



ANDRESSA MENDES DE SENE

**SEASONAL FISH DISTRIBUTION ALONG UNDAMMED
RIVERS TO RESERVOIR CASCADES**

LAVRAS – MG

2020

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Dissertação apresentada à Universidade Federal de Lavras, como parte das exigências do Programa de Pós-Graduação em Ecologia Aplicada, área de concentração em Ecologia e Conservação de Recursos em Paisagens Fragmentadas e Agrossistemas, para a obtenção do título de Mestre.

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Coorientadora

LAVRAS – MG

2020

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2020

À Deus, aos meus familiares, amigos, professores, orientadores, meu namorado e todos que de alguma forma contribuíram para a realização deste sonho.

Dedico

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*“Chamam de violento o rio que tudo arrasta.
Mas ninguém chama violentas as margens que o aprisionam.”*

Bertolt Brecht

RESUMO

Os reservatórios em cascata têm efeitos cumulativos sobre as espécies de peixes, que podem ser menos pronunciados na presença de tributários não barrados. No entanto, ainda é pouco compreendido como esses efeitos são sazonalmente processados. Nessa perspectiva, esse estudo teve como objetivo avaliar a distribuição sazonal das assembleias de peixe em um sistema composto por dois reservatórios em cascata, localizados na bacia do Alto Rio Grande, Brasil, e seus dois afluentes de rios não barrados. A dissertação foi organizada em dois artigos: o primeiro considera toda a assembleia de peixes e o segundo com enfoque nas espécies migradoras. As espécies foram coletadas bimestralmente durante o período de um ano ao longo do sistema, avaliando a composição, riqueza, biomassa, e abundância de espécies nativas e não nativas. Além disso, para as espécies migradoras, a presença de alevinos e juvenis no sistema foi observada, e o estágio de maturação gonadal foi avaliado. As áreas de transição entre rios e reservatório apresentaram os maiores valores de riqueza total de espécies e, ao longo da cascata, um aumento de espécies não nativas foi observado. Os resultados também demonstraram o papel dos rios livres a montante na estruturação da ictiofauna e na manutenção da riqueza de espécies nativas, especialmente as migradoras. Foi possível perceber que as áreas de transição não parecem ter um papel significativo para o recrutamento das espécies migradoras, que parece depender dos rios não barrados e suas lagoas marginais associadas. Destacamos, portanto, a importância da conservação desses rios e da integridade de suas planícies de inundação para a manutenção da diversidade regional de peixes em sistemas de reservatórios em cascata.

Palavras-chave: Alto Rio Grande. Peixes de água-doce. Rios não barrados. Reservatórios em cascata.

ABSTRACT

Reservoir cascades have cumulative effects on fish species, which may be less pronounced in the presence of free-flowing tributaries. However, it is still poorly understood how these effects are seasonally processed. Through this perspective, this study aimed to assess the seasonal distribution of fish assemblages within a system composed of two reservoirs in cascade, located in the Upper Grande River basin, Brazil, and its two undammed tributaries. The dissertation was organized in two articles: the first considered the entire fish assemblage and the second focused on migratory species. The species were collected bi-monthly during a one-year period along the system, assessing composition, richness, biomass, and abundance of native and non-native species. Furthermore, for migratory species, the presence of fingerlings and juveniles in the system was recorded, and the gonadal maturation stage was evaluated. The transition areas between rivers and reservoir presented the higher values of total species richness, and along the cascade, an increase in non-native species was observed. The results also show the role of upstream free flowing rivers in fish fauna structure and in maintaining the richness of native species, especially migratory species. It was possible to notice that the transition areas do not seem to have a significant role in the recruitment of migratory species, since the recruitment probably depends on the undammed rivers and their associated floodplain lagoons. We therefore highlight the importance of conserving these rivers and the integrity of their floodplains for maintaining regional fish diversity in reservoir cascade systems.

Keyword: Upper Grande river. Freshwater fish. Undammed rivers. Reservoir cascade.

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PRIMEIRA PARTE
INTRODUÇÃO GERAL

INTRODUÇÃO GERAL

Os reservatórios são formados com o propósito principal de geração de energia elétrica (AGOSTINHO *et al.*, 2016). No Brasil o recurso hídrico é responsável por 54,03% da energia elétrica total produzida, que advém de 1511 usinas (ANEEL, 2020). Embora a geração de energia elétrica através dos rios atenda à demanda populacional, sendo de suma importância para o desenvolvimento econômico (PELICICE E AGOSTINHO, 2008), é importante ressaltar que esses empreendimentos geram mudanças extremas no fluxo natural dos rios, transformando-os de lótico (águas correntes) para lêntico (águas lentas) e alterando o regime hidrológico (AGOSTINHO *et al.*, 2016; AGOSTINHO, GOMES E PELICICE, 2007a).

Essa mudança leva a modificações de habitats, alteração da disponibilidade de recursos e reestruturação de toda a biota aquática (AGOSTINHO, GOMES E PELICICE, 2007a), podendo ocorrer a proliferação de algumas espécies de peixes (AGOSTINHO, PELICICE E GOMES, 2008), que sobrevivem a essa nova condição (AGOSTINHO, GOMES E PELICICE, 2007b; GOMES E MIRANDA, 2001), e a redução ou mesmo a extinção local de outras (AGOSTINHO *et al.*, 2016; AGOSTINHO, PELICICE E GOMES, 2008; GOMES E MIRANDA, 2001). Aos poucos é esperado que ocorra a formação de um gradiente longitudinal de espécies ao longo do reservatório, em resposta ao gradiente de condições hidrológicas e limnológicas, que é formado pelo barramento do rio (AGOSTINHO, GOMES E PELICICE, 2007a; BAUMGARTNER, BAUMGARTNER E GOMES, 2018; GOMES E MIRANDA, 2001).

A compreensão desse gradiente longitudinal para sistemas de reservatórios em cascata se faz importante, já que representa uma realidade para boa parte dos rios brasileiros (AGOSTINHO *et al.*, 2016; SANTOS *et al.*, 2017). Estudos têm demonstrado que os reservatórios em cascata apresentam efeitos cumulativos sobre as espécies de peixes em direção a jusante, com tendência de diminuição da riqueza de espécies nativas e da abundância de espécies migradoras, e ao mesmo tempo, um aumento na similaridade taxonômica e na riqueza de espécies não nativas (PETESSE E PETRERE, 2012; SANTOS *et al.*, 2017; LOURES E POMPEU, 2018; SANTOS *et al.*, 2018). A presença de tributários nessas áreas barradas tem demonstrado importância para que esses efeitos sejam menos pronunciados (SANTOS *et al.*, 2017; LOURES E POMPEU, 2018).

Entretanto, ainda é pouco compreendido como esses efeitos são sazonalmente processados. Desta forma, o presente trabalho tem como objetivo contribuir para o preenchimento desta lacuna de conhecimento, utilizando como objeto de estudo os dois primeiros reservatórios em cascata da bacia do Alto Rio Grande e que possuem dois rios livres de barramentos à montante do sistema. O estudo foi organizado em dois artigos, o primeiro abordando toda a assembleia de espécies de peixes e o segundo com enfoque nas espécies migradoras, uma vez que estas são fortemente afetadas pela regulação dos rios por realizarem longos deslocamentos ao longo do seu ciclo de vida e seu recrutamento ser dependente de inundações.

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SEGUNDA PARTE

ARTIGOS

ARTIGO 1

SEASONAL FISH DISTRIBUTION ALONG FREE-FLOWING RIVERS TO RESERVOIR CASCADES

Artigo redigido conforme as normas da revista *Neotropical Ichthyology*.

Seasonal fish distribution along free-flowing rivers to reservoir cascades

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ABSTRACT

Reservoir cascades have cumulative effects on fish species that can be less pronounced with the presence of incoming tributaries. However, it is still poorly understood how these effects are seasonally processed. This study aimed to assess the seasonal fish assemblage distribution along the first two reservoirs in cascade within the Upper Grande River basin, which receive two long free-flowing rivers. Fish species were collected bi-monthly throughout one year along this system, and were evaluated by composition, richness, biomass, and abundance of native and non-native species. The transitional areas between the rivers and reservoir presented the highest fish richness, and an increase of non-native species was observed along the cascade. The results also showed the role of the upstream rivers for structuring the fish fauna and maintaining the native fish richness, especially for migratory species. We emphasize the relevant role of non-regulated rivers that flow into cascading reservoir systems in maintaining regional fish diversity.

Keywords: Freshwater fish, Grande River, Reservoirs, Tributaries.

RESUMO

Os reservatórios em cascata causam efeitos cumulativos em espécies de peixes, que podem ser menos pronunciados com a presença de tributários afluentes. Entretanto, ainda é pouco compreendido como esses efeitos são sazonalmente processados. O estudo objetivou avaliar a distribuição sazonal da assembleia de peixes ao longo dos dois primeiros reservatórios em

cascata no Alto Rio Grande, e que recebem dois grandes tributários livres de barramento. Espécies de peixes foram coletadas bimestralmente durante um ano ao longo desse sistema, e foram avaliadas a composição, riqueza, biomassa, e abundância de espécies nativas e não nativas. A região de transição entre os rios e o reservatório foi a que apresentou a maior riqueza de peixes, e um aumento de espécies não nativas foi observado ao longo da cascata. Os resultados também evidenciaram o papel dos rios a montante na estruturação da fauna de peixes e na manutenção da riqueza de peixes nativos, principalmente espécies migradoras. Salientamos o relevante papel dos rios livres de barramentos que fluem para sistemas de reservatórios em cascata, na manutenção da diversidade regional de peixes.

Palavras-chave: Peixes de água doce, Reservatórios em cascata, Rio Grande, Rios não barrados.

RUNNING HEAD

Seasonal fish fauna in a reservoir cascade.

INTRODUCTION

Reservoir cascades have cumulative effects on native fish species richness as well as abundance of migratory species, which tend to decrease in downstream direction, while taxonomic similarity and non-native species richness tend to increase (Petesse, Petreire, 2012; Santos *et al.*, 2017; Loures, Pompeu, 2018; Santos *et al.*, 2018). These effects, however, can be less pronounced by the presence of tributaries in dammed areas (Santos *et al.*, 2017; Loures, Pompeu, 2018). It is still poorly understood how these effects are seasonally processed, as well as the influence of undammed rivers in these systems.

According to the River Continuum Concept (RCC) (Vannote *et al.*, 1980), undammed rivers are expected to have a longitudinal resource gradient. Furthermore, biotic and abiotic variables are expected to change progressively from upstream to downstream, leading to gradual changes in fish-species composition. However, impoundments change the longitudinal gradient in flow intensity and direction (upstream to downstream) as a function of dam position, as postulated by the Serial Discontinuity Concept (SDC) (Ward, Stanford, 1983). Considering a cascade reservoir scenario, this effect is expected to intensify as proposed by Cascading Reservoir Continuum Concept (CRCC) (Barbosa *et al.*, 1999).

In regulated rivers, especially when a reservoir cascades are created, a proliferation of some fish species, which can survive in these new conditions, may occur (Gomes, Miranda,

2001; Agostinho *et al.*, 2007a; Agostinho *et al.*, 2008). Additionally, a reduction or even local extirpation of some fish species can be expected, like long-distance migratory fish (Gomes, Miranda, 2001; Agostinho *et al.*, 2008; Pelicice *et al.*, 2015; Agostinho *et al.*, 2016; Oliveira *et al.*, 2018). This change in fish composition and abundance occurs gradually as a result of environmental filters formed by the reservoirs (Gomes, Miranda, 2001). Also, when a lotic segment is found upstream, a longitudinal gradient of species along the reservoir is formed in response to the gradient of hydrological and limnological conditions as a consequence of river impoundment (Gomes, Miranda 2001; Agostinho *et al.*, 2007c; Baumgartner *et al.*, 2018). Here, there is a tendency to find rheophilic species (fish that usually prefer to live in moving water), including migratory species, in the lotic portions of the reservoir (Agostinho *et al.*, 2016). However in lentic areas, these species tend to be medium-sized sedentary species with low diet specificities (Agostinho *et al.*, 2007a; Agostinho *et al.*, 2016; Oliveira *et al.*, 2018). Although this gradient trend of fish assemblage is expected, variations may occur due to the peculiarities of local fauna and reservoir characteristics (Agostinho *et al.*, 2007a; Baumgartner *et al.*, 2018).

Recently, some studies have been trying to better understand the longitudinal gradient for reservoir cascade systems, as they represent a reality of the Brazilian river landscape (Agostinho *et al.*, 2016; Miranda, Dembrowski, 2016; Santos *et al.*, 2017; Loures, Pompeu, 2018, 2019). Additionally, the effects of these reservoir cascade systems on fish assemblages are expected to become more pronounced over time from one reservoir to another (Petesse, Petrere, 2012; Santos *et al.*, 2017; Loures, Pompeu, 2018). Native species richness and abundance of migratory species tend to decrease downstream of cascade reservoir systems as these reservoirs are generally smaller and clearer (Santos *et al.*, 2017; Loures, Pompeu, 2018). At the same time, taxonomic similarity and non-native species tend to increase consistently among the reservoirs (Petesse, Petrere, 2012; Santos *et al.*, 2018; Loures, Pompeu, 2018). It is suggested that changes in hydrological and limnological characteristics of water are responsible for changes in fish assemblages but also reservoir position in the cascade, reservoir water retention time, age, and connectivity are also important (Miranda, Dembkowski, 2016; Santos *et al.*, 2017, 2018).

The Paraná River basin has a sequence of reservoirs in its main course, however some important lotic remnants are still found, such as the Aiuruoca River as well as the higher part of Grande River, upstream of the Camargos Hydropower Plant (Suzuki *et al.*, 2011; Borges, Abjaudi, 2016). In this context, this study aimed to assess the seasonal fish assemblage

distribution along the two first reservoirs in cascade at the Upper Grande River basin. Specifically, this study sought to answer the following four questions: (1) Is there variation in fish-species richness, biomass, and abundance along the sites?; (2) Does temporal beta diversity vary along the reservoir cascade?; (3) How is fish assemblage structured along the system and between seasons?; and (4) Which are the factors that drive fish assemblage structure along the reservoir cascade? We expected a significant variation in fish assemblage along the cascade with a decrease in total and native richness, an increase in non-native species, and a decrease in fish biomass and abundance. We predict that temporal beta diversity varies along the cascade, and that the variation is higher in the upper part of the system due to the influence of river seasonality. We also predict a longitudinal gradient in fish assemblages along the cascade, with differences in species composition along the system, which will be more visible during the dry season. Lastly, we expect that water transparency and position of sites along the reservoir cascade are important predictors of fish assemblage structure.

MATERIALS AND METHODS

Study area. The Upper Grande River basin, part of the Paraná River basin, is located in southeastern Brazil and creates a natural border between the state of Minas Gerais and São Paulo, occupying an area of 143,437,79 km², where 60.2% belongs to the state of Minas Gerais (IPT, 2008). Along the main stem, there are 12 hydropower dams, leading to a dramatic loss of original riverine habitats. However, some important stretches of free-flowing rivers are still found, especially in its upper course (Suzuki *et al.*, 2011; Borges, Abjaudi, 2016). The regional climate is classified as mesothermal mild and semi-humid, with mean temperature ranging between 10 °C and 15 °C, presenting 4 to 5 dry months and a mean precipitation of 1,450 to 1,600 mm per year (Borges, Abjaudi, 2016).

This study took place in the first two upstream reservoirs: Camargos and Itutinga. The Camargos Hydropower Plant started operating in 1960; it has an installed capacity of 45 MW and an associated reservoir with an area of 73.35 km². The Itutinga Hydropower Plant, located immediately downstream of Camargos' dam, was inaugurated in 1955 and presents a run-of-the-river reservoir area of 1.72 km² and a power generation capacity of 52 MW (Cachapuz, 2006) (Fig. 1). Both plants coordinate operations (Cachapuz, 2006), with 14 days of water residence time (Suzuki *et al.*, 2011). While two long free-flowing rivers (the Aiuruoca and Grande) flow to the Camargos reservoir, no significant tributary reaches Itutinga's reservoir.

Ten sampling sites were distributed along the Aiuruoca (Sites 12 and 22) and Grande Rivers (Sites 10 and 20), draining into the Camargos reservoir, and along the Camargos (Sites 30, 40, 50, and 60) and the Itutinga's (Sites 70 and 80) reservoirs (Fig. 2). The distance among sites varied between 5 and 10 km apart from each other.

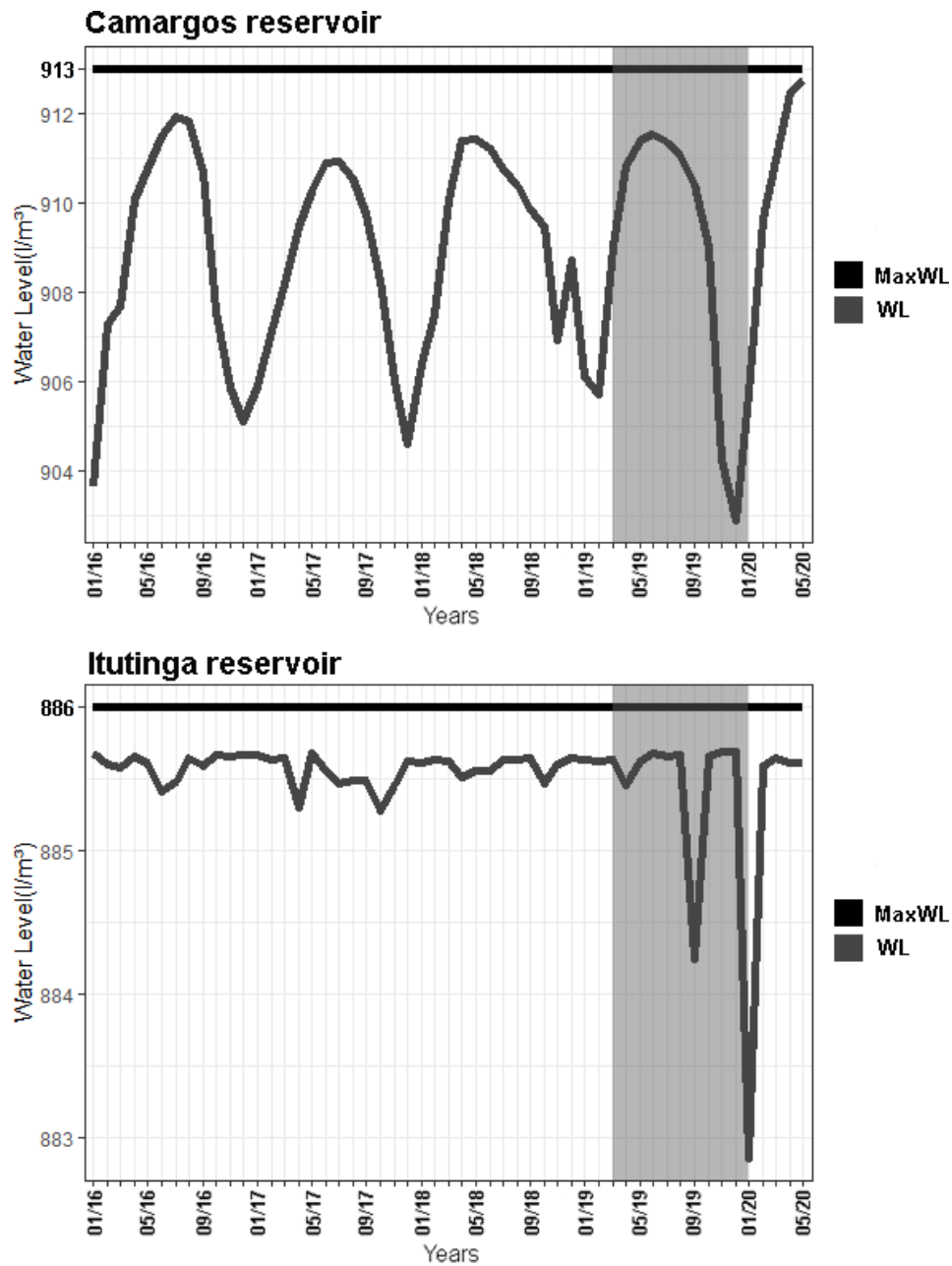


Fig. 1. Maximum and monthly water level along four years of the Camargos and Itutinga reservoirs. The highlighted period indicates the time in which data sampling was performed.

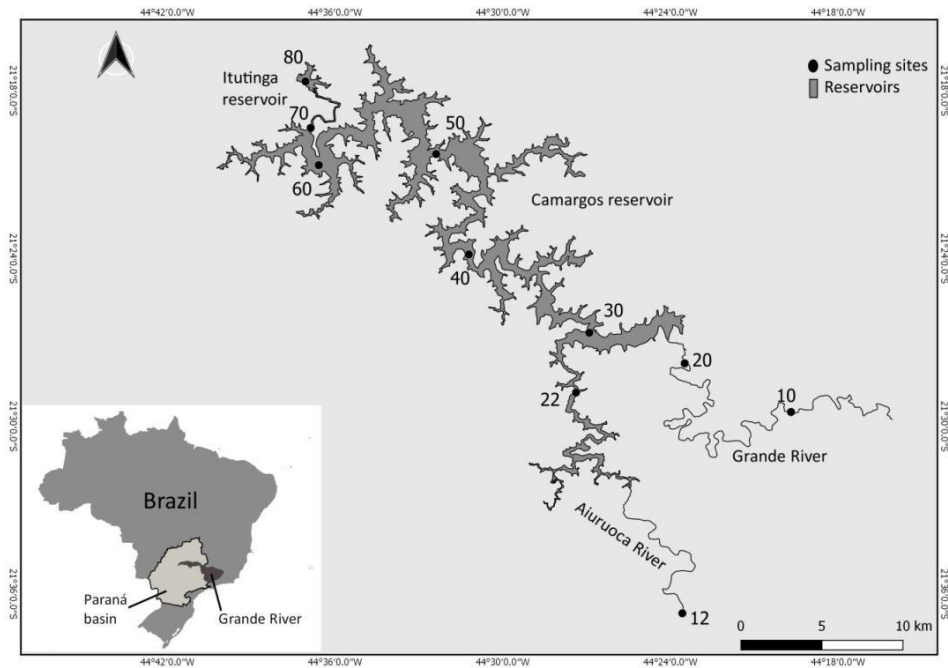


Fig. 2. Sampling sites (indicated by the numbers) in the Grande River basin in Minas Gerais, Brazil.

Sampling. Six fish surveys were performed bi-monthly at each sampling site during the period between March 2019 and January 2020. Fish were caught using gill nets set with mesh sizes of 3, 4, 5, 6, 7, 8, 10, 12, 14 and 16 cm opposite knots, with each net a length of 10 meters. They were placed early in the afternoon in littoral areas and removed the following morning, totalizing about 12 – 14 hours of exposure. Active sampling was performed with seines (5 m long, 2 m high, 5 mm mesh size) with a standardized effort of 5 beach seines pulled for 25 m per sampling point, excluding the first collection from point 12 (Fig.1), where littoral areas had depths of over 2 m and, therefore, gear use was not possible. Two semicircular hand nets (80 cm in diameter, 1 mm mesh size) were also used, with a standardized effort of 20 min. per site. The collected fish were anesthetized in Eugenol solution 50mg/l, fixed in 10% formalin solution, and then transferred to a solution of alcohol 70% for preservation. In the laboratory, each specimen was identified (Nakatani *et al.*, 2001; Ota *et al.*, 2018; Ribeiro *et al.*, 2019), measured (body length), and weighed. Voucher specimens were deposited in the Ichthyologic Collection of Federal University of Lavras – UFLA (CI – UFLA).

At each sampling event, pH and temperature were measured with a multiparameter water quality probe (YSI 556 MPS). Water transparency was estimated using a Secchi disc;

hydrological variables (water level and water flow) data were obtained from the local hydropower company (Companhia Energética de Minas Gerais – CEMIG).

Statistical analysis. The total abundance data was standardized by calculating catch per unit of effort (CPUE) in number of individuals (CPUE_n) per 100 m² of gillnets and in biomass (CPUE_b) per 100 m² of gillnets. Total fishing effort used in each sampling were 160 m². Catch per unit of effort were estimated by the formula:

$$CPUE_n = \sum_{i=1}^3 \left(100 \times \frac{N_i}{E_i} \right)$$

Where: N_i = number of fish captured by gillnet i (3, 4, 5, 6, 7, 8, 10, 12, 14 and 16 cm); E_i = fishing effort for gillnet i .

For CPUE_b catch per unit of effort were estimated by the formula:

$$CPUE_b = \sum_{i=1}^3 \left(100 \times \frac{B_i}{E_i} \right)$$

Where: B_i = biomass of fish captured by gillnet i (3, 4, 5, 6, 7, 8, 10, 12, 14 and 16 cm); E_i = fishing effort for gillnet i .

To answer the first question regarding native richness and non-native richness in relation to total fish richness, CPUE_n and CPUE_b were calculated for each site. To test if there was a significant difference in variables among sites, a Kruskal-Wallis test was performed. When a significant difference was detected ($p < 0.05$), the post hoc pairwise comparisons using the Wilcoxon rank-sum test was realized.

To address the second question, two approaches of beta diversity measurements were used for complementary results. Primarily, the additive partition of beta diversity (Lande, 1996) was calculated, which considers richness values given by regional richness (Gamma) minus the local average richness (Alpha). Homogeneity of dispersions tests (PermDisp) (Anderson *et al.*, 2008) were also performed considering species composition (presence/absence), based on an Euclidean distance similarity matrix. The results showed the mean of centroid distances, in which case we calculated the mean distance of the six samplings for each site. The average value indicates temporal variation – the higher the value, the greater the temporal variation in species composition at the site. Both analyses were performed for each sampling site, considering the six surveys.

The species composition (the taxonomic identity of species) was used to perform a non-metric multidimensional scaling (NMDS) in order to understand how fish assemblage is structured throughout the system and seasons. Presence/absence data were used because different fishing gears were used during surveys (gill nets, seines, and hand nets). The resemblance matrix was calculated based on the Jaccard similarity index (Clarke, Gorley, 2006). Fish assemblages were compared between seasons, considering four groups formed by sampling sites: i) River (sites 10 and 12) ii) Transition (sites 20, 22, and 30); iii) Camargos (sites 40, 50, and 60); iv) Itutinga (sites 70 and 80). These groups were formed considering their position along the cascade system and similar hydrological condition (Tab. 1). In order to test if the differences observed in NMDS results were statistically significant, an analysis of similarity (ANOSIM) was performed. ANOSIM analysis results in a statistic R with a significance level (P) tested for pairwise differences among groups. R-values closer to 1 indicate more dissimilarities between groups, while closer to 0 the more similar they are (Clarke, Gorley, 2006). To understand which species most contributed to the similarity in each group and season, a similarity percentage analysis (SIMPER) was performed based on the presence/absence matrix (Clarke, Gorley, 2006).

Tab. 1. Sampling sites and respective characteristics and coordinates. The groups were determined for data analysis purposed considering similar hydrological condition.

Sites	Groups	Characteristics	Coordinates
10	River	On the Grande river, in a lotic section upstream of the Camargos reservoir	-21.491529° -44.328130°
12	River	On the Aiuruoca river, in a lotic section upstream of the Camargos reservoir	-21.613229° -44.397045°
20	Transition	On the Grande river, in the transition region between a lotic stretch with the Camargos reservoir	-21.462530° -44.391532°
22	Transition	On the Aiuruoca river, in the transition region between a lotic stretch with the Camargos reservoir	-21.479907° -44.456347°
30	Transition	At the Camargos reservoir, at the confluence of the Aiuruoca and Grande rivers	-21.444272° -44.448429°

Sites	Groups	Characteristics	Coordinates
40	Camargos	In the Camargos reservoir, about 11 km downstream from the previous point	-21.397605° -44.520289°
50	Camargos	In the Camargos reservoir, about 11 km downstream from the previous point	-21.337780° -44.539758°
60	Camargos	In the Camargos reservoir, about 11 km downstream from the previous point	-21.344771° -44.609349°
70	Itutinga	Downstream of Camargos dam, near a escape channel and upstream of the Itutinga dam	-21.322170° -44.614583°
80	Itutinga	At the Itutinga reservoir, near its dam	-21.294487° -44.617696°

To answer the last question regarding the factors that drive fish assemblage structure along the reservoir cascade, distance-based linear model (DistLM) analyses (Anderson *et al.*, 2008), based on Jaccard dissimilarity matrix (forward with adjusted R), were performed. The variables explored were: water transparency, pH, temperature, water flow (Q), water level (dNA), season, habitat (lotic and lentic), and region.

Maps were made in QGIS (version 2.18.22) with GRASS 7.4.1 and adapted in Adobe Photoshop (version CS3) to display analysis results. Kruskal-Wallis tests and graphs were performed in the RStudio software (version 3.4.0) using “vegan” and “ggplot2” packages. The NMDS, ANOSIM, SIMPER, PermDisp, and DistLm was performed in the programs PRIMER 6 & PERMANOVA+ (Anderson *et al.*, 2008).

RESULTS

A total of 21,336 individuals were recorded belonging to 39 fish species, 31 genera, 15 families and 6 orders which were sampled using gill nets, seines, and semicircular hand nets (Tab. 2). Characiformes (64.1%), Siluriformes (17.9%), Cichliformes (7.7%), and Gymnotiformes (5.1%) were the most representative orders. Four species (10.2% of total richness) of non-native fish and seven (17.9%) species of migratory fish were found. Although 60 samplings were performed altogether, the accumulation curve did not stabilize (Fig. 3).

Taxon	Sampling sites									
	10	12	20	22	30	40	50	60	70	80
<i>Geophagus brasiliensis</i> (Quoy & Gaimard, 1824)	X		X	X	X	X	X	X	X	X
Cyprinodontiformes										
Poeciliidae										
<i>Poecilia reticulata</i> (Peters, 1859) ^a									X	X
Gymnotiformes										
Gymnotidae										
<i>Gymnotus</i> aff. <i>carapo</i> (Linnaeus, 1758)			X		X					
Sternopygidae										
<i>Eigenmannia virescens</i> (Valenciennes, 1836)	X		X	X	X	X	X		X	X
Siluriformes										
Loricariidae										
<i>Hypostomus</i> cf. <i>iheringii</i> (Regan, 1908)	X	X	X	X	X	X		X	X	X
<i>Hypostomus</i> cf. <i>regani</i> (Ihering, 1905)	X	X	X		X	X	X	X	X	X
<i>Neoplecostomus</i> cf. <i>paranensis</i> (Langeani, 1990)	X									
Pimelodidae										
<i>Iheringichthys labrosus</i> (Lütken, 1874)	X	X			X	X	X	X	X	X
<i>Pimelodus maculatus</i> (Lacepède, 1803) ^b	X	X	X	X	X	X	X	X	X	X
<i>Pimelodus microstoma</i> (Steindachner, 1877)							X	X		
Pseudopimelodidae										
<i>Pseudopimelodus mangurus</i> (Valenciennes, 1835)		X								
Synbranchiformes										
Synbranchidae										
<i>Synbranchus marmoratus</i> (Bloch, 1795)						X				
Total Richness	21	22	27	25	27	26	21	21	22	20

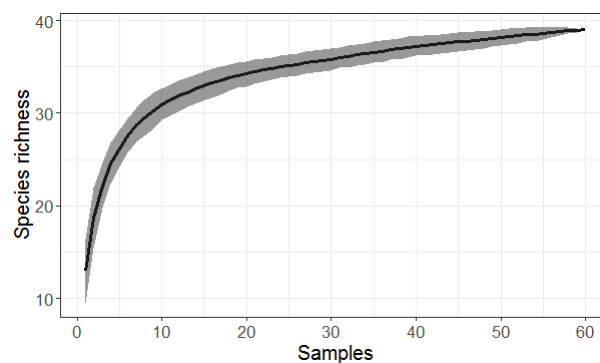


Fig. 3. Species accumulation curve, with 95% confidence interval, considering all samples at all points.

There was a variation in fish assemblage along the cascade, but not in a linear gradient. Total native fish species had higher values at the transitional sites (20, 22, 30) and in the first Camargos site (40) (Fig. 4), and non-native fish species richness tended to increase downstream, and represented 20% of the local species richness at Itutinga's reservoir (Fig. 5).

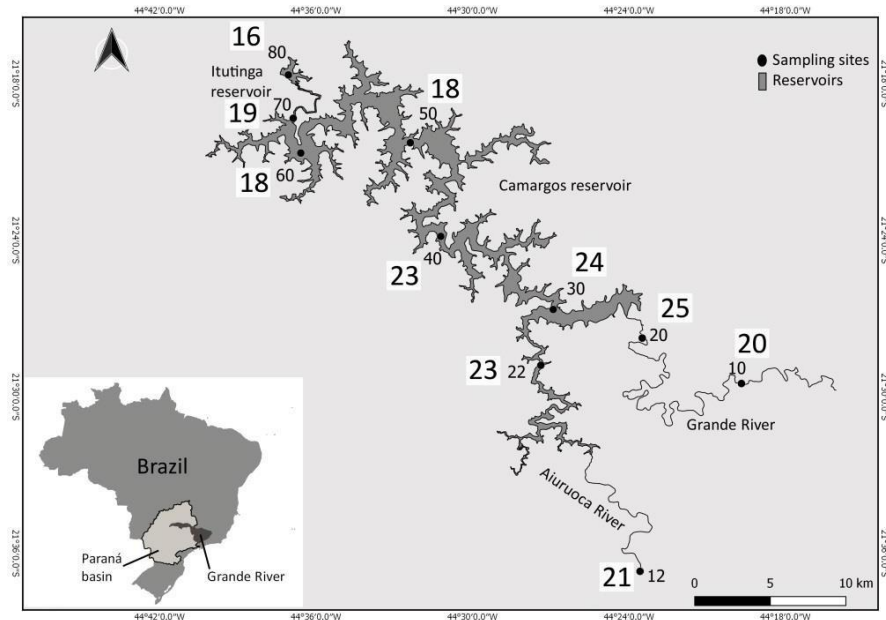


Fig. 4. Total native species richness by sampling site.

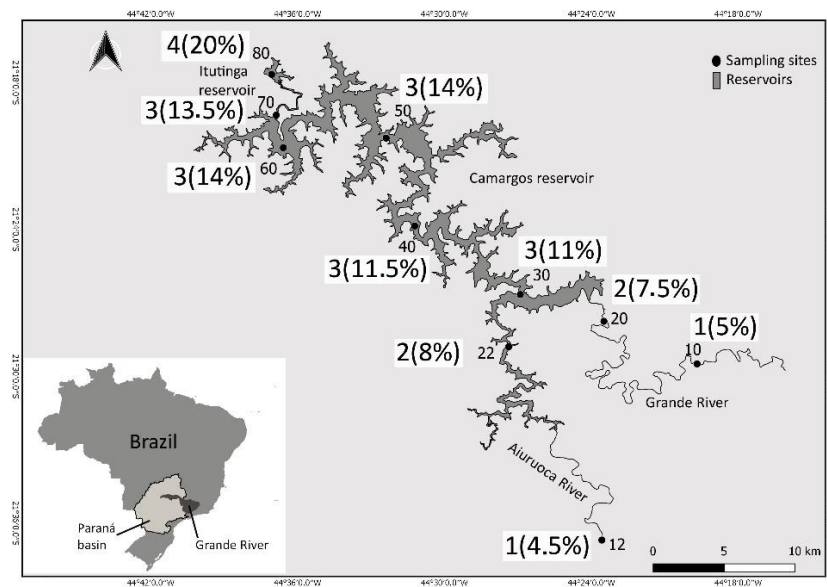


Fig. 5. Absolute non-native species richness and respective frequency (in parenthesis) by sampling sites.

No significant differences were observed in abundance CPUE_n (KW = 9.42; $p = 0.39$) and biomass CPUE_b (KW = 10.99; $p = 0.27$) between sites (Figs. 6a-b). However native richness (KW = 36.49; $p < 0.01$) and non-native relative richness (KW = 25.46; $p < 0.01$)

varied along the studied gradient. Despite that, when pairwise multiple comparisons tests were performed, no significant difference between sites were detected.

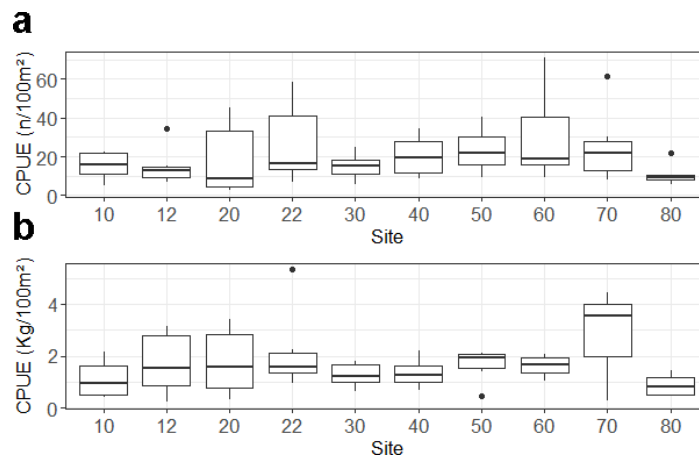


Fig. 6. Variation (median \pm interquartile range and amplitude) in fish abundance along the sampling sites. **a.** Variation in number (CPUE_n); **b.** Variation in biomass (CPUE_b).

Higher values of gamma diversity were observed at the transitional sites (20, 22, and 30) and at the first site in the Camargos reservoir (40), reflecting higher values of alpha. Temporal beta diversity (additive partitioning) did not present a distinctive pattern along the gradient (Fig. 7). However, as indicated by the PermDisp analyses, species composition in transition zones (20, 22 and 30) and at the Itutinga (80) reservoir presented the lowest temporal variation (Fig. 8).

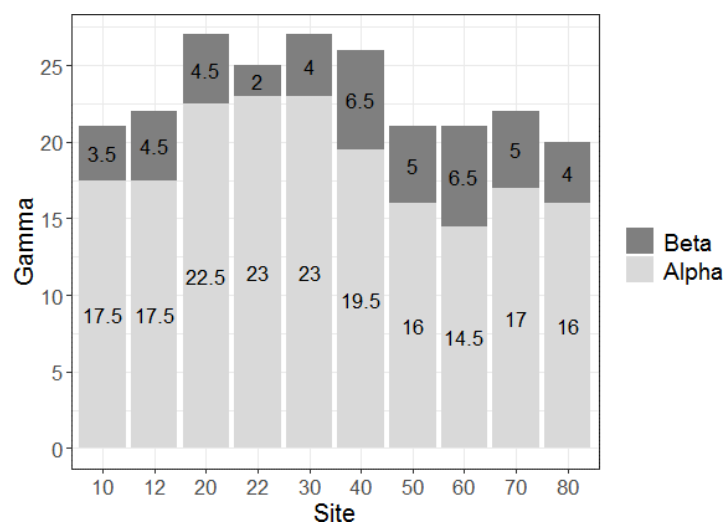


Fig. 7. Additive diversity partitioning along the sampling sites in reservoir cascade.

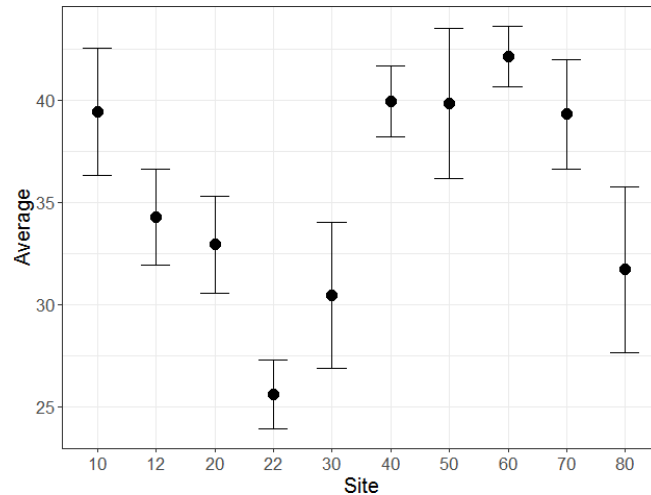


Fig. 8. Mean centroid distance (mean \pm standard deviation) of species composition for the sampling sites along the reservoir cascades.

The four regions (River, Transition, Camargos, and Itutinga) were distinct in the nMDS analyses, based on the assemblage composition, and such differences were confirmed in both dry (ANOSIM: global $R=0.718$, $P<0.01$) and wet (ANOSIM: global $R=0.567$, $P<0.01$) seasons. However, riverine points (10 and 12) and those of the transition sites (20, 22, and 30) were more similar to each other in the wet season (Fig. 9).

SIMPER analyses indicated that the transition samplings points were the ones with higher average similarity compared to the others. While few species, like *Astyanax fasciatus*, were widespread along the gradient, some were associated to specific regions and with a seasonal pattern. *Characidium aff. zebra*, for instance, was frequent at the riverine sites and found at the transition only during the wet season. The wet season was also related to higher frequency of migratory species at the riverine sites (Tab. 3).

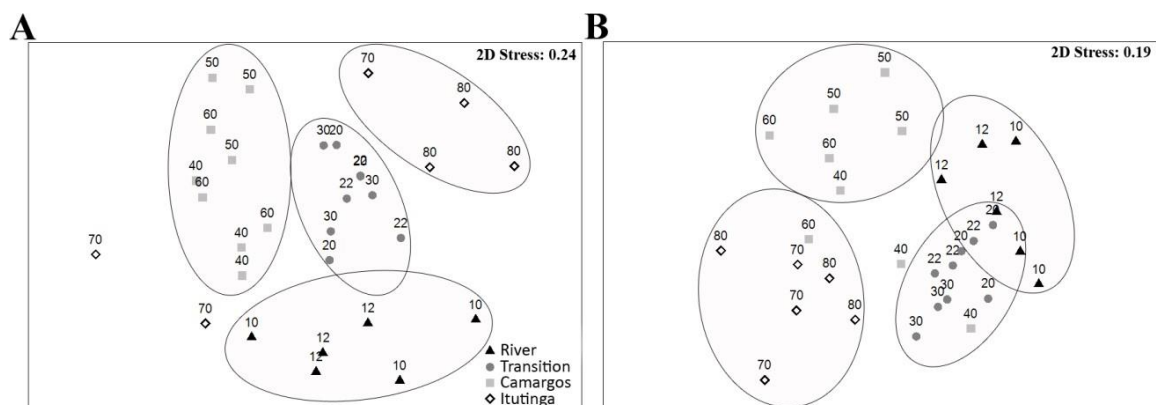


Fig. 9. Non-Metric Multidimensional Scaling (nMDS) with total richness, based on Jaccard distance index in dry (A) and wet season (B).

Species	Rivers		Transition		Camargos		Itutinga	
	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet
<i>Salminus hilarii</i> ^B	0.67	0.75	-	-	-	-	-	-
<i>Schizodon nasutus</i>	0.5	-	1	1	1	1	0.83	0.83
<i>Serrapinnus heterodon</i>	-	-	0.89	0.89	-	-	-	-
<i>Serrapinnus notomelas</i>	-	-	1	1	-	-	-	-
Accumulated contribution (%)	93.94	90.25	92.15	90.31	90.31	90.87	91.57	91.79
contribution (%)								
Average similarity (%)	51.37	53.19	69.35	69.64	60.88	51.74	50.54	56.78

The region along the gradient was the most important variable in explaining fish composition, accounting alone for 14% of fish assemblage structure. In the sequential test, the best significant model included six variables that together explained 21% of the variation in fish assemblage composition (Tab. 4).

Tab. 4. Distance-based linear models (DistLM) results from marginal and sequential tests. Water flow was represented by Q and water level by dNA.

Variable	P	Explained variation (%)	Cumulative explained variation (Adj R ²)
<i>Marginal tests</i>			
Season	0.324	1.88	
Region	0.001	14.00	
Habitat	0.001	10.00	
Temperature	0.001	4.18	
pH	0.038	3.18	
Transparency	0.001	5.58	
dNA	0.002	5.66	
Q	0.299	1.94	
<i>Sequential test – Best Model</i>			
Region	0.001	14.50	12.99

Variable	P	Explained variation (%)	Cumulative explained variation (Adj R ²)
+Transparency	0.005	3.64	15.23
+Temperature	0.005	3.64	17.55
+Season	0.041	2.52	18.75
+Ph	0.030	2.51	19.99
+dNA	0.035	2.47	21.23

DISCUSSION

Our hypotheses were partially supported. Although we observed an increase of non-native species richness along the cascade, the highest richness values occurred in the transition areas, and no differences in captures (CPUE) or trend of temporal beta diversity along the cascades were observed. Differences in species composition along the system were detected, and they were more pronounced during the dry season. Still, as expected, region along the cascade was one of the main drivers of fish assemblage composition.

The number of registered species in this study represents about 13% and 44% of the fish fauna recorded for the Upper Paraná (Langeani *et al.*, 2007) and the Upper Grande River (Casarim *et al.*, 2012), respectively. The dominance of Characiformes and Siluriformes orders represents the regional pool of species. The fish fauna from the reservoirs studied were previously known from a single paper which recorded 18 fish species in Itutinga's reservoir (Alves *et al.*, 1998). Our study added four new occurrences for this reservoir.

Instead of a linear decrease in fish richness along the cascade system as expected, richness was higher at the transitional sites. A downstream decrease in native species richness is the most observed pattern observed in cascade reservoir systems (Santos *et al.*, 2017; Loures, Pompeu, 2018), but higher richness at the transitional zones have also been reported (Santos *et al.*, 2010; Terra *et al.*, 2010; Yang *et al.*, 2012; Nobile *et al.*, 2019; Sandhya *et al.*, 2019; Guedes *et al.*, 2020). Transition zones are considered an ecotone area (Willis, Magnuson, 2000), sharing physical, chemical, biological, and ecological connections with the river and the reservoir. Thereby, such zones provide a coexistence of species adapted to both lotic and lentic conditions (Willis, Magnuson, 2000; Terra *et al.*, 2010; Buckmeier *et al.*, 2014; Nobile *et al.*, 2019; Sandhya *et al.*, 2019). The presence of long stretches of free rivers

upstream from the Camargos reservoir is possibly one of the main factors related to the observed pattern, as such environments contribute to the occurrence of rheophilic species in the upper part of the studied system.

The increase in non-native fish species along the cascade was expected because the impoundments are considered one of the main vectors for non-native fish species introduction, which is facilitated by fish stocking, aquaculture, and sport angling activities in this environment (Casimiro *et al.*, 2017; Gubiani *et al.*, 2018). Non-native fish species can impact the system in many ways: competing for resources, introducing pathogens and parasites, modifying the functioning of the system, and changing habitats and prey availabilities (Agostinho *et al.*, 2007b). Studies have already shown that non-native species tend to increase consistently along the reservoir's cascade in the Paranapanema (Casimiro *et al.*, 2017; Pelicice *et al.*, 2018) and Araguari River (Loures, Pompeu, 2018), both in the Paraná River basin. The greater presence of non-native species in the lacustrine regions may partially explain the absence of differences in catches (CPUE) throughout the studied system. Due to the absence of natural lakes in Brazil, few species evolved traits to cope with lentic habitats (Gomes, Miranda, 2001; Agostinho *et al.*, 2016). As a result, rheophilic species, including migratory fish (usually larger fish sizes), are usually found in higher abundance in lotic portions of the reservoir (Agostinho *et al.*, 2016), while non-native species and a few small-sized sedentary species became abundant in lentic areas (Gomes, Miranda, 2001; Pelicice *et al.*, 2018).

Temporal beta diversity did not present a distinctive pattern along the gradient, but this may be related to some local characteristics. The Camargos reservoir presents extreme water level fluctuations due to operational requirements, which could explain the temporal instability of its inner regions (sites 40, 50, and 60). Adversely, the inner region of the Itutinga, a run-of-the-river reservoir, presented lower values of temporal beta diversity, similar to the transition zone. A factor that could contribute to the stability of fish assemblages in the transitional area is the successful recruitment of some species (Yang *et al.*, 2012) and the greater availability of resources, which could maintain stable fish assemblages (Terra *et al.*, 2010).

The four defined regions along the studied cascade (river, transition, Camargos, and Itutinga) presented distinct fish species compositions in both seasons. This longitudinal gradient is created in response to hydrological and limnologic gradients of conditions formed by river impoundments (Gomes, Miranda, 2001; Agostinho *et al.*, 2007c; Baumgartner *et al.*,

2018). Such spatial variation in fish composition have been described for several cascade systems (Santos *et al.*, 2017; Loures, Pompeu, 2018; Pelicice *et al.*, 2018). The higher similarity among the river and transition sites during the wet season was also expected and points to the effects of the increased flows in the upper portion of the reservoir (Thomaz *et al.*, 2007; Terra *et al.*, 2010;), expanding to downstream riverine conditions.

Differences among regions were related to differential occurrences of most species. *Characidium* aff. *zebra*, for instance, was frequent at the riverine sites and found at the transition sites in the wet season. Its presence has been associated to low flow river conditions over sandy substrates (Leal *et al.*, 2011), and congeneric species have been registered in riverine and transitional areas of reservoirs (Santos *et al.*, 2010; Terra *et al.*, 2010; Leal *et al.*, 2011). Migratory fish species also increased their occurrence in the riverine region in the wet season. These species rely on the seasonal flood regime to complete their life cycles, depending on free-flowing rivers to reproduce (Pompeu *et al.*, 2012; Agostinho *et al.*, 2016). One of the few species widespread along the gradient was *Astyanax fasciatus*. This species is able to reproduce in different kinds of environments, especially in lentic water, presenting an omnivorous diet and low parental care (Agostinho *et al.*, 2007c). This genus is common to find in different environments, including rivers, transitions, and reservoirs, in both seasons (Santos *et al.*, 2010; Terra *et al.*, 2010) as well as in a cascade systems (Loures, Pompeu, 2018; Pelicice *et al.*, 2018).

The significance of the region along the cascade as the main driver of fish assemblage structure stresses the importance of free-flowing upstream rivers. The connectivity represents one important factor for fish species distribution, and the role of such non-regulated rivers for the reservoir have been already described (Carvajal-Quintero *et al.*, 2019). Transparency, temperature, and season have also contributed to the best model aiming to explain fish assemblage structure. The progressive increase in water transparency along reservoirs has been related to differential mortality of eggs and larvae (Pelicice *et al.*, 2015), while water temperature is one of the most important factors that influence fish distribution (Buisson *et al.*, 2008). The seasonality, in turn, has frequently been described as an important driver of fish communities in reservoir (Terra *et al.*, 2010) and probably reflects several aspects of the studied system such as seasonal river flow changes, reservoir level, and local precipitation patterns.

By assessing the fish assemblage seasonal distributions along the two first reservoirs in cascade at the Upper Grande River basin, we verified the role of free rivers upstream for the structuring of the fish fauna. We have also highlighted the importance of free rivers and

transition areas between lotic and lentic environments for maintaining native fish richness, especially migratory species in rivers during the wet season. This study also reinforces the role of cascade systems in the increase of non-native species, as well as the importance of free-flowing rivers for fish species in a cascade system, indicating that the construction of dams in these free rivers should be avoided.

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ARTIGO 2

**MIGRATORY FISHES FROM RIVERS TO RESERVOIRS: SEASONAL AND
LONGITUDINAL PERSPECTIVES**

Artigo redigido conforme as normas da revista Pan-American Journal of Aquatic Sciences.

Migratory fishes from rivers to reservoirs: seasonal and longitudinal perspectives

Running headline: Migratory fishes in a reservoir cascades.

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Abstract: Migratory fishes have a high ecological, social, and commercial value and they are strongly affected by the regulation of river water levels. This study aimed to understand how migratory fishes use the longitudinal gradient, in an upstream to downstream direction, along two free-flowing rivers and two reservoirs in a cascade within the Upper Grande River basin. Migratory fish abundance, biomass, richness, fingerlings and juveniles presence, and macroscopic gonadal maturation stage were evaluated by bi-monthly collection during one year along the system. Migratory fish recruitment seems to occur on depending of free-flowing rivers upstream, and transition areas do not seems have a significant role for recruitment. Therefore, we highlighted the importance of the maintenance of free-flowing rivers and the integrity of their floodplains.

Keywords: Recruitment, reservoir cascade, free rivers, freshwater fish

Resumo: Peixes migradores de rios a reservatórios: perspectiva sazonal e longitudinal. Os peixes migradores têm um alto valor ecológico, social e comercial e são fortemente afetados pela regulação do nível de água dos rios. Este estudo teve como objetivo compreender como os peixes migradores utilizam o gradiente longitudinal, na direção montante a jusante, ao longo de dois rios de fluxo livre e dois reservatórios em uma cascata na bacia do Alto Rio Grande. A abundância, biomassa, riqueza, presença de alevinos e juvenis e o estágio de maturação gonadal macroscópico das espécies migradoras foram avaliados por coleta bimestral durante um ano no sistema. O recrutamento de peixes migradores parece ocorrer dependendo do rio que flui livremente à montante, e as áreas de transição não parecem ter um papel significativo para o recrutamento. Destacamos, portanto, a importância da manutenção dos rios de fluxo livre e da integridade de suas planícies de inundação.

Palavras-chave: Recrutamento, reservatório em cascata, rios livres, peixes de água doce

Introduction

Migratory fishes have a high ecological value, as well as social and commercial (Harvey & Carolsfeld 2003, Agostinho *et al.* 2007a, Pelicice & Agostinho 2008, Agostinho *et al.* 2016, Pelicice *et al.* 2018). Since they perform long displacements along their life cycle, and their recruitment

depends on flooding, they are strongly affected by regulated water levels in rivers (Gomes & Miranda 2001, Pelicice & Agostinho 2008, Pompeu *et al.* 2012, Agostinho *et al.* 2016, Winemiller *et al.* 2016).

A general pattern for reproductive migration includes the upstream displacement in rivers and tributaries at the beginning of the wet season and the following spawning during high flow events when the waters are turbid (Harvey & Carolsfeld 2003, Agostinho *et al.* 2007b, Pelicice & Agostinho 2008, Pompeu *et al.* 2012, Lopes *et al.* 2018). After reproduction, eggs develop and hatch as they are passively transported by the river currents to lateral depressions (marginal lagoons), which are flooded due to overflow of the rivers; fingerling development also can occur in the riverbed (Harvey & Carolsfeld 2003, Agostinho *et al.* 2007a, Agostinho *et al.* 2007b, Pelicice & Agostinho 2008, Pelicice *et al.* 2015, Lopes *et al.* 2019). Adult migrants return to areas of greater resource availability where juvenile fish can eventually be recruited (Pompeu *et al.* 2012, Lopes *et al.* 2019).

Although this pattern has been observed for many river systems, there are several variations, such as that observed in the lower Uruguay River, where lateral flooding areas are restricted by the landscape. In that case, the fish development occurs in transient environments between tributaries and the main river channel, providing conditions close to those found in floodplain lagoons (Zaniboni-Filho & Schulz 2003). In cases of regulated rivers, the presence of free-flowing rivers upstream of dams have demonstrated importance in maintaining the diversity of rheophilic fish as they allow migratory species to complete their life cycle (Marques *et al.* 2018, Carvajal-Quintero *et al.* 2019, Lopes *et al.* 2019). Thus, it is necessary to perform studies to evaluate if the transition of a river with a reservoir can function as a place of recruitment of these species, because this transition area can provide conditions similar to those found in floodplain lagoons, such as less water turbidity and lentic areas with lateral vegetation providing refuge and food resources, conditions favorable for fingerlings and juvenile development (Zaniboni-filho & Schulz 2003).

Some studies have observed the presence of eggs and larvae in the upper part of reservoirs (Suzuki *et al.* 2011, Couto & Pompeu 2013), but without confirmation of their survival and recruitment based on the presence of fingerlings and juveniles. The presence of these stages in the transition areas, river to reservoir, can show that migratory fishes can complete their life cycles, not only along the free-flowing rivers but also in upper areas of reservoirs. Such information for migratory fishes is needed especially in rivers transformed into reservoirs cascades because these cascades can intensify the impact on these species (Santos *et al.* 2017, Loures & Pompeu 2018, Santos *et al.* 2018). Reservoir cascades tend to decrease migratory fish abundance towards downstream reservoirs (Santos *et al.* 2017), while richness tends to be higher in reservoirs that present lotic stretches upstream of the impounded area (Loures & Pompeu 2018).

This study aimed to understand how migratory fishes use the longitudinal gradient, in an upstream to downstream direction, along two free-flowing rivers and two reservoirs in a cascade

located in the Upper Grande river basin, Minas Gerais, Brazil. We tested three hypotheses: (1) due to their reophylic behavior, migratory fish abundance, biomass, and richness will decrease from the free-flowing rivers towards the reservoirs; (2) the areas of transition of the two free-flowing rivers (the Aiuruoca and Grande) with the Camargos reservoir will allow the early development of migratory species; and (3) the number of migratory fishes, in mature and post-spawning gonadal maturation stage, will increase in free-flowing rivers during the wet season.

Materials and methods

Study area

The study was conducted in the Upper Grande river, part of the upper Paraná river basin, at the first two upstream reservoirs from the Camargos and Itutinga hydroelectric dams, and in two important stretches of free flowing rivers that are still found upstream of Camargos dam, the Aiuruoca and Grande rivers (Suzuki *et al.* 2011). The Grande river basin presents 12 hydropower dams along the main stem. In its upper course, is possible to find stretches of free flowing rivers (Suzuki *et al.* 2011, Borges & Abjaudi 2016), however, important original riverine habitats have already been lost in the basin. The basin occupies an area of 143,437,79 km² and creates a border between the states of Minas Gerais and São Paulo, where 60.2% of the area belongs to Minas Gerais (IPT, 2008). The climate of the study area is classified as semi-humid and mesothermic mild, presenting average annual temperatures ranging from 10 to 15 °C and annual mean precipitation from 1,450 to 1,600 mm, with 4 to 5 dry months (May to September) (Borges & Abjaudi 2016).

Ten permanent sampling sites, each separated by approximately 10 km in distance, were distributed along the Aiuruoca and Grande Rivers and Camargos and Itutinga reservoirs. In Itutinga, there are no significant tributary flowing to the reservoir (Fig. 1). Conversely, the Aiuruoca and Grande rivers merge to become the Camargos reservoir. The Camargos Dam started operating in 1960, with a power generation capacity of 45 MW and a reservoir with an accumulated area of 73.35 km². The Itutinga reservoir, built in 1955, is located immediately downstream of the Camargos Dam and presents an installed capacity of 52 MW and a reservoir area of 1.72 km² (Cachapuz 2006). Both plants coordinate operation (Cachapuz 2006), with a 14 days water residence time (Suzuki *et al.* 2011).

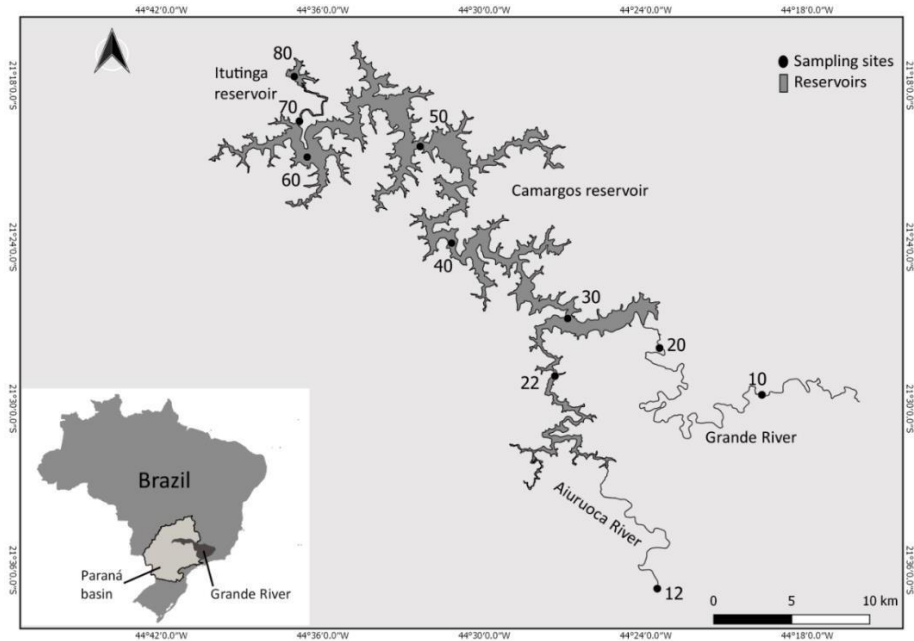


Figure 1. Geographic location and samplings sites in the Grande river basin, Minas Gerais.

Sampling

Sampling was performed every two months between March 2019 and January 2020. Fish were captured using gill nets with different mesh sizes 3, 4, 5, 6, 7, 8, 10, 12, 14 and 16 cm, measured by opposite knots, with each gill net measuring 10 m long. The gill nets were set in littoral areas in the afternoon and removed the following morning, totalizing 12 hours of exposure.

We also used active sampling with two semicircular hand nets (80 centimeters in diameter, 1 mm mesh size) and beach seines (5 m long, 2 m high, and 5 mm mesh size between opposite knots) to collect fingerling and juvenile migratory fishes. We standardized the semicircular hand nets sampling effort by doing 20 minutes per sampling point. Standardized sampling effort of beach seines was of five hauls, 25 m long per sampling. At sampling site 12 (Fig. 1), it was not possible to perform beach seine sampling in March due to depths over 2 m in littoral areas.

Fishes were anesthetized in Eugenol 50mg/l, and the ones belonging to migratory fishes were evaluated for gonadal maturation stages (GMS) based on macroscopic characteristics. These were dissected to determine sex and gonadal stage according to Vazzoler (1996) classifications (Table I).

Table I. Classification of gonadal maturation stages (GMS) of male and female based on macroscopic characteristics (Vazzoler, 1996).

Stage	Female	Male
Immature	F1: Thin and transparent ovaries with low vascularity evident, very small in size.	M1: Thin, translucent and reduced testicles.

Stage	Female	Male
Initial maturation	F2: Bulky ovaries occupying about 1/3 to 2/3 of the celomatic cavity, oocytes are visible to naked eye.	M2: Bulky testicles with lobed shape, milky white in color.
Mature	F3: Ovaries reach maximum volume, turgid and with numerous oocytes visible to the naked eye.	M3: Testicles are bulky, turgid, whitish. With weak pressure the membrane breaks, releasing sperm.
Post-spawning	F4: Flaccid ovaries with hemorrhagic areas, occupying less than 1/3 of the celomatic cavity.	M4: Flaccid testicles with a hemorrhagic aspect.

After the gonadal characterization, fish were fixed in 10% formalin solution and transferred to a solution of alcohol 70% for conservation. In the laboratory, each individual was measured (body length), weighed, and their identification confirmed (Nakatani *et al.* 2001, Ota *et al.* 2018, Ribeiro *et al.* 2019). The specimens were deposited in the Ichthyologic Collection of Federal University of Lavras – UFLA (CI – UFLA).

Data analysis

Species were classified as migratory following specific literature (Agostinho *et al.* 2003, Agostinho *et al.* 2007a), and the registered pool was compared with a survey of migratory species and their respective maximum length (cm) from the Upper Paraná basin, obtained through literature.

To test the first hypothesis, which predicts that migratory fish abundance, biomass, and richness decrease from free-flowing rivers towards the reservoirs, total abundance, and total biomass data were standardized by calculating catch per unit of effort (CPUE) in number of individuals (CPUE_n) per 100 m² of gillnets and in biomass (CPUE_b) per 100 m² of gillnets. Total fishing effort used in each sampling was 160 m² of gillnets, exposed for 12 hours. Catch per unit of effort were estimated by the formula

$$CPUE_n = \sum_{i=1}^3 \left(100 \times \frac{N_i}{E_i} \right)$$

Where: N_i = number of fish captured by gillnet i (3, 4, 5, 6, 7, 8, 10, 12, 14, and 16 cm); E_i = fishing effort for gillnet i.

For CPUE_b catch per unit of effort were estimated by the formula:

$$CPUE_b = \sum_{i=1}^3 \left(100 \times \frac{B_i}{E_i} \right)$$

Where: B_i = biomass of fish captured by gillnet i (3, 4, 5, 6, 7, 8, 10, 12, 14 and 16 cm); E_i = fishing effort for gillnet i .

To test for differences in abundance, biomass and richness among sites were compared using a Kruskal-Wallis test. When a significant difference was detected ($p < 0.05$), the post-hoc pairwise comparisons using the Wilcoxon rank-sum test was performed.

Considering the catches using semicircular hand nets and seines, fingerlings and juveniles of migratory species were quantified for each species per sampling site. The classification of fingerling and juvenile stages were considered using literature of the fingerlings maximum sizes as well as the sizes of first sexual maturation for each species (Table II).

Table II. Total length of fingerlings at maximum size and at first sexual maturation, used to classify fish species in fingerlings and juvenile stage at respective references.

Migratory species	Fingerlings (cm)	First sexual maturation (cm)	References
<i>Brycon orbignyanus</i>	3.1	25	(Nakatani <i>et al.</i> 2001)
<i>Leporinus friderici</i>	3.1	11.5	(Lopes <i>et al.</i> 2000)
<i>Megaleporinus obtusidens</i>	3.4	19	(Nakatani <i>et al.</i> 2001)
<i>Megaleporinus piavussu</i>	3.4	19	(Nakatani <i>et al.</i> 2001)
<i>Pimelodus maculatus</i>	4.8	12.3	(Nakatani <i>et al.</i> 2001)
<i>Prochilodus lineatus</i>	1.8	19	(Nakatani <i>et al.</i> 2001)
<i>Salminus hilarii</i>	1.8	21	(Esguícero & Arcifa 2010, Nakatani <i>et al.</i> 2001)

To assess the second hypothesis and confirm if transition areas, rivers to reservoir, can allow for the development of migratory species, and to understand how adults of migratory species use the system, all stages that were collected (fingerlings, juveniles, and adults) were plotted along the system and season when present.

To assess the third hypothesis, data was grouped by sites with similar hydrological conditions and characteristics to understand general patterns along the longitudinal gradient (Table III), in both wet and dry seasons.

Table III. Sampling sites and groups formed in relation to similar hydrological condition and characteristics.

Sites	Groups	Characteristics	Coordinates
10	River	On the Grande river in its lotic section upstream of the Camargos reservoir	-21.491529° -44.328130°
12	River	On the Aiuruoca river in its lotic section upstream of the Camargos reservoir	-21.613229° -44.397045°
20	Transition	On the Grande river in the transition region between its lotic stretch with the Camargos reservoir	-21.462530° -44.391532°
22	Transition	On the Aiuruoca river in the transition region between its lotic stretch with the Camargos reservoir	-21.479907° -44.456347°
30	Transition	At the Camargos reservoir at the confluence of the Aiuruoca and Grande rivers	-21.444272° -44.448429°
40	Camargos	In the Camargos reservoir about 11 km downstream from the previous point	-21.397605° -44.520289°
50	Camargos	In the Camargos reservoir about 11 km downstream from the previous point	-21.337780° -44.539758°
60	Camargos	In the Camargos reservoir about 11 km downstream from the previous point	-21.344771° -4.609349°
70	Itutinga	Downstream of Camargos dam near its escape channel and upstream Itutinga dam	-21.322170° -44.614583°
80	Itutinga	At the Itutinga reservoir near its dam	-21.294487° -44.617696°

Table V. List of migratory species sampled in the Upper Grande River in relation to migratory species that occur in the Upper Paraná basin. The superscript letter ^a denotes nonnative species.

Migrants Upper Paraná basin	Sampled	Maximum length (cm)
<i>Brycon orbignyanus</i> (Valenciennes, 1850)	X	79.5
<i>Leporinus friderici</i> (Bloch, 1794)	X	40.0
<i>Megaleporinus obtusidens</i> (Valenciennes, 1837)	X	76.0
<i>Megaleporinus piavussu</i> (Britski, Birindelli & Garavello, 2012)	X	38.0
<i>Pimelodus maculatus</i> (Lacepède, 1803)	X	51.0
<i>Prochilodus lineatus</i> (Valenciennes, 1837)	X	80.0
<i>Salminus hilarii</i> (Valenciennes, 1850)	X	50.0
<i>Hemisorubim platyrhynchos</i> (Valenciennes, 1840)		61.0
<i>Leporinus tigrinus</i> (Borodin, 1929) ^a		20.0
<i>Piaractus mesopotamicus</i> (Holmberg, 1887)		40.5
<i>Pirinampus pirinampu</i> (Spix & Agassiz, 1829)		120
<i>Pseudoplatystoma corruscans</i> (Spix & Agassiz, 1829)		166
<i>Pterodoras granulosus</i> (Valenciennes, 1821) ^a		70.0
<i>Rhaphiodon vulpinus</i> (Spix & Agassiz, 1829)		80.0
<i>Rhinelepis aspera</i> (Spix & Agassiz, 1829)		49.0
<i>Salminus brasiliensis</i> (Cuvier, 1816)		100.0
<i>Steindachneridion scriptum</i> (Miranda Ribeiro, 1918)		90.0
<i>Zungaro jahu</i> (Ihering, 1898)		140.0

No significant differences were observed in abundance (CPUE_n: KW = 15.97; p = 0.06) and richness (KW = 15.25; p = 0.08) among sites (Fig. 2a and C). However, biomass (CPUE_b) changed (KW = 19.03; p = 0.02) along the studied gradient (Fig. 2b). Although higher biomass was observed

in the lotic remnants (sites 10, 12, and 20) and immediately downstream of Camargos Dam (site 70), when pairwise multiple comparison tests were performed no significant difference between sites were detected.

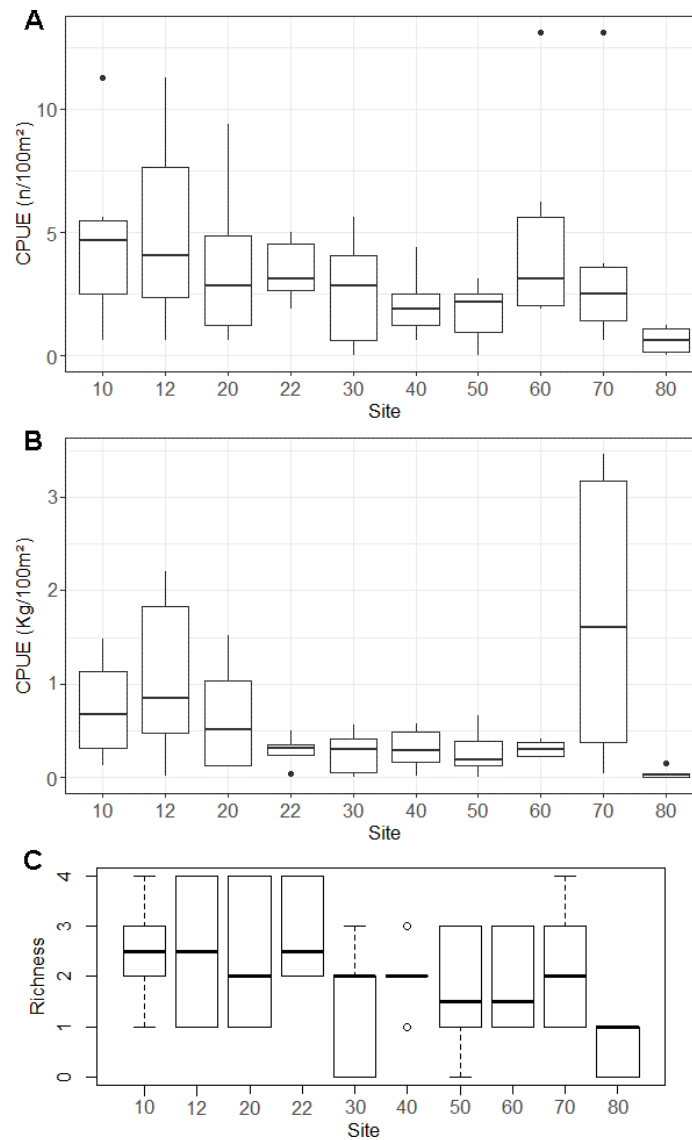


Figure 2. Variation (median \pm interquartile range and amplitude) in migratory fish abundance in number (CPUE_n) (A), biomass (CPUE_b) (B), and richness (C) along the sampling sites.

Fingerlings, juveniles, and adults from migratory species were registered along the system. While the different species did not show a unique pattern along the system, some trends could be noticed. In general, migratory species tended to be found in greater abundance in the stretches of free rivers during the wet season. Juveniles belonging to six of the seven migratory fishes sampled were registered. For most of them, such occurrences were related to the lotic stretches, while *Pimelodus maculatus* were registered throughout the entire sampled system. Fingerlings of only one species (*Leporinus friderici*) were collected in the system (Fig. 3).

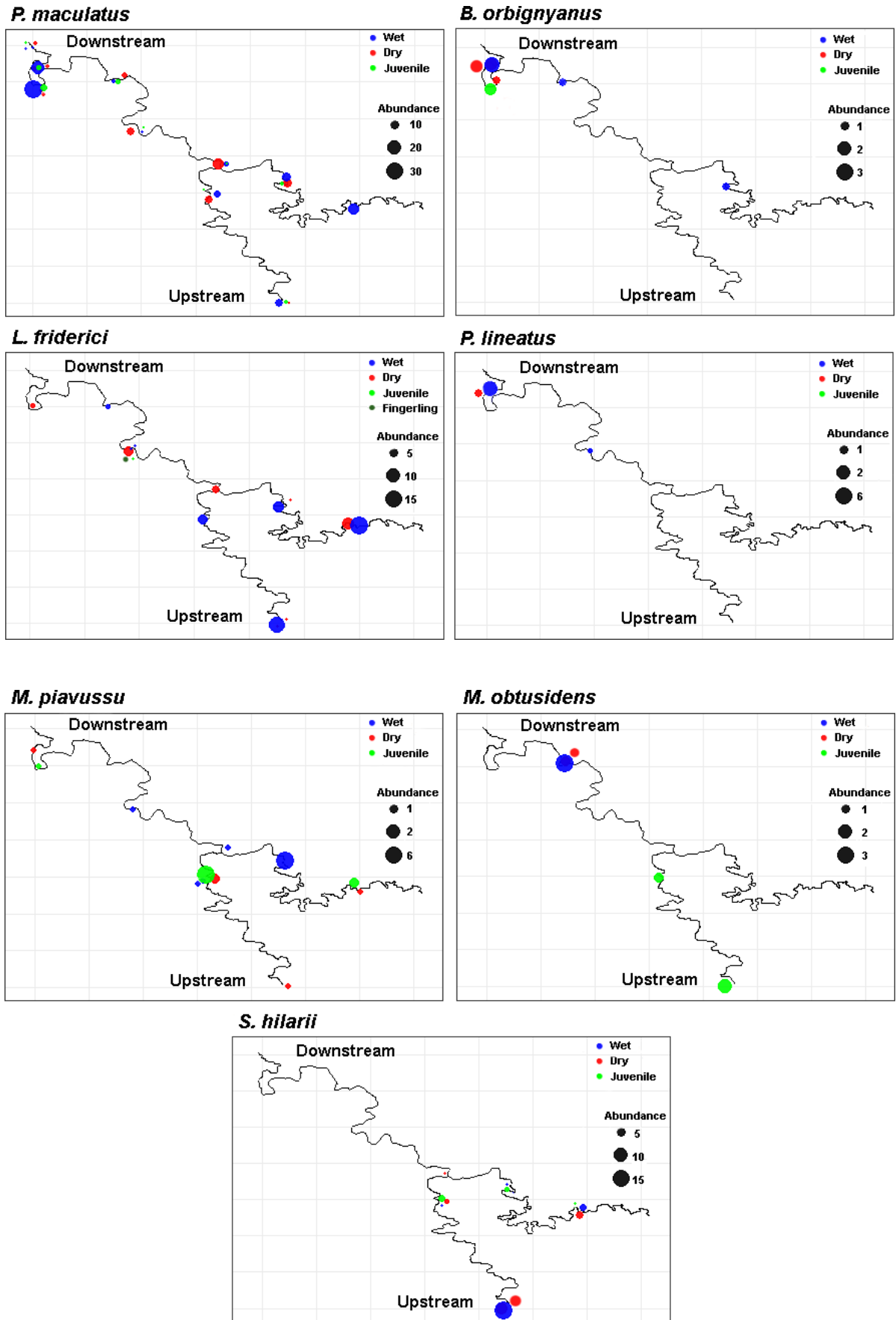
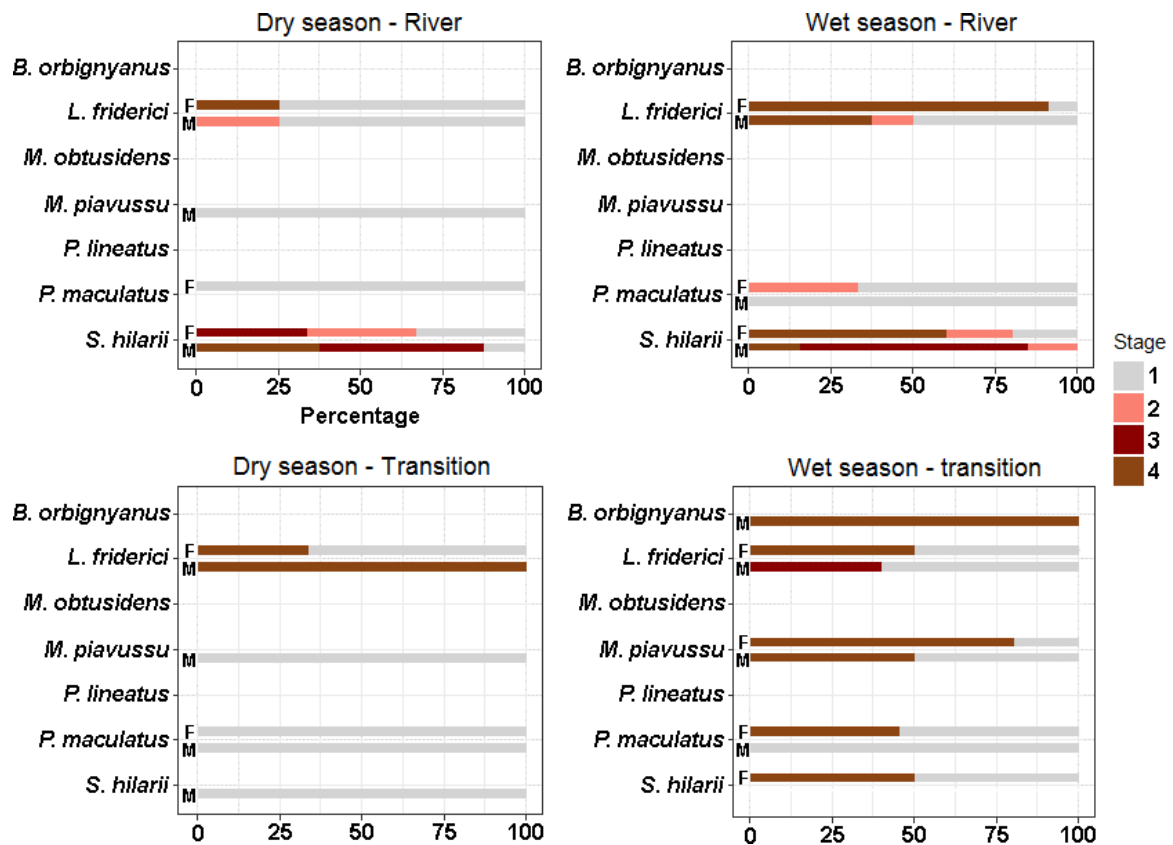


Figure 3. Distribution of adults, juveniles, and fingerling stages of migratory fishes during wet and dry seasons along the sampled system.

The prevalence of the different gonadal maturation stages varied among groups and seasons. In general, stages related to the reproduction itself (mature and post-spawning) were prevalent during the wet season and more frequent in free-flowing rivers and transition zones (Figure 4). The species *Pimelodus maculatus* presented juveniles at almost all sampling points, however individuals with initial maturation and post-spawning stages were only found in rivers and transition areas during the wet season. The species *Brycon orbignyanus* and *Prochilodus lineatus* presented individuals in the stage post-spawning in the Itutinga reservoirs, although no juvenile or fingerlings were collected. Abundance of *Leporinus friderici* increased in rivers during the wet season at the same time as an increased prevalence of individuals with post-spawning stage in this area. This species was also the only one in which fingerlings were collected. The greater abundance of *Megaleporinus piavussu* adults and juveniles was found in transition areas with increased individuals in post-spawning stage. Adults of *Megaleporinus obtusidens* were not found in rivers and transition areas, however some juveniles were collected in these areas during the wet season. *Salminus hilarii* presented adults with mature and post-spawning stages as well as juveniles, but only in rivers and transition areas and primarily in the wet season.



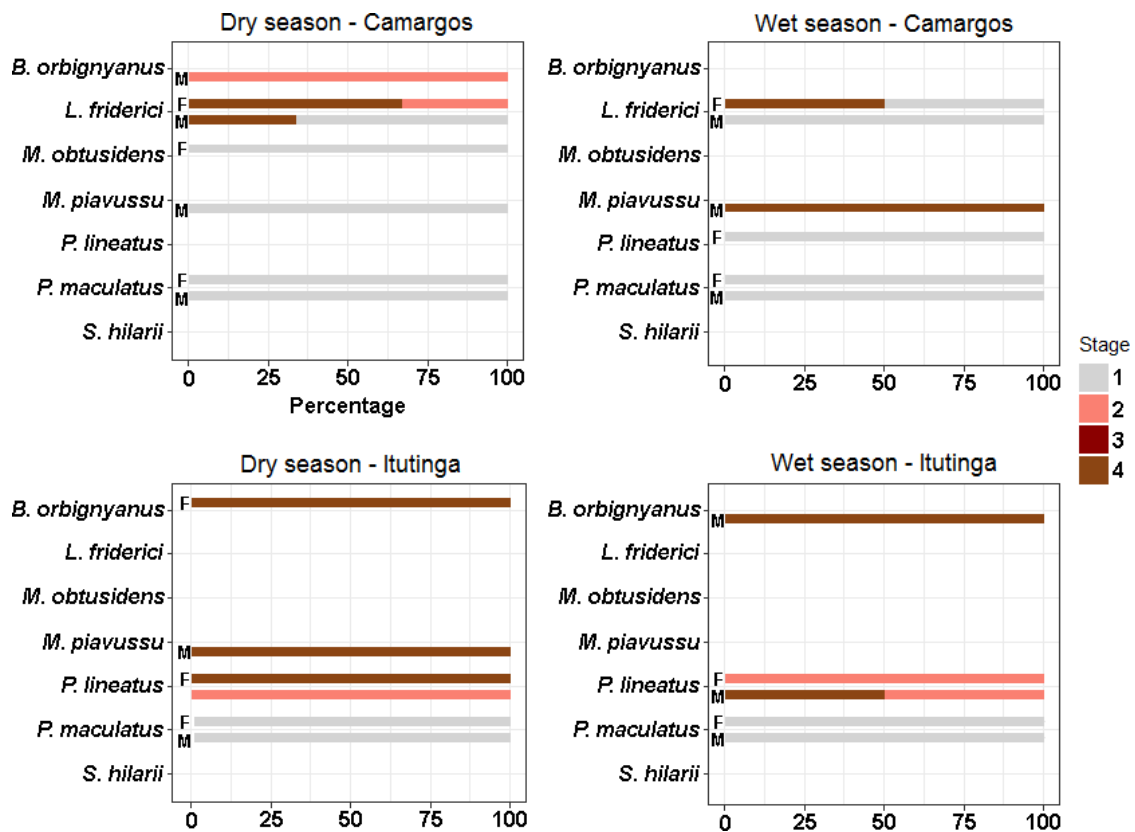


Figure 4. Gonadal maturation stage (GMS) of migratory species during the wet and dry seasons along the groups formed in the system (F1/M1 = females/males: immature; F2/M2 =females/males: initial maturation; F3/M3= females/males: mature; F4/M4=females/males: post-spawning).

Discussion

No differences in abundance, biomass, and richness of migratory species were verified. However, species tended to be found in greater abundance in the stretches of free rivers during the wet season. Although juveniles and fingerlings were registered in the system, the low abundance indicates that recruitment is not happening in the transitional area, between the rivers and the reservoir. Mature individuals were found during the wet season and were more frequent in rivers and transition zones. The system is used distinctly by the different migratory species; most of them presented low abundance along the system and seem to depend on stretches of free rivers to complete their life cycles.

The number of migratory fishes species sampled in this study represents 39% of the total migratory species from the Upper Paraná basin (Agostinho *et al.* 2003, Agostinho *et al.* 2007b), however large migrants were not sampled in the upper part of the basin. Loss of connection, due to sequence of impoundments, can impede large migrants from accessing upper parts of the basin (Petesse & Petrere 2012, Pelicice *et al.* 2015).

Migratory species abundance and biomass tend to decrease along reservoir cascades, because downstream reservoirs tend to have shorter water residence times and be smaller and less turbid (Agostinho *et al.* 2007a, Santos *et al.* 2017, Pelicice *et al.* 2018). However, our study does not present a significant difference along the system in both abundance or biomass. Despite that, higher biomass was observed in the free flowing tributaries, likely because these species prefer to live in running waters (Pompeu *et al.* 2012, Agostinho *et al.* 2016). Higher abundance was also observed immediately downstream of the Camargos dam, possibly due to stocking programs that release migratory fishes (*Brycon orbignyanus* and *Prochilodus lineatus*) in the Itutinga reservoir (Alves *et al.* 1998).

A reservoir cascade system reduces connectivity along the river, leading to a loss of habitats for migratory species and, consequently, a loss of richness (Cheng *et al.* 2015, Loures & Pompeu 2018). Such a pattern was not evident in our study, possibly because this system is composed of only two medium-sized reservoirs, or possibly because the presence of migratory fish stocking in the Itutinga reservoir may be masking this pattern.

The greater abundance of migratory species were in the stretches of free river in the wet season because are related to their reproductive period, since these species depend on the lotic environment and on the natural flow regime to complete the life cycle (Pompeu *et al.* 2012, Agostinho *et al.* 2016). The prevalence of stages related to the reproduction itself (mature and post-spawning) during wet season in lotic and transitional zones reinforce such pattern.

Fingerlings and juvenile stages did not occur in abundance within transition zones, indicating that these areas did not contribute to migratory fish recruitment. The extreme water level fluctuations due to operational requirements of the Camargos impoundment decreases the available habitats and the refuge areas (Nobile *et al.* 2019). Therefore, the migratory species found in the studied systems rely on the abundant floodplain lagoons along the Aiuruoca (Lima *et al.* 2010) and the Grande rivers to complete their life cycle. Presumably, when the water level dropped, these juveniles returned to the river searching for lentic water (Agostinho *et al.* 2003).

The species *Pimelodus maculatus* presented juveniles and adults in almost all sampling sites and seasons, however individuals with mature and post-spawning stages were found only in rivers and transition areas during the wet season. To note, this species has a controversial migratory condition (Santos *et al.* 2012), can be considered migratory or not (Zaniboni-Filho & Schulz 2003, Oldani *et al.* 2007, Arcifa & Esguícero 2012). According to Agostinho *et al.* (2003), the species is migratory but needs fewer free stretches of river to complete the life cycle. In the Paraná basin, *P. maculatus* is considered widely distributed (Agostinho *et al.* 2003), even in reservoirs presenting relatively short, obstruction-free stretches (Agostinho *et al.* 2007a), as demonstrated by the dominance of the species in five reservoir cascades in the Araguari river (Loures & Pompeu 2018). Although juveniles have previously been collected in Itutinga reservoir, which has no free stretches, all adults

presented immature gonadal stage and no fingerlings were registered, indicating that their local occurrence may be from individuals passing through the spillway or Kaplan turbines of the Camargos dam (Alves *et al.* 1998).

The species *Brycon orbignyanus* and *Prochilodus lineatus* presented individuals in the post-spawning stage within the Itutinga reservoir, although no juvenile or fingerlings were collected in this area. The first is categorized as an endangered species (Akama *et al.* 2018), and the decline of its population have been related to changes in natural flood regime and riparian vegetation removal (Tonella *et al.* 2019). Both species also depend on flowing water to complete their life cycles (Agostinho *et al.* 2003, Zaniboni-Filho & Schulz 2003), and their presence is probably related to fish stocking realized by the local power company (CEMIG – Centrais Elétricas de Minas Gerais) (Alves *et al.* 1998).

As expected for a species depending of free flowing rivers for reproduction (Resende 2003, Agostinho 2007), the abundance of *Leporinus friderici* increased in rivers during the wet season at the same time as an increase of post-spawning stage individuals in these areas. The dependence of *L. friderici* individuals, which inhabit reservoirs, on lotic environments to reproduce was reported in another study (Lopes *et al.* 2000). This species was the only one in which fingerlings and juveniles were collected, suggesting that its recruitment could occur at the transitional area. However, such captures were in a low number, leaving it hard to confirm whether this area is used for recruitment or occurred just occasionally.

The remaining species, in general, were also found during the wet season in transition and river areas with increases in post-spawning stage individuals, reinforcing that these species need flowing waters to reproduce (Vazzoler 1996, Nakatani 2001). Therefore, the lotic stretches of the Grande and Aiuruoca rivers seem to maintain self-sustainable populations of the registered migratory species, acting as source areas for the individuals that use the reservoirs.

In this cascade system, we verified that migratory fish recruitment seems to depend on free-flowing rivers upstream while transition areas, on the other hand, do not seem to play a significant role for recruitment. In this sense, we highlight the importance of maintaining these free-flowing rivers and the integrity of their floodplains. Finally, we encourage further research aimed to investigate migratory fish along Grande and Aiuruoca rivers as well as the use of floodplains. Furthermore, we emphasize the importance of the Camargos reservoir water level and its influence on the river's connection to marginal lagoons during the wet season and, consequently, the effect on the recruitment.

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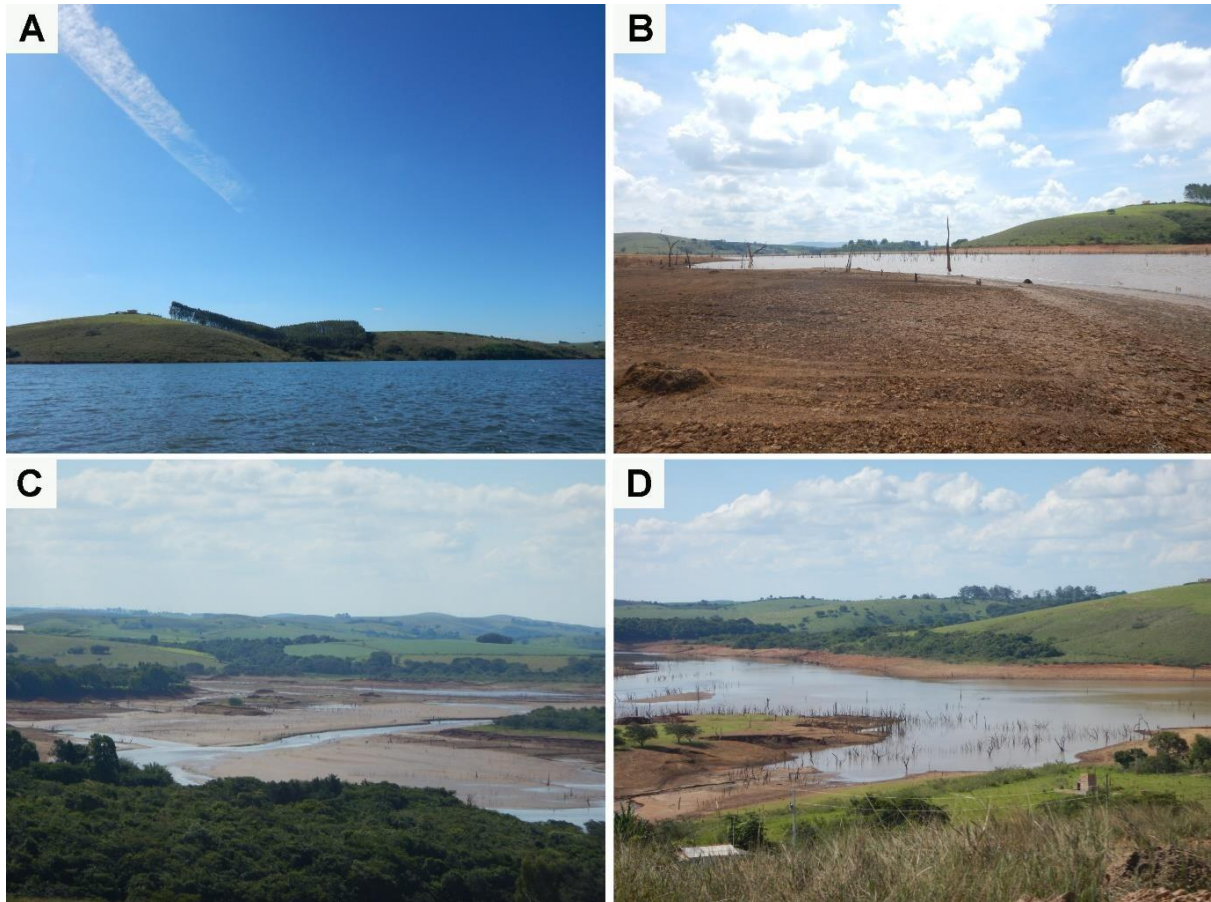
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ANEXO – Panorama geral da região de transição.

Legenda: Área de encontro dos rios Aiuruoca e Grande com o reservatório de Camargos. A = Época de seca; B = Época chuvosa; C = Rio Aiuruoca prestes a desaguar no reservatório de Camargos, época chuvosa; D = Encontro do Rio Grande com o reservatório de Camargos, época chuvosa. É possível observar o efeito do reservatório de acumulação sobre o nível de água na área de transição.