevators) with no consideration of the availability of adequate habitats for the species in the upstream stretches or in the region. Tagging studies on fish movements are recent (Hahn et al., 2007; Fontes et al., 2012; Wagner et al., 2012), and these studies have not eliminated the controversies regarding the adequacy and the efficiency of fish passages. The controversial aspect on the fish passage issue refers mainly to its simplicity and convenience for management programs that are mandatory in Brazil, but with low significance for conservation, i.e. aiding recruitment of migratory fish (Pelicice and Agostinho, 2008; Pompeu et al., 2012).

Other relevant aspects that should be considered in discussions on fish passages are their high selectivity (Agostinho et al., 2007d), the difficulty in controlling which species go through the passage (Pompeu et al., 2012), and the absence of downstream movement of adults and their offspring (Agostinho et al., 2007c, 2011; Suzuki et al., 2011; Pelicice and Agostinho, 2012). Solutions to the existing bottlenecks concerning recommendations of fish passages as a tool to mitigate impacts on migratory species must address the following issues: (i) whether the passages are efficient to attract fish and to allow free movements; (ii) whether the reservoirs represent a barrier to downstream movement of adult fish or to the drift of their eggs and larvae (Agostinho et al., 2007c; Pelicice et al., in press), (iii) whether long-distance migratory species have distinct behaviors and the swimming ability to be attracted to and to overcome the water flow in a fish passage; (iv) whether the passage is safe, with low rates of injury or predation (Agostinho et al., 2012), (v) whether clear objectives exist (e.g. genetic and/or demographic) to justify the use of fish passes, and (vi) whether the regional context



(i.e. distribution of critical habitats) supports the use of fishways to achieve conservation goals (Pelicice and Agostinho, 2008; Pompeu et al., 2012). While these aspects are neglected, the decision on the construction of fish passages will remain nebulous, with the risk of causing further impacts and complicating alternative conservation efforts.

Another controversial management action has been fish stocking. The first stocking initiatives were conducted with non-native species in northeastern Brazil and were successful in producing self-sustaining populations and improving fishing yields (Pava et al., 1994). This experience, especially with non-native species, spread to other regions of Brazil and was the main fishery management activity conducted by the Brazilian fishery-related institutions and by power companies. Until 1990, non-native species were emphasized in stocking programs developed in southeastern and southern Brazil. Some of the stocked non-native species were successful colonizers and are currently widespread in many basins (e.g. silver croaker *P. squamosissimus*; peacock basses *Cichla* spp.). Other species were successful in some reservoirs, where they appear in high abundance (e.g. tilapias—mainly *Oreochromis niloticus*, oscar *Astronotus ocellatus*, and freshwater sardine *Triporthus angulatus*). Although stocking activities currently emphasize native species, monitoring of commercial (artisanal) fishery outputs shows that stocking has not been efficient and might even represent an additional source of impacts (Agostinho et al., 2004, 2010). There are no relationship between stocking efforts and captures (landed fish) in artisanal fisheries in the reservoirs of southeastern and southern Brazil, where stocking was more intense. Some of the stocked species were never captured in the fisheries (AES-Tietê, 2007).

Stocking programs were historically conducted based on a precarious knowledge of the system to be managed, of the species to be released, and of the real need for the action. In addition, inexperience regarding how to conduct stocking (which species, the necessary quantities, the appropriate location, the size of the fish, and the time of release, among others) led to the practice of “trial and error.” Furthermore, stocking has been conducted without monitoring and without learning from the past actions, which can be helpful in avoiding future mistakes (Gomes et al., 2004; Agostinho et al., 2007a; Pelicice et al., 2009). For example, knowledge of the carrying capacity of the receptor environment and the size of wild stocks are fundamental assumptions in stocking for supplementation (Coxw, 1999), and such knowledge has been ignored in the stocking programs conducted in Brazil. Additionally, the processes used to rear fish for stocking programs are frequently the same used to produce fish for farming; in fact, fishes for both purposes have been reared together in fish farms. Thus, by ignoring the genetic quality of the brooders and other possible negative impacts on natural populations, stocking became a potential and constant threat to local populations and to the fishery itself, although such consequences were never empirically studied (Agostinho et al., 2010). It should be highlighted that stocking programs are supported by society, based on the naïve belief that fish populations were impacted, declined and must be recomposed in the reservoirs; stocking, in this sense, is a valid compensation or mitigation measure to address the impact of impoundments on fish diversity and fishery resources (Agostinho et al., 2007a). This is a common-sense explanation used in legislative initiatives to make stocking mandatory in the entire country, recently approved in Law Project 5989-09 (Lima et al., 2012; Pelicice et al., 2014). Ideally, stocking strategies should consider (i) the need for stocking, based on detailed information about the environment, the target species, and the intensity of the exploration; (ii) an understanding of the processes that drove the wild stock to depletion; (iii) the establishment of clear and quantifiable objectives; (iv) the capacity to rear and distribute fries with a genetic quality equivalent to the wild

stock (Flagg and Nash, 1999); (v) the compatibility of the quantity of fish, size, place and timing of the release with the distribution and structure of natural populations (Molony et al., 2003); and (vi) monitoring of the stocking and wild populations. In fact, monitoring programs should be an integral and indissoluble component of stocking, and the results obtained should be the base for adjusting or even halting the procedures.

Aquaculture, in a strict sense, is not considered a management activity destined to mitigate impoundment impacts. However, aquaculture has been conducted under the argument that it minimizes fishing pressure on wild stocks, either by the involvement of the fishermen in production activities (farming) or by a reduction in the demand for wild fish (Agostinho et al., 2007a). Although considered an important food production activity, aquaculture, as any other production method, affects the environment with an intensity that varies according to the type (intensive or extensive) and the species farmed. Such impacts are evident in the intensive farming conducted in caging nets installed in Brazilian reservoirs, which has received subsidies from the governmental financial agencies related to fish production (Agostinho et al., 2008b; Lima et al., 2012). Although fish farming in cages has not been adequately monitored, preliminary studies already indicate some distortions with regard to proposed objectives, conflicts among users, profitability, introduction of species, and aquaculture as a source of water quality degradation (Agostinho et al., 2007a; Strictar-Pereira et al., 2010; Azevedo-Santos et al., 2011; Pelicice et al., 2014). Given the common occurrence of escapes in aquaculture, the use of non-native species was prohibited in reservoirs where these species were not established. However, this restriction was removed by a Federal Decree, which provided the status of “native” to several species from other continents (i.e. tilapias species), as a mean of fostering aquaculture in large reservoirs (Vitule et al., 2012; Pelicice et al., 2014). This decision may increase non-native dispersion across South American basins; it is well known that aquaculture is the main source of non-native species to Neotropical reservoirs (Ortega et al., 2015). In addition, fish farming of native species in cages conducted by traditional fishermen has not been promising due to the high costs of production, difficulties in commercialization, and small-scale production stemming from the investment capacity of the fishermen. Regardless of these negative points, aquaculture in public waters (reservoirs) may be environmentally sustainable and may promote social development, generating income and jobs. However, such a system requires a program with ample interaction with other activities related to fishery resources, created with rigorous planning and sustained by technical studies on production, impacts and marketing (Agostinho et al., 2008b). Unfortunately, aquaculture in Brazilian reservoirs does not follow these high environmental standards, and constitutes an additional source of disturbance to wild freshwater fish (Agostinho et al., 2007a; Pelicice et al., 2014).

Control of the fishery activity is an ongoing alternative to managing reservoirs in Brazil. However, there are also huge practical and conceptual difficulties to overcome. In general, fishing in reservoirs has already begun in the heterotrophic phase just after filling, when the harvest is high. In this phase, a great number of fishermen engage in the activity. Thus, the fishermen who traditionally fished in the river are included among the unemployed people who worked in the construction of the dam and the farmers who lost part of their land to the impoundment and who need a complementary source of income for subsistence. With the natural decrease in the harvest after the “trophic upsurge” period, fish stocks do not support the fishery pressure, causing poverty in the area. This type of fishery is not characterized by initial planning, and control becomes virtually impossible due to the high demand for a scarce resource. Overfishing is constant and acts synergistically with other disturbances such as those resulting from

impoundment (e.g. the reduction in large-sized migratory species), leading to a severe depletion of stocks (Agostinho et al., 2007a). Brazilian fishery legislation imposes temporal restrictions (periods of reproductive migration), spatial restrictions (places where fish stocks are more vulnerable to capture or nurseries), restrictions on fishing gear and methods (gear with low selectivity or that captures many fish), and restrictions on the size of the landed fish (capture of juveniles). In addition, entrance to the fishery requires a license, which should theoretically control access. However, enforcement efforts are minimal, and access to the fishery is facilitated by federal laws. Furthermore, there is no monitoring of the effectiveness of legal restrictions. It is clear, then, that the rigor of the law is not sufficient, except for a certain reduction in fishing effort during the period of the reproductive migration.

## 9. Final considerations

Large reservoirs are noticeable landscape features in most of the main hydrographic basins in Brazil. Long-distance migratory fish are the most impacted by impoundments, as a result of three fundamental characteristics inherent to their life history strategy: (i) the huge home range these species occupy in the hydrographic basin, including migration routes to areas critical for completion of life cycles, such as spawning areas and nurseries; (ii) a strong dependency of this life strategy on the natural flow regime controlled by the dams; and (iii) a demand for specific habitats, with shelter and adequate food for the initial stages of development, which are lost or degraded after river impoundment (Agostinho et al., 2007a). Species in this group of fish usually are large in size and in greatest demand in all fisheries in the region because of their high commercial value. Thus, the depletion of their local stocks is a concern in relation to biodiversity but also represents a loss in profitable fishing activities (Petrere et al., 2002; Hoeinghaus et al., 2009). The corollary of our review is that river regulation in South America affected permanently fish diversity and fishery resources, and that biodiversity and ecosystem services are currently threatened in many basins. Society must be aware of this scenario, so better decisions can be made in the near future (especially for pristine Amazon rivers).

Although poor management protocols proposed to mitigate the impacts of impoundments are still in effect and some backlash in terms of conservation-related legislation is occurring, the available knowledge on the reservoir environments and their impacts on the fish fauna has increased substantially in the last two decades. This knowledge has to be popularized so that common sense (which is not always correct) becomes good sense and poor management practices are abandoned. To this end, evaluation of the results of management practices is an essential step in management, and ignoring such results increases the likelihood of failure, of wasting resources and effort or, even worse, of causing new and greater impacts. Thus, the reevaluation of all current management or mitigation activities is urgent, and alternative strategies must be identified, such as habitat management or planning related to undammed basins and leaving some stretches with large free-flowing tributaries. For example, the 230 km undammed stretch of the Upper Paraná River and the undammed tributaries that flow into it are still sufficient to maintain the original fish fauna of the basin. The fact that the Upper Paraná is among the most regulated rivers in the world suggests that a similar strategy should be implemented in impoundments planned for the Amazon or other basins worldwide. In conclusion, alternative management actions must be seriously considered if we are to conserve fish diversity in a context of intense river regulation. Yet, we emphasize that impoundments affect profoundly the structure of the fish fauna, and that there is no simple solution to mitigate impacts or to restore biodiversity once a dam is constructed.

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