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Large reservoirs as ecological barriers to downstream movements of Neotropical migratory fish

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Abstract

Most large rivers in South America are fragmented by large dams, and a common management strategy to mitigate impacts has been construction of fish passes. Recent studies, however, indicate that downstream passage of adults and young fish is nil or minimal. Better understanding of this phenomenon is needed if fishways are to provide any tangible conservation value in South America. We propose, in this article, that large reservoirs impose a different kind of barrier to migrating fish: impoundments create a diffuse gradient of hydraulic/limnological conditions that affects fish behaviour and functions as an extensive environmental filter that discourages downstream movements. To develop this idea, we characterize the barriers created by dams and reservoirs by describing their distinct nature, the effects on fish migration and potential solutions. We show, for example, that dams generally prevent upstream movements, whereas reservoirs impede mainly downstream movements. In this context, we explain how fish passes, in some instances, can partially mitigate fragmentation caused by dams, but there is no technical solution to solve the barrier effect of reservoirs. In addition, we present a body of empirical evidence that supports the theory that large reservoirs are important barriers to fish migration in South America, we offer an overview of the size of reservoirs to show that impoundments typically have large dimensions, and we discuss the significance of this theory for other regions. Based on current and proposed river regulation scenarios, we conclude that conservation of Neotropical migratory fish will be much more complicated than previously believed.

Keywords Conservation, fishway, management, potamodromous fish, river regulation, South America

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Introduction

Habitat loss and fragmentation are major threats to aquatic biodiversity. Most of the world's large rivers are fragmented by dams, with many fluvial systems converted into series of impoundments (Nilsson *et al.* 2005). In South America, major river networks are impacted by channel fragmentation and flow regulation (Nilsson *et al.* 2005; Finer and Jenkins 2012). Hydroelectric generation now accounts for more than 76% of the electric energy produced in Brazil (EPE 2013), with most large rivers in the more densely populated southern region having been converted into a series of large impoundments (e.g. Paraná River Basin; Agostinho *et al.* 2008). Hydropower development also has been advanced in the Amazon region with many dams recently constructed and others planned for the future (Tollefson 2011).

River regulation impacts the entire Neotropical fish fauna (reviewed in Agostinho *et al.* 2007a), but rheophilic and long-distance migratory fishes are the most affected (Carolsfeld *et al.* 2003; Hoeinghaus *et al.* 2009). These migratory fishes include many species with high commercial/social value, including the large Characiformes and Siluriformes that require distinct habitats and natural flow regimes to perform seasonal migrations for completion of their life cycles (Carolsfeld *et al.* 2003). During the wet season, adults migrate upstream to spawn, after which eggs and larvae are passively transported with the current to productive nursery habitats in floodplains downstream. Spent adults undergo a return migration downstream to suitable habitats for feeding (Agostinho and Zalewski 1995; Lowe-McConnell 1999; Pompeu *et al.* 2012). Although this pattern appears to be common in rivers throughout South America, variations do exist, including river basins where migratory fish complete their life cycles using in-channel habitats (Zaniboni Filho and Schulz 2003; Godinho and Kynard 2008) and more complex movements, such as upstream and downstream migration among different systems, which has been observed in the Amazon region (Barthem *et al.* 1991; Lucas and Baras 2001; Araújo-Lima and Ruffino 2003).

Brazilian authorities recognize that impoundments obstruct migratory movements and/or decrease the connectivity between specific habitats, and they have required hydropower companies to take measures to protect migratory fishes. A common mitigation practice is installation of fish passes, and dozens of Brazilian dams have been equipped with ladders and similar structures (Agostinho *et al.* 2008). Despite substantial financial investments and engineering efforts, several recent studies have shown that fish passes in South America are largely ineffective (e.g. Agostinho *et al.* 2002; Pelicice and Agostinho 2008; Pompeu *et al.* 2012), basically because constructed fishways have failed to restore viable populations of migratory fishes. Multiple problems have been identified (Agostinho *et al.* 2007a; Pompeu *et al.* 2012), but a critical limitation is the virtual absence of downstream passage for adults and young fish (Agostinho *et al.* 2007b, 2011; Pelicice and Agostinho 2008, 2012; Brito and Carvalho 2013). The lack of downstream passage, although historically neglected by managers, may compromise the use of fishways as a management tool, because fish dispersal towards lower reaches is impeded. In addition, deficient downstream passage may create one-way fishways with significant negative consequences for population structure and stock recruitment. There is now growing recognition that hindrance of downstream passage poses a serious impediment for restoration of migratory fish stocks in large impounded rivers of South America (Pelicice and Agostinho 2008; Agostinho *et al.* 2011; Pompeu *et al.* 2012).

Understanding the causes for lack of downstream passage past dams is imperative for successful application of fishway technologies for fish conservation in South America; fish passes initially were developed for salmonid fish in temperate rivers. In this context, we propose a mechanism to explain why Neotropical migratory fish do not pass downstream from reservoirs and dams: impoundments are obstructive because large reservoirs function as additional, distinct barriers to fish migration. These impoundments have gradients of hydrological and limnological conditions that negatively impact fish behaviour, impeding free movements along the river. In this sense, the reservoir exerts a behavioural obstacle to downstream movements of adults and young fish. To develop this idea, we address the following objectives: (i) to characterize and compare the barrier imposed by a dam versus a barrier imposed by a large reservoir, including descriptions of their distinct natures, effects on fish migration and potential solutions; (ii) to summarize empirical evidence that supports the theory that large reservoirs function as barriers to downstream migration; (iii) to present data revealing that most impoundments in South America are large; (iv) to discuss the significance of the theory for other regions; and (v) to discuss management implications of this theory for the conservation of migratory fish. In this article, we focus on the Brazilian scenario, because the country is representative of the Neotropical context: it encompasses a large fraction of the tropical landmass, contains the highest freshwater fish diversity in the world and has most of the largest reservoirs of South America, with many more planned for construction.

The reservoir as an ecological barrier

Research on impacts of dams has historically considered the dam as the principal or sole barrier blocking longitudinal fish movements. The dam is indeed an unquestionable barrier, but we believe it is not the only barrier preventing fish movements, nor the most severe in some cases. We discuss here that the reservoir itself, by presenting environmental conditions completely different from the original fluvial regime, constitutes a strong ecological barrier to free movements along the river. In this sense, when a large river is dammed, two main obstacles are formed: the dam and the reservoir. To clarify this distinction, we describe the nature of these two barriers and present their main characteristics, the movements that are prevented by each and the technical solutions available (summarized in Table 1). In this section, we propose the theory and make some predictions that are examined in the next section with a review of empirical evidence.

Dams are physical vertical obstructions (Table 1) at discrete positions in space that clearly constitute significant blockage to longitudinal connectivity of river channels. Blockage of upstream fish movement is abrupt and complete (Fig. 1), but downstream movements are possible if fish use dam structures, such as spillways or turbines (in hydropower dams). Fish often crowd below the dam wall, especially during spawning events (Loures and Pompeu 2012). This phenomenon, which is easily observed at any dam, has long concerned scientists, managers and laypersons and thus eventually led to proposals for fishways. These technologies, including ladders, lifts, bypass channels, locks and trap-truck systems, are devices or procedures that aid migratory fish to overcome dams and complete their life cycle requirements, designed to connect fragmented stretches and restore fish movement (Fig. 1) (Clay 1995; Larinier 2002; Agostinho *et al.* 2007a). Depending on the region and the species, fishways may facilitate significant upstream passage; most fish passes, however, have proven deficient (Noonan *et al.* 2012; Brown *et al.* 2013). In South America, in particular, the fishways only permit passage by a fraction of migratory individuals for a few species (e.g. Fernandez *et al.* 2004; Agostinho *et al.* 2007c; Pompeu *et al.* 2012). Improvements in

Table 1 Characteristics of the barrier represented by dams and reservoirs, their relationship with fish movements and technical solutions available to mitigate the barrier effect.

	Dam	Reservoir
1. Barrier		
Characteristics of the barrier	Vertical Abrupt Structural	Horizontal Gradient Hydraulic/limnological
Relation to fish biology	Physical	Behavioural
Restriction to upstream migration	High to adults and juveniles	Low to adults and juveniles
Restriction to downstream migration	Unknown	High to adults, juveniles, eggs and larvae
2. Solution		
Technical solution for upstream passage	Ladders, lifts, locks and canals	Unavailable, but most likely unnecessary
Technical solution for downstream passage	Screening, bypass devices, spillway management	Unavailable
Efficacy of solution	Low/moderate to upstream movements Unknown to downstream movements	Unavailable Unavailable

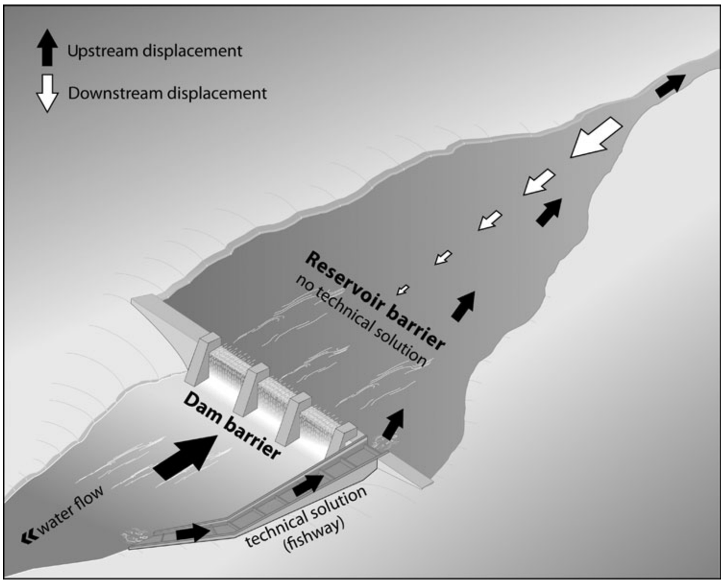

Figure 1 Schematic model indicating the two barriers created by the impoundment of large rivers. In this scenario, the dam is a barrier to upstream movements, while the reservoir is a barrier to downstream movements. Fish passes are technical solutions to overcome the barrier of the dam, whereas no solution exists to cope with the ecological barrier imposed by the reservoir. Arrow size is proportional to the quantity of migrant fish.

planning, engineering and hydraulics are possible, and much progress has been achieved since the installation of the first ladders in Brazil. More effective fish passes have been developed (Agostinho *et al.* 2007a), and knowledge about the swimming capabilities of native species has advanced (Santos *et al.* 2007, 2008, 2012). Nevertheless, all facilities evaluated so far have shown problems and limitations, perhaps due to the high behavioural and ecological diversity of the Neotropical fish fauna. Little is known, however, about downstream passage through fishways and other dam structures (Agostinho *et al.* 2007a), despite recent studies have shown that fish do not use ladders as a descending route (Agostinho *et al.* 2007b, 2011; Pelicice and Agostinho 2008, 2012; Brito and Carvalho 2013). This inefficiency may be related to the low density of fish above the dam, which may be a consequence of the barrier imposed by the reservoir.

The barrier created by reservoirs is different than that caused by dams. The reservoir is not a distinct physical structure; it extends longitudinally and horizontally over a much greater distance along the river corridor than a dam (Table 1). The reservoir barrier is a gradient of hydrological and limnological conditions that creates a gradual transition of lotic, semi-lentic and lentic environments between upstream and downstream reaches (Thornton *et al.* 1990; Okada *et al.* 2005). A large reservoir, in particular, is a huge compartment with very low flow velocity and is long (tens to hundreds of kilometres), with greater depth and water transparency than adjacent river reaches. These conditions interact with fish behaviour and represent a hydrological/limnological obstacle to downstream fish migration; for example, migratory fishes in the Neotropics, as in other regions of the world, evolved within a fluvial context, with life histories adapted to the natural flow regime (Fernando and Holčík 1982; Winemiller 1989; Gomes and Miranda 2001). As a consequence, these fishes are usually rheophilic and remain associated with running waters or riverine environments. Adult fish likely lack appropriate orientation for downstream migration across the long stretch of standing waters that lies between upper lotic areas and the dam and therefore remain in upstream areas that retain riverine conditions. In addition, the absence of flow in reservoirs prevents downstream drift of eggs and larvae that normally would be passively transported to nursery habitats. In this scenario, non-buoyant eggs and larvae sink in lentic waters of the reservoir and are either deposited in harsh environments that are inappropriate for development or are exposed to higher predation pressure due to high water transparency (Agostinho *et al.* 2007b). Therefore, while dams physically prevent upstream movements, the reservoir exerts a behavioural obstacle to downstream movements of adults and young fish (Fig. 1). Importantly, the reservoir is not a strong obstacle to upstream movements of adult fish (Fig. 1). Although some fish may become disorientated, most fish that pass through the dam can traverse the reservoir to find suitable habitat in upper reaches (Agostinho *et al.* 2002; Antonio *et al.* 2007; Makrakis *et al.* 2007a; Makrakis *et al.* 2007b; Brito and Carvalho 2013).

No technical solution exists to cope with the barrier imposed by a reservoir (Table 1 and Fig. 1). In the absence of downstream migration through the reservoir, use of the most effective fishway technology (allowing fish to pass in both directions) would not restore free movements between river reaches. In this scenario, migratory fish could ascend through the ladder and reach upper sites but would have low return rates to downstream areas. Individual fish, once upstream, rarely would reach the dam area where downstream passage could occur. Genetic exchange is also affected, because gene flow (via downstream migration of adults or larvae drift) will be significantly reduced by the reservoir. Consequently, fishways cannot restore demographic dynamics and gene flow of migratory fish in areas fragmented by large dams – even though some fish are passed successfully upstream. Alternatively, improvements in downstream passage may lie in the manipulation of hydraulic conditions of the dam (i.e. flow restoration), an action that has been proposed to improve ecological integrity of river systems (King and Brown 2009) and to increase downstream passage (Williams 2008). Manipulations of river flow (e.g. using the spillways), however, are procedures that conflict with other uses of the impoundment – mainly hydroelectricity generation. In addition, these actions are constrained by operation restrictions, and therefore, net benefits are questionable. Flow management may be feasible in small reservoirs during the rainy season when water residence is shorter and significant flows might be possible. However, flow management is technically and economically unrealistic in large reservoirs (e.g. >50 km long) with high water residence time (e.g. >50 days). This situation would make the reservoir a more significant barrier than the dam itself and would also impede use of fish passes as a management tool. In this sense, the ecological barrier of reservoirs may represent a major obstacle for the restoration of migratory movements in rivers fragmented by large dams.

Based on the theory that reservoirs act as ecological barriers (see Fig. 1), we make broad predictions for migratory fish abundance along reservoir gradients and their associated dams (Fig. 2). We predict that (p.1) density of adults decreases abruptly within a reservoir from the upstream riverine area towards the dam; these declines should follow reductions in water velocity and increases in water transparency, which are functions of reservoir length, size and retention time. We also predict (p.2) strong reductions in eggs and larvae of migratory species because they respond directly to reductions in water flow during the movement of drifting. Therefore, very low densities of eggs and larvae are predicted within reservoirs and immediately below dams [exceptions include species that, due to stressful conditions, spawn just downstream of the dam or inside fishways, e.g. Freitas *et al.* (2009)]. We also predict (p.3) persistent high densities of adult and juvenile fish below the dam, a response to stimulus of water flow. When fishways are present (p.4), abundance of adult and juvenile fish must decline along the facility because fishways are selective to many species. In this case, the abundance of migratory fish may increase in the area above the dam; however, this trend is short-lived as fish migrate towards upper riverine sites.

Empirical evidence

In this section, we gather a body of empirical evidence to support the theory that large reservoirs function as a barrier to downstream movements. We present evidence from studies that indicate the following: (i) migratory/rheophilic fish remain in upper reaches of large impoundments and have a low abundance within the reservoir; (ii) adult fish actively avoid inner areas of the reservoir; (iii) downstream passage through fishways is virtually absent; and (iv) eggs/larvae do not drift through the reservoir. These data are in agreement with predictions derived in the previous section, that is, p.1 and p.2, related to the barrier caused by the reservoir (Fig. 2).

A series of studies conducted across different basins of South America have shown that the

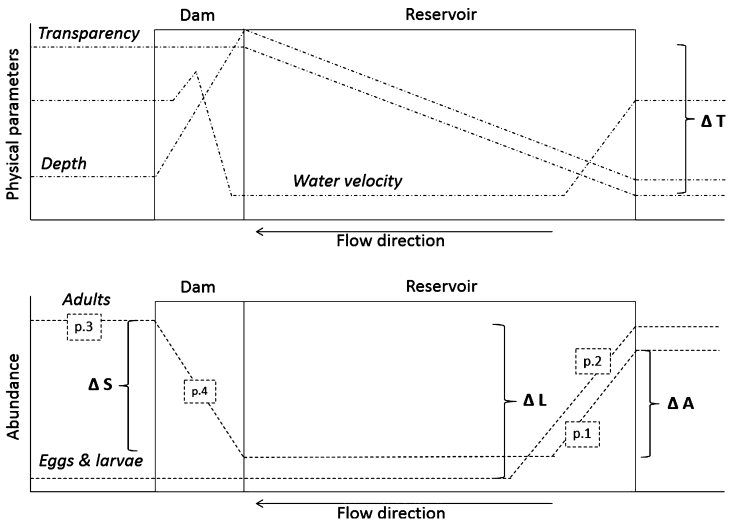

Figure 2 Schematic representation of the physical parameters (water velocity and transparency) and predictions for migratory fish abundance (adults, eggs and larvae) along the reservoir gradient and across the dam. ΔT = variation in transparency, related to reservoir length; ΔS = selectivity/effectiveness of upstream adult passage; ΔL = variation in eggs and larvae abundance, related to reservoir length; ΔA = variation in the abundance of adult fish, related to reservoir length.

abundance of migratory and/or rheophilic fish is a function of the distance from the dam (i.e. p.1). A higher abundance is found in tributaries, or riverine zones and transitional areas of reservoirs, and they are rare or absent in the inner areas of reservoirs (e.g. Petrere *et al.* 2002; Hoffmann *et al.* 2005; Luiz *et al.* 2005; Okada *et al.* 2005; Oliveira *et al.* 2005; Agostinho *et al.* 2007b, 2011; Esguicero and Arcifa 2010; Terra *et al.* 2010; Pelicice and Agostinho 2012; Petesse and Petrere 2012). The paucity of migratory species in reservoirs is a well-recognized trend and has directly affected fisheries (Petrere *et al.* 2002; Okada *et al.* 2005; Hoeinghaus *et al.* 2009). We emphasize that Neotropical fishes, especially potamodromous species, are typically rheophilic and adapted to live in riverine environments and associated habitats, with life history strategies that are coupled to the natural flow regime (Fernando and Holčík 1982; Winemiller 1989; Gomes and Miranda 2001). Hence, behavioural and ecological demands cause fish to remain associated with remnant lotic environments where they have a better chance of encountering conditions suitable to complete their life cycle. Downstream movements towards the dam would involve swimming across the reservoir, which is a lentic environment where flows are low or non-existent.

Mark–recapture and tagging studies support these trends and have shown that migratory fish tend to move away from reservoir areas (i.e. p.1). These studies, conducted in different reservoirs of the Paraná River Basin, have shown that migratory fish released in reservoirs tend to avoid lentic conditions and migrate rapidly through the impounded area towards upper lotic reaches or lateral tributaries (Agostinho *et al.* 2002, 2007a; Alves *et al.* 2007; Antonio *et al.* 2007; Makrakis *et al.* 2007a,b; Silva 2012; Brito and Carvalho 2013). For example, in Porto Primavera Reservoir, one of the largest impoundments in Brazil (2250 km^2 of surface area, 190 km long), Antonio *et al.* (2007) showed that fish released close to the dam travelled long distances in relatively short time intervals, indicating orientation and fast movements towards upper reaches. These authors also showed that some fish may disorientate or leave the reservoir (returning downstream) soon after entering the impoundment. Agostinho *et al.* (2002) reported that fish caught downstream from the Itaipu Reservoir (1350 km^2 of surface area, 160 km long) and then marked and released upstream near the dam abandoned this area quickly. A recent mark–recapture study (Makrakis *et al.* 2012), carried out in an extensive stretch between Yacyreta and Porto Primavera reservoirs, also revealed that marked fish perform mainly upstream and lateral movements. As a final example, Brito and Carvalho (2013) showed that migratory fish ascend through the fish ladders at

Canoas I and Canoas II dams and remain permanently in upper reaches, revealing that small, short reservoirs (<40 km long; <40 km^2 area; see Table 1) also prevent downstream displacement. Although studies that tag fish (e.g. mark–recapture, telemetry) are scarce, they clearly show that migratory fish tend to avoid the lentic conditions of impoundments. More tagging studies are needed to elucidate patterns of orientation and movement of fish following introduction into a reservoir.

The absence of downstream movement through fishways is strong evidence that migratory fish rarely visit inner areas of the reservoir (i.e. p.1). Several recent studies conducted in different basins consistently show that fish do not use ladders and other facilities as a descending route (Agostinho *et al.* 2007b, 2011; Lopes *et al.* 2007; Pelicice and Agostinho 2008, 2012; Brito and Carvalho 2013). We highlight studies carried out in the Tocantins River (Peixe Angical and Lajeado dams) that used a rigorous assessment protocol to evaluate downstream passage (Agostinho *et al.* 2011; Pelicice and Agostinho 2012). In both fishways (weir & orifice fish ladders), there was a striking contrast between the number of ascending and descending fish in the ladder, with a great prevalence of ascending individuals and a small number of descending fish (a typical one-way passage). Few migratory species were caught during downstream movements, which resulted in a high numerical ratio of ascending/descending fish (approximately 2700:1 in Lajeado and 1069:1 in Peixe Angical). Both studies also reported low abundance of migratory species in the area above the dam, indicating that fish were rare within the main body of the impoundment. Visual surveys carried out in the proximity of the Lajeado fish ladder (C.S. Agostinho, personal communication) revealed that few fish visited the exit of the ladder. Taken together, these findings suggest that migratory fish do not use fishways as a descending route because few of them approach the dam region of the reservoir.

Finally, the lack of downstream transportation of fish larvae is another strong piece of evidence that large reservoirs impede downstream movements (i.e. p.2). Some recent studies have consistently shown that the density of eggs and larvae along the river canal declined dramatically when they drifted into large impoundments (Agostinho *et al.* 2007b; Pinto *et al.* 2009; Suzuki *et al.* 2011). Additionally, there is clear evidence that eggs and larvae of migratory fish do not pass through fish ladders (Agostinho *et al.* 2007b; Freitas *et al.* 2009), which supports the idea that these life stages do not reach the dam. Even in small reservoirs, the downstream passage of eggs and larvae seems to be limited and dependent on variations in water residence, and this was demonstrated in the Santa Clara Dam, a short and small reservoir of 7.5 km^2 surface area (Pompeu *et al.* 2011). Based on this evidence, the reservoir seems to interrupt the downstream drift of ichthyoplankton towards lower reaches.

In conclusion, this body of evidence is in agreement with predictions 1 and 2 (Fig. 2), supporting the theory that large reservoirs act as a barrier to downstream migration: adult fish actively avoid inner areas of the impoundment and remain in remnant lotic areas, and eggs and larvae lack behavioural mechanisms to survive under low-flow conditions.

Large reservoirs in South America

In this section, we examine the South American scenario to show that large reservoirs (area, length and water residence) are common across freshwater landscapes. These water bodies are common because large rivers drain all major basins of the continent (Agostinho *et al.* 2007a); this prevalence implies that barrier effects might be common throughout the region.

We gathered information about reservoirs located in the main channels of major rivers in Brazil (Table 2) and collected information about surface area (km^2), length (km) and water residence time (days) – variables that might serve as proxies of the barrier effect. All reservoirs were geographically located and identified using the Sigel interface (National Agency of Electric Energy; http://sigel.aneel.gov.br/). Surface area was obtained from Agostinho *et al.* (2007a), and the length of each reservoir was measured using the Path tool in Google Earth 7.0. We obtained an approximate length value, which considered the fluvial distance (km) between the dam and the upper lotic stretch, that is, where the reservoir width decreases to a condition similar to the flowing river. In the case of a cascade of reservoirs, we considered the distance between dams. Water residence time was obtained from the literature and websites (hydropower companies).

We identified a total of 66 reservoirs in the main channel of Brazilian large rivers (Table 2),

Table 2 Reservoirs located in the main channel of the major fluvial courses in Brazil. Sequence = sequence of reservoirs along the river (upstream to downstream).

Reservoir	Basin	River	Sequence	Area (km^2)	Length (km)	Water residence (days)	Fish pass
Curuá-Una	Amazon	Curuá-Una		78	50	39	
Samuel	Amazon	Jamari		656	90	143.3	
Balbina	Amazon	Uatumã		2360	160	351	
Serra Da Mesa	Tocantins	Tocantins	1	1784	150	770	
Cana Brava	Tocantins	Tocantins	2	139	20	27.8	
São Salvador	Tocantins	Tocantins	3	104	60	12	
Peixe Angical	Tocantins	Tocantins	4	294	70	18	Ladder
Luis Eduardo Magalhães	Tocantins	Tocantins	5	630	150	24	Ladder
Estreito	Tocantins	Tocantins	6	400		15	
Tucurui	Tocantins	Tocantins	7	2875	150	51	
Três Marias	São Francisco	São Francisco	1	1142	130	120	
Sobradinho	São Francisco	São Francisco	2	4214	200	104.4	
Itaparica	São Francisco	São Francisco	3	828	180	72	
Moxotó	São Francisco	São Francisco	4	93	25	5	
Paulo Afonso	São Francisco	São Francisco	5	5.2	5	31	
Xingó	São Francisco	São Francisco	6	60	50	16	
Nova Ponte	Paraná	Araguari	1	446.58	100	507	
Miranda	Paraná	Araguari	2	50.61	60	39	
Amador Aguiar 1	Paraná	Araguari	3	18	10	8	
Amador Aguiar 2	Paraná	Araguari	4	45		27.8	
Corumba	Paraná	Corumbá		65	50	41	
Emborcação	Paraná	Paranaiba	1	485	60	419	
Itumbiara	Paraná	Paranaiba	2	778	90	129	
Cachoeira Dourada	Paraná	Paranaiba	3	74	40	3	
São Simão	Paraná	Paranaiba	4	722	120	62	
Camargos	Paraná	Grande	1	73.3	40	69.4	
Itutinga	Paraná	Grande	2	1.73	5	0.5	
Funil	Paraná	Grande	3	38.3	40	10.1	Lift
Furnas	Paraná	Grande	4	1440	130	160	
Mascarenhas de Moraes	Paraná	Grande	5	250	90	51	
Estreito	Paraná	Grande	6	46.7	20	18	
Jaguara	Paraná	Grande	7	36	20	4.87	
Igarapava	Paraná	Grande	8	40.94	35	2.6	Ladder
Volta Grande	Paraná	Grande	9	221.7	70	21	
Porto Colômbia	Paraná	Grande	10	143	50	14	
Marimbondo	Paraná	Grande	11	438	130	39	
Água Vermelha	Paraná	Grande	12	647	140	60.9	
Barra Bonita	Paraná	Tietê	1	308	70	90.3	
Bariri	Paraná	Tietê	2	62.5	45	14.2	
Ibitinga	Paraná	Tietê	3	113.5	70	21.6	
Promissão	Paraná	Tietê	4	530	105	134.1	
Nova Avanhandava	Paraná	Tietê	5	210	45	45.7	
Três Irmãos	Paraná	Tietê	6	785	130	217.9	
Jurumirim	Paraná	Paranapanema	1	425	90	322.8	
Piraju	Paraná	Paranapanema	2	17	30	5.7	
Paranapanema	Paraná	Paranapanema	3	1.5	9		
Chavantes	Paraná	Paranapanema	4	400	40	418	
Ourinhos	Paraná	Paranapanema	5	5	6	1	Ladder
Salto Grande	Paraná	Paranapanema	6	12	15	1.5	
Canoas II	Paraná	Paranapanema	7	22.51	30	5.5	Ladder

Table 2 Continued.

Reservoir	Basin	River	Sequence	Area (km^2)	Length (km)	Water residence (days)	Fish pass
Canoas I	Paraná	Paranapanema	8	30.85	30	3.8	Ladder
Capivara	Paraná	Paranapanema	9	576	110	119	
Taquaruçu	Paraná	Paranapanema	10	80.1	60	10	
Rosana	Paraná	Paranapanema	11	220	90	18.6	
Ilha Solteira	Paraná	Paraná	1	1195	180	47.6	
Jupiá	Paraná	Paraná	2	330	50	6.9	
Porto Primavera	Paraná	Paraná	3	2250	190	33.9	Ladder
Itaipu	Paraná	Paraná	4	1350	160	30	Channel
Salto Caiacanga	Paraná	Iguaçu	1				
Foz Do Areia	Paraná	Iguaçu	2	139	60	102	
Segredo	Paraná	Iguaçu	3	84.88	70	47	
Salto Santiago	Paraná	Iguaçu	4	208	70	50.8	
Salto Osório	Paraná	Iguaçu	5	62.9	35	16	
Salto Caxias	Paraná	Iguaçu	6	144.2	75	33	
Machadinho	Uruguai	Uruguai	1	79	45	53	
Itá	Uruguai	Uruguai	2	141	100	55	

which included water bodies with high dimensions. Considering the surface area (range: 1.5–4214 km^2; $n = 65$), 78% of the reservoirs had areas larger than 50 km^2, while 28% had areas larger than 500 km^2. We recorded high mean values in all basins (Fig. 3a), including some with mean values >1000 km^2. Analysing reservoir length, we recorded long water bodies in all basins (range: 5–200 km; $n = 63$) and observed that 67% had lengths >50 km and 30% had lengths >100 km. All basins showed high mean values (Fig. 3b), especially those located in rivers with a high discharge, such as the Paraná River. Water residence varied considerably among reservoirs (range: 0.5–770 days; $n = 64$), but 56% had residence time >1 month and 23% showed residence >100 days. Most basins had mean residence time >50 days (Fig. 3c), an indication of low flow rates through large reservoirs in South America. These patterns are supported by the analysis of Avakyan and Iakovleva (1998) who compared reservoir size in different continents. From these data, we note that the amount of water stored per reservoir (volume/reservoir, km^3) is high in South America (Fig. 4). This pattern is even clear if we consider Brazil, which holds the largest rivers of the continent and whose reservoirs show twice the average volume recorded in North America or Europe. The South American scenario is, therefore, characterized by large reservoirs (i.e. large in length, area and volume stored) installed in the main course of major rivers of the continent.

Studies that have provided evidence that the reservoir is a barrier to downstream movements (see previous section) have analysed reservoirs with varied dimensions, including short (<40 km) and small (<40 km^2) water bodies, with low water retention times (<10 days), for example Canoas 1 and 2 (Lopes *et al.* 2007; Brito and Carvalho 2013), Funil (Suzuki *et al.* 2011) and Santa Clara (Pompeu *et al.* 2011). Note that area, length and water residence of these reservoirs are far below the average observed across all Brazilian basins (Fig. 3). For the downstream passage of eggs and larvae, the minimum dimension in which passage occurred (Santa Clara Dam: 7 km long, 7.5 km^2, 2 days residence time) and the minimum dimension in which it was prevented (Funil Dam: 40 km, 38 km^2, 10 days) were much lower than those of other studied reservoirs (Fig. 5). For the descending passage of adults, there is no information about the minimum dimension in which passage is possible, but the minimum known dimension where downstream passage is prevented (Canoas II: 30 km, 28 km^2, 5.5 days) is also far below other reservoirs.

Although the number of impoundments in South America is much lower in comparison with other continents, for example, North America or Europe (Avakyan and Iakovleva 1998; Pringle *et al.* 2000; Nilsson *et al.* 2005), the density of

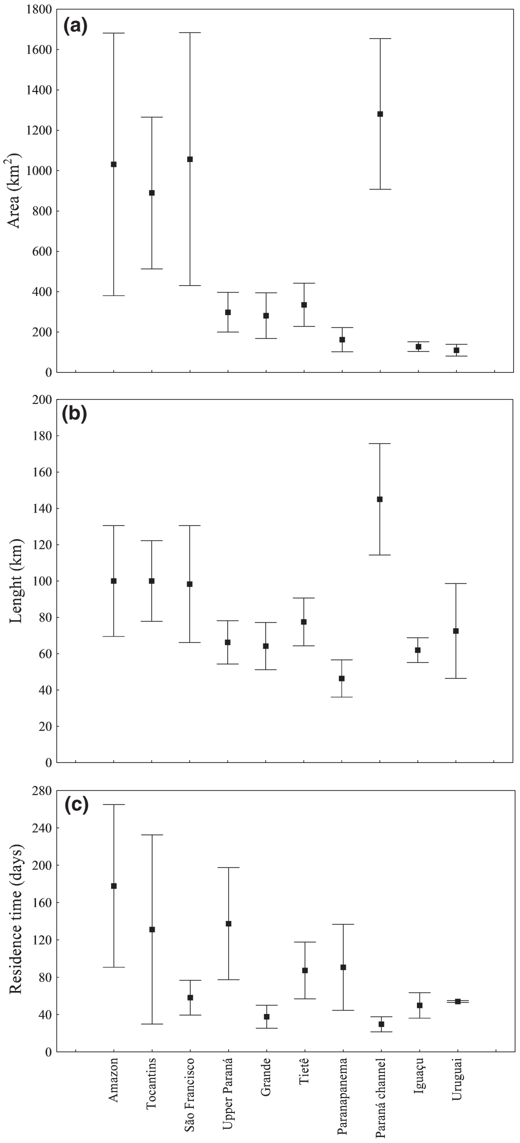

Figure 3 Dimensions of reservoirs located in the main river basins of Brazil. (a) surface area (km^2), (b) length (km) and (c) water residence time (days). Values are the means ± SE. See Table 2 for further information.

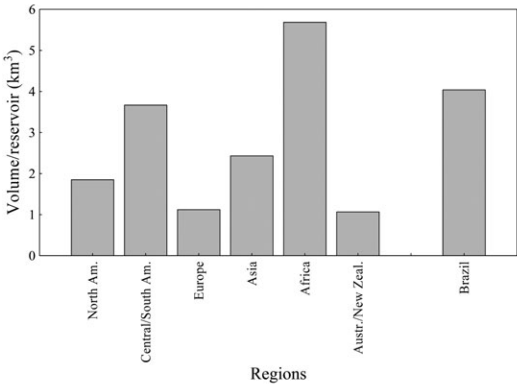

Figure 4 Mean water stored per reservoir (volume/reservoir, km^3) in different continents (plus Brazil). The average volume was obtained by dividing total volume/number of reservoirs in each continent, considering impoundments constructed over the 20th century (1900–1990). Data obtained from Avakyan and Iakovleva (1998).

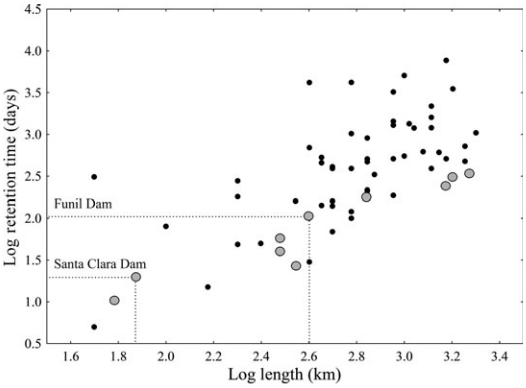

Figure 5 Relationship between length (km, log) and water residence time (days, log) of the reservoirs analysed in this study, indicating the minimum reservoir dimension (length × residence) in which the downstream passage of eggs and larvae was recorded (Santa Clara Dam; Pompeu *et al.* 2011) and prevented (Funil Dam; Suzuki *et al.* 2011). Reservoirs with fishways are indicated by larger symbols (grey).

large reservoirs is very high in some basins (e.g. Paraná, São Francisco, Tocantins rivers). In addition, reservoirs in many basins are arranged in cascades along the longitudinal gradient (Table 2), which creates a series of ecological barriers. Moreover, some large dams have been built or are being constructed within the Amazon basin (e.g. Madeira, Tapajos, Xingu and Tocantins sub-basins), and there are plans to regulate some important tributaries, including upper Andean catchments (Tollefson 2011; Finer and Jenkins 2012; Castello *et al.* 2013). Therefore, the barrier effect of reservoirs will impact biodiversity in the most species-rich region of the earth.

Significance for other regions

Although the domain of the theory is the Neotropical context, we believe it has greater scope, with application to other river systems in the world. The validity will depend on regional settings, that is, the dimension of reservoirs and the nature of fish communities. We expect that reservoirs will be particularly impactful as ecological barriers in large river system with many rheophilic and migratory species. Thus, the theory would be valid for all continents, as large river systems and migratory fish are found worldwide (Lowe-McConnell 1999; Lucas and Baras 2001; Nilsson *et al.* 2005).

This theory may have particular significance for tropical and subtropical systems in Africa and Asia. The context of these geographical regions has similarities with South America: they have large river systems and a diverse assemblage of potamodromous species. Furthermore, many countries in these regions have emerging economies, with pressure for the construction of new hydroelectric dams (Dugan *et al.* 2010). The impoundment of large river systems in Asia and Africa (e.g. Zaire, Nile, Congo, Zambezi, Ganges, Mekong, Yangtze) will naturally create large reservoirs. In fact, Asian and African reservoirs have higher volume if compared to other continents (Fig. 4). The African continent, for example, has more than 30 reservoirs with area >50 km^2 (Bernacsek 1984), some with colossal surface areas (Volta = 8270 km^2; Nasser = 6850 km^2; Kariba = 5550 km^2; Kafue Gorge = 4340 km^2). Moreover, the fish fauna in these regions has developed adaptations, behaviours and life history traits to cope with fluvial environments, and they depend on the natural flow regime to complete their life cycles; as a consequence, many species are potamodromous, rheophilic and/or migratory (Lowe-McConnell 1999; Dudgeon 2000; Poulsen *et al.* 2004; Tedesco *et al.* 2008; Baran 2010). In South-East Asia, in particular, the fish fauna is essentially composed of riverine species (Fernando and Holčík 1982; Gomes and Miranda 2001). Even in the African continent, characterized by a high diversity of lacustrine-adapted species, riverine fish are conspicuous (Fernando and Holčík 1982; Tedesco *et al.* 2008; Melcher *et al.* 2012).

The Mekong River Basin, which drains several countries in South-East Asia and sustains a very productive inland fishery, is a special case. Freshwater fish assemblages in this basin are among the most diverse in the world, which includes iconic and endangered species (Dudgeon 2011). This river is also characterized by a high diversity of rheophilic and migratory species (potamodromous, anadromous and catadromous), which show complex patterns of longitudinal and lateral migration (Poulsen *et al.* 2004). Some species, such as the catfish *Pangasius krempfi* (Pangasiidae), migrate over long distances (>700 km) between marine and freshwater environments to reproduce (Hogan *et al.* 2007). The region, however, has been targeted for hydropower development: some dams were constructed in upper reaches and tributaries (e.g. Xiaowan, Dachaoshan), but several others have been planned (e.g. Nuoshadu, Pak Beng, Luang Prabang, Xayaburi, Pak Lay, Sanakham, Stung Treng, Sambor), including the main channel (Baran 2010; Dugan *et al.* 2010; Dudgeon 2011). This process will fragment the river continuum, regulate the natural flow regime and create large reservoirs. In this context, fish passes have been proposed to rehabilitate and conserve fish stocks (Baran 2010; Dugan *et al.* 2010; Baumann and Stevanella 2012). However, considering the size of the reservoirs (some >50 km^2; Baran 2010) and the diversity of migratory behaviours, with prevalence of potamodromous fish (Poulsen *et al.* 2004), the formation of large reservoirs may prevent downstream movements – preventing also the use of fish passes as efficient management tools.

This scenario is also expected in the Yangtze River (China), which holds high levels of fish diversity and endemism (Fu *et al.* 2003; Dudgeon 2011) – including endangered species such as the giant paddlefish *Psephurus gladius* (Polyodontidae) and sturgeons. Like the Mekong, the Yangtze and its main tributaries have been targeted for intense hydropower development (Dudgeon 2011), an activity that will naturally create large impoundments. The construction of the Three Gorges Dam, for example, created a large reservoir in the main course of the Yangtze River (c.a. 1000 km^2 surface area), affecting more than 500 km upriver and altering the structure and distribution of fish populations (Xie *et al.* 2007; Gao *et al.* 2010). There is also evidence that the reservoir has prevented downstream movements of young and adult fish, supporting predictions 1 and 2 (Fig. 2). For example, Jiang *et al.* (2010) showed that large quantities of eggs and larvae flow into the reservoir, but authors concluded that losses might occur due to adverse conditions in the impoundment. In fact, after the construction of the Three Gorges Dam, Duan *et al.* (2009) observed a marked decline in the drift of larvae of Chinese carps in the stretch downstream from the dam.

Authors attributed the decline to the loss of spawning grounds and the suppression of reproductive stimuli, but larvae from upstream sites would have to drift through a huge lentic reservoir. We highlight that carps continue to spawn in sites located upstream from the dam (Jiang *et al.* 2010), but larvae captured downstream do not come from these upstream sites (Duan *et al.* 2009). It is very likely, therefore, that larvae cannot reach downstream sites because of the barrier imposed by the reservoir. In addition, other study have shown that sturgeons (subadults) marked and released in the upper lotic section tended to move downstream towards the impoundment, but few visited inner sites of the reservoir (Du *et al.* 2013). Authors also showed that travelling speed declined when fish reached lentic zones. These results, therefore, suggest that the Three Gorges Reservoir is working as a barrier to downstream movements, a pattern that may repeat in other large reservoirs of the region.

In temperate regions (North America, Europe, Asia, Australia, Japan), the barrier effect imposed by reservoirs may also be important. These regions present a different context, but there are indications that impoundments have affected downstream migration of adults and young. The context is different because most dams are small sized (weirs and low-head dams installed in streams, creeks and small rivers) and fish assemblages are less diverse and include many lentic-adapted species (Fernando and Holčík 1982; Gomes and Miranda 2001). However, these regions also have large river systems, for example Colorado, Columbia, Mississippi, Rhine, Danube, Volga, Lena and Murray Darling; most of these have been intensely regulated, including construction of large reservoirs (Avakyan and Iakovleva 1998). Migratory fish species are found in these systems (e.g. salmon, eels, shads, sturgeons, lampreys), and these often encompass diverse migratory behaviours that include residence in rivers during some part of the life cycle (Lucas and Baras 2001; Carolsfeld *et al.* 2003). Many species are rheophilic (e.g. Logez *et al.* 2013) and demand downstream migration, with some laying buoyant eggs and larvae that rely on river flow to drift downriver (Lucas and Baras 2001; Carolsfeld *et al.* 2003; Zitek *et al.* 2004; Pavlov *et al.* 2008). For these taxa, reservoirs may impede the downstream movement of adults and drift of eggs and larvae towards nursery grounds. In fact, several studies conducted in regions with different migratory species present findings in agreement with predictions 1 and 2 (see Fig. 2). For example, migratory and rheophilic fish tend to be absent or rare within the lentic portions of reservoirs (e.g. Poddubny and Galat 1995; Gehrke *et al.* 2002; Kruk and Penczak 2003; Falke and Gido 2006; Gido *et al.* 2009) and mainly occur in lotic upper reaches (e.g. Harris and Hightower 2011; Yoon *et al.* 2012). In addition, downstream movements decline as fish enter impoundments due to reduced water velocity and turbulence (e.g. Tiffan *et al.* 2009; Pedersen *et al.* 2012), and downstream passage through weirs is reduced (e.g. O'Connor *et al.* 2006). There is also evidence that drifting eggs and larvae are retained within the reservoir where they are exposed to unsuitable habitats (e.g. Humphries and Lake 2000; Humphries *et al.* 2002; Gilligan and Schiller 2003). Finally, studies revealed that the drift, settlement and retention of synthetic particles with size and buoyancy similar to eggs of rheophilic fish have been shown to be strongly affected by variation in river discharge (e.g. Dudley and Platania 2007; Widmer *et al.* 2012; Worthington *et al.* 2014). These studies show that reservoirs, including small impoundments, affect the downstream migration of fish in temperate latitudes.

It is important to note that salmon and eels, dominant migratory fauna in many temperate systems (Carolsfeld *et al.* 2003; Leveque *et al.* 2008), often are able to migrate downstream through reservoirs. These fishes have migratory behaviour and life history patterns that probably reduce the barrier effect of reservoirs. For example, many salmon species are semelparous (e.g. Pacific salmon *Onchorhynchus*), so adults do not migrate downriver after spawning; the dam, consequently, constitutes the principal barrier preventing migration (i.e. upstream). Moreover, dispersal of young life stages occurs at more advanced developmental stages and larger sizes; physiological, morphological and behavioural adaptations of smolts, for instance, are related to the motivation to migrate downstream (McCormick *et al.* 1998). Young fish, in this case, actively migrate downriver and are not in danger of sinking in lentic waters of the reservoir. However, we are hesitant to conclude that the barrier imposed by reservoirs has no effect on these migratory fishes. Reduced downstream migration of smolts (*Oncorhynchus*) has been recorded for decades in the Columbia River (Williams 2008; Muir and Williams 2012). This case is complex, considering that substantial resources (i.e. management and research) have been applied to improve downstream passage and other aspects, yet recovery and maintenance of wild stocks have proven difficult (Williams 2008). Similar patterns have been recorded for eels (Acou *et al.* 2008; Carr and Whoriskey 2008; Pedersen *et al.* 2012), which become disorientated in reservoirs during downstream migration. Disorientation reduces the speed of migration (Williams 2008; Noorgard *et al.* 2013), which increases mortality due to predation by fish and birds (Rieman *et al.* 1991; Jepsen *et al.* 1998). Reservoirs can, therefore, significantly impact downstream migrations of salmon and eels.

The theory that reservoirs function as barriers to downstream movement appears valid for other regions, and confirmation will require further study. We stress that investigation of downstream migration and passage has been neglected by scientific research and management (Marmulla 2001; Larinier and Travade 2002; Agostinho *et al.* 2011; Katopodis and Williams 2012; Noonan *et al.* 2012), so the barrier imposed by reservoirs may go unnoticed in many cases. As a consequence, research on downstream passage must investigate more than dams as physical barriers or agents of mortality and must consider the impact of reservoirs on downstream movement.

Implications for conservation

The obstacle imposed by dams has attracted the attention of managers, scientists and the public, while the ecological barrier created by the reservoir has remained largely neglected and uninvestigated. Common sense suggests that a mass of lentic water, unlike a concrete physical structure, offers little physical resistance to fish movement. However, this is not the case for fishes of the Neotropics and other regions of the world. Dams and reservoirs create dual barriers that prevent fish migration via distinct mechanisms. While dams block mostly upstream movements, large reservoirs create a diffuse gradient of hydraulic/limnological conditions that discourages downstream migratory behaviour and traps drifting eggs and larvae. Recognition that large reservoirs are barriers to downstream movements and that there is no simple solution to this problem indicates that the conservation of Neotropical migratory fish is much more complicated than that considered by current management approaches – which typically entail the installation of fishways.

Fishway construction is now commonplace and employed as the principal solution to fisheries impacts from impoundments (Pompeu *et al.* 2012). In some Brazilian states, the construction is mandatory. However, despite intense public demand for more and better fishways in South America, there is no scientific evidence showing that any existing facility has played a role in conservation of fish stocks. There are many problems related to their functioning (Agostinho *et al.* 2007a; Pompeu *et al.* 2012), and the barrier created by reservoirs may compromise their use. The absence of downstream migration causes fishways to fail in re-connecting the fragmented river; even if the facility allows complete passage in both directions, the reservoir barrier will prevent fish from entering areas close to the dam where descending passage could occur. In this case, fishways have little conservation value (Pompeu *et al.* 2012). In addition, the absence of downstream dispersal may lead to undesirable population effects, including one-way routes, source-sink dynamics or ecological traps and thereby compromising conservation efforts (Pelicice and Agostinho 2008, 2012; Agostinho *et al.* 2011; Pompeu *et al.* 2012). Therefore, in the light of the barrier imposed by the reservoir, proposals for fishways require revision; passages become innocuous in the context of large reservoirs and pose a risk of complicating alternative management actions. There is a growing worldwide recognition that fishways have important limitations (Kraabøl *et al.* 2009; Noonan *et al.* 2012; McLaughlin *et al.* 2013) and do not serve the expected conservation role, that is, fishways are a half-way technology (Brown *et al.* 2013). We believe that part of the failure is related to an extreme reductionist approach, which has only considered the barrier imposed by the dam and the need for upstream migration, but has not considered migration as a complex biological dynamic process that involves multiple movements and demands.

The findings elucidated in this study inspire a careful reanalysis about the conservation of fish populations in a scenario where large dams are built in a sequence along the river continuum (including tributary rivers). Most of the major rivers in South America are now intensively regulated, and because there is no management action that can restore the original fauna, the decline of migratory fish is a clear consequence. This decline is a matter of great concern, as these fishes provide important ecosystem functions and services (Hoeinghaus *et al.* 2009), including habitat coupling via energy transport and trophic effects (Freeman *et al.* 2003; Bauer and Hoye 2014). Perhaps, society is not sufficiently informed to understand that the extensive use of hydropower is not compatible with the conservation of fish diversity. The public must be educated about the loss of biodiversity and ecosystem services that occurs at local and regional levels when a large river is dammed (e.g. local extirpation, homogenization, decreased recruitment and fishery yields, disruption of gene flow). Given these negative impacts, the most promising conservation alternative involves the preservation of free-flowing rivers or long fluvial segments with habitats for spawning and early fish development. Maintaining populations of migratory species is possible when critical habitats are present, even in moderate river stretches (c.a. 100–300 km) such as the last fluvial remnants of the Paraná, the São Francisco and Tocantins rivers (Agostinho *et al.* 2004, 2011; Godinho and Kynard 2006; Godinho *et al.* 2007). In some small basins of eastern Brazil, almost all fish species could be preserved if <10% of the hydropower potential was lost to maintain a free-flowing river (Pompeu 2012). More informed decisions about the construction of future dams could hold great significance for the Amazon region, which still preserves pristine hydrological conditions, but has suffered strong Brazilian federal pressure for hydroelectric development. It should be emphasized that river regulation in the Amazon will lead to the creation of large reservoirs in a system that harbours thousands of fish species with various migratory behaviours (Barthem *et al.* 1991; Lowe-McConnell 1999; Lucas and Baras 2001; Araújo-Lima and Ruffino 2003). Authorities should understand that there will be no effective action to restore ecological integrity, biodiversity and ecosystem services after river regulation occurs. The delimitation of whole basins and/or stretches for preservation may represent the only effective measure to maintain some aspects of the regional biodiversity. In this case, systematic conservation planning (Abell *et al.* 2007; Barmuta *et al.* 2011) may be valuable to decide where to build new dams and how to manage existing ones, following local and regional particularities of the system.

In conclusion, we have proposed the theory that large reservoirs function as major barriers to downstream movements of Neotropical migratory fish, and we gathered a body of empirical evidence to support this idea. We also showed that the South American scenario is characterized by large reservoirs, and therefore, the barrier effect must be a common and important phenomenon in river systems of the continent. Although our analysis focused primarily on South America, the theory likely is valid for other river systems throughout the world. We hope that the barrier effect of large reservoirs becomes a major focus of new research, conservation and planning for potential river regulation projects in South America and other regions of the world. Actually, the physical and ecological barriers caused by the dam and the reservoir, respectively, must be considered together when assessing the construction of new dams and managing existing impoundments. Impacts from these dual barriers are pervasive and, in many circumstances, irremediable.

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