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Original Research Article

Artificial flow regime promotes abiotic and biotic gradients: Testing the concept of longitudinal zonation in an off-river reservoir

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ABSTRACT

Fragmentation and interconnection of water bodies cause severe changes in the natural flow regime of continental water systems. However, assessments of these impacts on the freshwater fish distribution are still scarce. We investigated whether an artificial flow regime generated by discharges from an aqueduct would promote a longitudinal environmental gradient in an off-river reservoir. We tested the hypothesis that the incoming water from aqueduct discharges promotes environmental gradient between lotic and lentic conditions. We expect that environmental changes and the artificial flow regime promote the structuring of fish assemblage and that the lotic-lentic transition areas present the highest fish species richness. A longitudinal gradient in environmental characteristics with differing fish assemblage structure was found. Temporal changes in the fish assemblages occurred only in areas near the discharge of the aqueduct. The highest fish richness and diversity were recorded in the transition zone during the wet season, associated with the greater environmental heterogeneity of this ecotone, whereas the lowest was found in the lotic zone, probably associated with the altered flow regime. The greatest abundance was recorded in the upper lentic zone in the wet season, whereas the lowest was found in the lower lentic zone in both seasons. Our results corroborate the hypothesis that the artificial flow regime, modulated by the seasonality of discharges and the influence of environmental variables, promotes longitudinal gradients in reservoirs when rivers are not present. The findings are relevant in a scenario where ever more interconnections of aquatic bodies have been diffused around the world.

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1. Introduction

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Reservoir construction and water diversion have multiplied in the world, disfiguring the landscape and flow regime of continental water systems. Nowadays, more than half of the world's largest river systems are fragmented

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by dams (Grill et al., 2019; Nilsson et al., 2005), with severe implications for the global diversity of freshwater fish (Liermann et al., 2012). In addition to fragmentation, the rivers have been exposed to the spread of large interand intra-basin water interconnection and transfer programmes. State and private investments of over US \$ 2.7 trillion in water transfer megaprojects is expected over the next few years, mainly in North America, Asia and Africa with a total water transfer volume reaching 1910 km³







per year, and a total transfer distance greater than twice the length of the equator (Shumilova et al., 2018). In the US, for example, the number of inter-basin water transfer projects has risen from 256 in 1985–1986 to 2161 in 2017 (Dickson and Dzombak 2017). Recently, one of the largest water crises in modern history has led the Indian government to formulate an unprecedented program of linking 30 major rivers through more than 15,000 km of concrete channels (Lakra et al., 2011). Fragmentation and interconnection of water bodies originate a complex artificial hydrological network, with unpredictable long-term consequences.

The construction of reservoirs breaks the natural river flow regime and results in a set of abiotic and biotic modifications, equivalent to the formation of a new ecosystem, with hybrid characteristics between a river and a lake (Baxter, 1977; Fernando and Holčík, 1991; Poff et al., 1997). The environmental contrast between rivers and lakes can be observed in the longitudinal axis of the reservoirs, where the new lentic regimes formed near the dam can be observed, as well as the presence of free flow regimes upstream of the enterprise. Longitudinal zonation patterns in reservoirs are often based on a common conceptualization proposed by Thornton (1990), where the environment is categorized into three distinct zones: I. Riverine, pluvial or lotic; II. Transition and III. Lacustrine or lentic. The area occupied by each zone varies according to each reservoir and is influenced by the magnitude of the barred river. morphometry, retention time, thermal stratification, season and geographical location (Straškraba and Tundisi, 2013). The degree of connectivity between the river and reservoir systems is essential in the function, the dynamics of the ecological nuclei and the reservoir integrity (Fullerton et al., 2010; Larsen et al., 2012).

Many studies have shown that the distribution of fish in the longitudinal river-reservoir gradient is not random (e.g., Nobile et al., 2019; Prchalová et al., 2009; Sandhya et al., 2019; Vašek et al., 2016). For example, lentic zones tend to support fewer species due to a lower number of species pre-adapted to exclusively lentic conditions (Fernando and Holčík, 1991; Affonso et al., 2016). Lentic habitats are generally characterized by low levels of organic nutrients, clear water and greater depths (Kimmel et al., al., 1990). In the lotic zone, the flow is intense, the nutrient levels are higher, and the abiotic characteristics are more similar to those of a river (Straškraba and Tundisi, 2013; Thornton, 1990). Fish that colonize the lotic zone are adapted to river conditions, and this zone supports, for example, a greater number of rheophilic species (Agostinho et al., 2007). The transition zone shares characteristics of the lotic and lentic zones. A higher species richness may occur in the transition areas due to greater habitat heterogeneity in this ecotone (Buckmeier et al., 2013; Willis and Magnuson, 2000). River-reservoir transition ecotones may temporarily promote coexistence between species adapted to both lentic and lotic conditions, or those tolerant of hydrological variations (Nobile et al., 2019; Sandhya et al., 2019; Terra et al., 2010). The seasonality of rainfall and flow changes also result in changes in nutrient inputs and habitat availability, which interact in a complex manner

in the longitudinal gradient and modulate the distribution of assemblages (Agostinho et al., 2004; Junk et al., 1989; Nobile et al., 2019).

Several reservoirs were built outside of the main channel of a river (e.g., off-stream; off-river, or polders), in flooding areas adjacent to water bodies, and can be supplied by inter- and / or intra-basin water transposition mechanisms. In these types of reservoirs, the direct absence of an upstream river may not favour the formation of marked longitudinal gradients. However, water discharges from hydraulic mechanisms produce artificial flow regimes and have the potential to promote longitudinal environmental gradients in reservoirs

The hydrological regime is a main driver of freshwater ecosystems, structuring the physical habitat model, providing connectivity, framing biotic interactions, and ultimately selecting the specific life histories of aquatic organisms (Mims and Olden, 2012, 2013). Water movement through landscapes and complex interactions with substrates, local geology and relief promote heterogeneous habitats (Bunn and Arthington, 2002), which influence fish distribution, abundance and diversity (Poff and Zimmerman, 2010).

Alteration of natural flow regimes often results in negative effects on the biota (e.g., Brown and Bauer, 2010; Bunn and Arthington, 2002; Poff et al., 1997). Many studies show that the conversion of a lotic to a lentic environment caused by river fragmentation is harmful to the native fish assemblages (e.g., Liermann et al., 2012; Loures and Pompeu, 2019; Wu et al., 2019). However, the reverse, that is, the effects of the conversion of a lentic environment to a lotic one caused by artificial flow regime in reservoirs are still scarce in the literature. Even more scarce are studies that attempt to predict how these contrasting effects (fragmentation and interconnection) interact and affect fish distribution.

The present study aimed to investigate for the first time whether water inflows reaching an off-river reservoir, through a transposition between adjacent watersheds, would be responsible for spatiotemporal changes in the fish assemblages and in the descriptors of abundance, species richness and diversity. Specifically, we aimed to (i) identify whether there is a longitudinal abiotic gradient through environmental variables (habitat + physicochemical), (ii) determine how species are distributed along this gradient, (iii) compare fish assemblages and their descriptors between zones and seasons, and (iv) examine the fish-environment relationships in these non-natural conditions. The tested hypothesis was that the incoming water from aqueduct discharges promotes environmental gradient between lotic and lentic conditions. We expect that environmental changes and the artificial flow regime promote the structuring of fish assemblage, since flow is one of the main modulators of the environmental conditions and, consequently, of the communities (Poff et al., 1997). In addition, we expect that the lotic-lentic transition areas present the highest fish species richness because of the great environmental heterogeneity of this ecotone (Buckmeier et al., 2013; Willis and Magnuson, 2000). Achieving these goals can serve to identify the environmental effects caused by changing flow patterns



Fig. 1. Elevation map of the Lajes Reservoir, with longitudinal zone indications (red dashed line - lotic zone (Lo); orange dashed line - transition zone (Tr); and yellow dashed line - i. upper lentic (ULe); ii. middle lentic zone (MLe); and iii lower lentic zone (LLe); generated by Atlas 1.3- 3D Map Generator Terrain. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

and to improve our understanding of the impacts on the fish distribution imposed by river fragmentation and interconnection.

2. Methods

2.1. Study area

The Lajes Reservoir (22°42′-22°50′S; 43°53-44°32′W), State of Rio de Janeiro, Brazil, was formed between 1905 and 1907 and is one of the oldest reservoirs designed for the primary purpose of generating electricity in Brazil (Brazilian Committee on Dams, 2011). The mean inflow of water is 13.7 m³/s⁻¹, of which most of the flow $(8.3 \text{ m}^3/\text{s}^{-1})$ is received by transposition from an interbasin diversion (From Paraíba do Sul River Basin to Guandu River Basin) (Fig. 1). Water transposition occurs by gravity through the rock-carved artificial underground aqueduct, built in 1914, with a length of 8.4 km. Aqueduct flow oscillations follow natural rainfall patterns, with higher discharges in the wet season (January-March) and lower discharges in the dry season (July-September) (Fig. 2). The remaining flow is natural (\approx 5.4 m³/s⁻¹), coming from the streams of the Atlantic Forest biome, which discharge into different areas of the reservoir. Lentic conditions predominate in the longitudinal extent of the reservoir, because of the low connectivity with natural tributaries and dendritic morphology, associated with a high retention time (\approx 297 days). The banks present dense vegetation cover of the Atlantic Forest biome in different stages of ecological succession. Water transparency is high (euphotic zone = 9.2 m) and mesotrophic conditions predominate (Total phosphorous = 1.0 μ M) with low phytoplankton biomass (Chlorophyll-*a* = 1.9 μ g L⁻¹) (Soares et al., 2008). The climate is seasonal tropical with dry winters (Aw), according to the Köppen–Geiger classification.

2.2. Sampling locations

Monthly standardized samplings were carried out between April 2016 and March 2018 in five zones, covering an extent from the mouth of the aqueduct discharge to the dam (Fig. 1). The zones were defined according to the flow, physicochemical parameters and depth, following Thornton (1990) and Agostinho et al. (2007). The lotic zone (hereinafter, Lo) begins at the mouth of the aqueduct and extends for 1.8 km in a narrow flowing channel, with shallow depth (2.0-6.1 m); the transposed waters reach the reservoir colder (17.6-25.8 °C) and more turbid (~1.4-97.3 NTU) than in the other zones. The transition zone (Tr) is structured without apparent flow, with a slightly deeper depth (2.4-6.9 m), and less turbid water (~2.6-37.9 NTU). The lentic zone, outside the influence of aqueduct discharges, occupies a large longitudinal extension, and is subdivided into three zones (upper lentic, ULe; middle lentic, MLe; and lower lentic, LLe). Overall, the three lentic zones have similar physicochemical and habitat characteristics, such as low turbidity (1.6-4.2 NTU) and high temperature (21.1–31.1 °C), differing only in depth (ULe = 6.3-16.2 m, MLe = 7.7-31 m and LLe = 31.7-46 m).



Fig. 2. Mean and standard error of monthly rainfall (mm, dashed line) and flow (m³ s⁻¹, dark line) variations from April 2016 to March 2018 in the Lajes Reservoir.

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2.3. Environmental variables

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····· Flow (m³/s⁻¹)

Water temperature (°C) and turbidity (NTU) were measured using a Horiba U-52 G multiprobe (Japan, Horiba, Ltd.). Water transparency (cm) was obtained with a Secchi Disk. Depth was measured using a centimetre-accurate digital probe (Speedtech model SM-5). Underwater videos (~ 20 min) recorded on a 200 m² (50 \times 4 m) area transect from the shore to the reservoir bed were taken using a remote operated vehicle (ROV) model Titan Genneino (Shenzen, China). The ROV is capable of operating to a depth of 150 m and is equipped with a camera attached (1 / 2.5 inches SONY CMOS, 4k resolution, FOV 160°), operating at a speed of 3.3 ft / s and angled filming of 30° towards the bed. From the videos, the coverage of each item of substrate type (% of rocks, clay and sand) and aquatic macrophytes was estimated, using a rating protocol of 0-4 corresponding to coverage area: 0 = no coverage $(0 m^2)$; $1 = low coverage (1-60 m^2); 2 = moderate coverage (60.5-$ 120 m²); 3 = high coverage (120.5-180 m²); 4 = completecoverage (200 m²).

2.4. Fish sampling

Six gill nets (35×2.8 m; mesh of 15–110 mm between adjacent nodes) were set near the margins at dusk and retrieved the next morning. The sampling unit was defined as the number of individuals collected per 590 m² / 14 h, totalling 120 samples (5 zones \times 2 years \times 2 seasons \times 6 months). Fish were caught alive, and their total length (TL) was measured; they were then returned alive to the water. This study was authorized by the Ethics Council of Animal Use (CEUA / ICBS / UFRRJ), through Permission 12,179, CEUA 03/2017, and the Brazilian Environmental Agency (SISBIO/IBAMA/ICMBio- Permit no. 10,707).

2.5. Statistical analyses

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A Permutational Analysis of Variance (PERMANOVA) based on Euclidean distance and permutation of residuals under a reduced model was performed to ascertain the abiotic longitudinal gradient by comparing the environmental variables, substrate type and aquatic macrophytes coverage between the fixed factors: i. seasons (dry, April-September \times wet, October-March); and ii. longitudinal zones (lotic, Lo; transition, Tr; upper lentic, ULe; middle lentic, MLe; and lower lentic, LLe). Significant differences among the factors were followed by PERMANOVA pairwise comparison tests.

A PERMANOVA was also applied to compare the structure of the fish assemblage between seasons and longitudinal zones (fixed factors). Fish abundance data were previously transformed (square root) to reduce the influence of abundant species but preserve information on their relative abundance, and the triangular matrix was constructed using Bray-Curtis similarity. PERMANOVA was applied using the Type III square sum (partial) to calculate the p values. When significant differences were detected (p <0.01), paired comparisons were conducted between the groups. In addition, comparisons of the total number of individuals (N), total number of species (S) and Shannon-Wiener diversity (H') were performed between zones and seasons using this PERMANOVA analysis. We also used a Similarity Percentage (SIMPER) analysis to determine species that most contributed to within-group average similarity of the seasons and zones, thus identifying their distribution patterns along the spatial-temporal gradient. The relationship between environmental variables and the fish assemblage structure was investigated using distance-based redundancy analysis (dbRDA, McArdle and Anderson, 2001). This analysis is suitable to measure the relationship between variation in the species data and some linear combination of the environmental variables

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Variable	Season	Zone	Season \times zone	Significant differences
Temperature (°C)	170.6**	32.6**	0.4	Dry < Wet Lo < Tr IIIe MIe IIe
Transparency (m)	18.1**	59.1**	1.4	Wet $<$ Dry Lo $<$ Tr $<$ ULe $<$ MLe. LLe
Turbidity (NTU)	12.1**	6.5**	4.7*	Dry < Wet LLe, MLe, ULe < Tr, Lo
Depth (m)	4.2*	449.0**	1.0	Wet < Dry Lo < Tr < ULe < MLe < LLe
Macrophytes	1.3ns	361.7**	1.3	ULe, MLe, LLe $<$ Lo $<$ Tr
Clay	3.5ns	52.1**	0.8	Lo < Tr < MLe, LLe, ULe
Sandy	0.3ns	52.2**	0.4	LLe, MLe, ULe $< Tr < Lo$
Rocks	0.6ns	118.1**	0.4	LeU $<$ MLe $<$ LLe, Tr $<$ Lo

Pseudo-F values from PERMANOVA and significant differences in environmental variables between seasons and zones in the Lajes Reservoir.

ns. non-significant; ** p < 0.001; * p < 0.05.

(Legendre and Anderson, 1999). Pearson correlations with the first two dbRDA axes were examined to identify the strength and direction of the species-environmental relationship (Anderson et al., 2008). Taxa with low abundance (%N < 1) were excluded from analysis. Univariate and multivariate analyses were performed with the software PRIMER-E v.6.1.13 and PERMANOVA + 1.0.3 (www.primer-e.com; Anderson et al., 2008).

3. Results

3.1. Environmental variables

Environmental variables differed between seasons and along the longitudinal gradient from the aqueduct to the dam, with irrelevant interactions between these two factors, except for the turbidity (Table 1; Table S1 and Fig. S1 in the Supplementary information). Higher temperatures were detected in the wet season (t = 13.0; p < 0.001) compared with the dry season and in the lentic zones (ULe, MLe and LLe) compared with the lotic zone (p < 0.001). The turbidity was significantly higher in the wet season (t = 3.4; p < 0.001) compared with the dry season, and in the lotic zone (p < 0.001) compared with the lentic zones. Zone \times season interactions were detected for turbidity in Lo and Tr zones, with higher values during the wet season compared to the dry season (Lo, t = 2.4, p < 0.001; Tr, t = 2.6, p < 0.001) only in this two zones (Table S1 in the Supplementary information). The transparency was highest in the dry season (t = 4.2; p < 0.001), between the lower and middle lentic zones (p < 0.001). The depth presented a spatial gradient, with lower values in the lotic zone and higher values in the lower lentic zone (p < 0.001). Higher depths were found in the dry season (t = 2.0; p < 0.05) compared to the wet season due to the operation of the hydroelectric plant that keeps the water accumulated in the dry season.

Regarding the habitat components, aquatic macrophytes (p < 0.001) occurred in higher percentages only in the lotic and transition zones. Clay substrate predominated in four (Tr, ULe, MLe and LLe) of the five reservoir zones (p < 0.001), while rocky substrate (p < 0.001) predominated only in Lo. Sandy substrate records (p < 0.001) occurred only in the lower proportion, in the transition and lotic zones (Table 1).

3.2. Diversity indices

The community descriptors (N, S and H') changed significantly between the zones and seasons (Table S2, and Fig. S2 in the Supplementary information). The number of individuals (N) was significantly higher in the ULe, Lo and Tr compared with the other zones (p < 0.001), and in the wet season than in the dry season (t = 2.7; p < 0.001). Significant interaction season vs. zone was found only for ULe (t = 3.6; p < 0.001), which exhibited the highest abundances during the wet season, whereas in the other zones no marked seasonal variation was found (Table S2; Fig. S2 in the Supplementary information).

The number of species (p < 0.001) and Shannon diversity (p < 0.001) were significantly higher in the transition zone during the wet season, and lower in the lotic and ULe zones in both seasons (Table S2; Fig. S2 in the Supplementary information). Significant differences in community descriptors between the seasons were detected only for the number of individuals (N) and number of species (S). The number of individuals (t = 2.7; p < 0.001) and the number of species (t = 3.4; p < 0.001) were lower in the dry season and higher in the wet season.

3.3. Fish assemblages

A total of 5129 specimens comprised in 5 orders, 14 families, 27 genera and 31 species were captured (Table S3 in the Supplementary information). Most individuals were Siluriformes (% total number, N% = 66.3%), followed by Cichliformes (N% = 12.4%) and Characiformes (N% = 11.2). Of the 31 species recorded, 12 were common in all zones. In the Lo zone, there was exclusive occurrence of the native Siluriformes Hypostomus luetkeni, Microglanis parahybae and Trichomycterus giganteus, whereas in the Tr zone there were exclusive records of the Characiformes Hoplerythrinus unitaeniatus and Colossoma macropomum. Loricariichthys castaneus (N% = 31.1; FO% = 61.7), Trachelyopterus striatulus (N% = 10.4; FO% = 59.2), Rhamdia quelen (N% = 7.7; FO% = 81.7), Metynnis maculatus (N% = 7.4; FO% = 51.7) and Cichla kelberi (N% = 4.3; FO% = 58.3) were the most abundant and frequent species. Hoplias malabaricus, Astyanax cf. bimaculatus and Copdoton rendalli were frequent but not abundant. Hypostomus luetkeni was abun-

Table 1

dant in the Lo zone and not frequent in the rest of the reservoir (Table S3 in the Supplementary information).

Differences in the fish assemblage structure were detected among the zones (Pseudo-F = 19.27; p < 0.001) and seasons (Pseudo-F = 4.30; p < 0.001), according to PER-MANOVA. Spatial changes accounted for 32.9% of the estimated component of the variation - ECV, whereas seasonal changes accounted for 4.31% of the ECV (Table 2).

Significant differences (p < 0.001) in the assemblage structures were found between all zones, according to the paired comparisons, and between the dry and wet seasons for the pooled samples, according to PERMANOVA. When each zone was considered separately, seasonal changes were detected only for the Lo, Tr and ULe zones (Table 2).

The species that most contributed to the average similarity (SIMPER) in Lo zone was *H. luetkeni*, followed by *R. quelen, H. malabaricus* and *L. copelandii*, whereas in Tr were *M. maculatus, R. quelen* and *C. gilbert* (Table S4 in the Supplementary information). *Rhamdia quelen* and *T. striatulus* contributed to average similarity in the three lentic zones. Other species were typical and had high contribution to average similarity in ULe (e.g., *L. castaneus* and *G. brasiliensis*), MLe (e.g., *C. rendalli, H. affinis*, and *C. kelberi*), and LLe (e.g., *C. kelberi*) (Table S4 in Supplementary information). *Cichla kelberi* was most representative of the dry season, whereas *L. castaneus* and *M. maculatus* of the wet season, according to SIMPER analysis.

Table 2

Results from PERMANOVA for comparing differences in the fish assemblage structure between the five zones and two seasons.

Source	Df	MS	Pseudo-F	ECV		
Zone	4	27,186	19.27**	32.91		
Season	1	6079	4.31**	8.80		
Zone x Season	4	3130	2.22**	12.04		
Res	111	1410		37.55		
Total	120					
Pair wise test for the fixed factors						
Zone	t		Season	t		
LLe vs. MLe	1.91**		$Dry \times Wet$	2.07**		
LLe vs. ULe	3.66**					
LLe vs. Tr	3.66**					
LLe vs. Lo	4.77**					
MLe vs. ULe	3.31**		Zone \times Season	t		
MLe vs. Tr	4.01**		LLeDry \times LLeWet	1.11		
MLe vs. Lo	5.41**		$MLeDry \times MLeWet$	1.23		
ULe vs. Tr	4.47**		ULeDry \times ULeWet	2.19**		
ULe vs. Lo	5.92**		TrDry \times TrWet	1.59*		
Tr vs. Lo	5.93**		LoDry \times LoWet	2.06**		

The *t*-test values are shown for post hoc, pair-zone and station tests. df, degrees of freedom; MS, mean sum of squares; ECV, estimated percentage components of variation; F, Pseudo-F; * p < 0.05; ** p < 0.001.

3.4. Species-environment relationship

A total of 28.2% of the variation in the structure of the fish assemblages was explained by the environmental variables according to the first two axes of dbRDA (Fig. 3).



Fig. 3. Ordination diagram (triplot) of the two first axes of the distance-based Redundancy Analysis (dbRDA) on the relationships between fish assemblage and environmental variables. Samples coded by zones: Lo, lotic; Tr, transition; ULe, upper lentic; MLe, middle lentic; LLe, lower lentic; and seasons: W, wet; D, dry. Species code: Asbim, Astyanax cf. bimaculatus; Aspar, Astyanax parahybae; Cikel, Cichla kelberi; Coren, Coptodon rendalli; Cygil, Cyphocharax gilbert; Homal, Hoplias malabaricus; Hyaff, Hypostomus affinis; Hylue, Hypostomus luetkeni; Lecop, Leporinus copelandii; Locas, Loricariichthys castaneus; Memac, Metynnis maculatus; Olhep, Oligosarcus hepsetus; Ornil, Oreochromis niloticus; Rhque, Rhamdia quelen; Trstr, Trachelyopterus striatulus.

The first dbRDA axis presented positive correlation with clay (r = 0.81), transparency (r = 0.64) and temperature (r = 0.64), and negative correlation with rocks (r = -0.89) and turbidity (r = -0.23). For the second dbRDA axis, only macrophytes (r = 0.77) and sandy substrate (r = 0.35) had significant positive correlation, whereas depth (r = -0.68) had negative correlation.

Hypostomus luetkeni (r = -0.81) and L. copelandii (r = -0.49) had strong correlation with RDA1 (Fig. 3, Table S5 in the Supplementary information) and were associated to rock substrate and high turbidity of the Lo zone. Trachelyopterus striatulus (r = 0.39), L. castaneus (r = 0.35), C. kelberi (r = 0.3), H. affinis (r = 0.27) and O. nilloticus (r = 0.28) were associated with clay substrate, high transparency and temperature of the lentic zones (LLe, MLe, ULe). Cyphocharax gilbert (r = 0.52), H. malabaricus (r = 0.61), A. cf. bimaculatus (r = 0.52), H. malabaricus (r = 0.5) had strong positive correlation with RDA2 and were associated with high macrophyte cover and low depth and transparency of the Tr zone.

4. Discussion

The main finding of this study is that water transposition from an adjacent watershed, through a hydraulic mechanism, promoted longitudinal changes in the physicochemical parameters and habitats and consequently influenced the structure of fish assemblages in an off-river reservoir, thus corroborating our hypothesis. Temporal changes in fish assemblages occurred only in areas located near the discharges, which may be associated with periodic fluctuations of the aqueduct flow. Given the often-cited relationships between flow, habitat structure, and fishes, it is not surprising that temporal modifications to flow regimes affect fish assemblage structure (Bunn and Arthington, 2002; Poff et al., 1997). Hydrological regime is of crucial importance in the modulation of fish ecological processes and assemblage structure. Species select physiologically convenient habitats throughout the life cycle. Changes in flow can influence phenological aspects of individual fish species (e.g., gonad maturation, migration, growth) and habitat availability and heterogeneity, with consequent effects on biotic interactions (Agostinho et al., 2007; Bunn and Arthington, 2002; Junk et al., 1989; Mims and Olden, 2012; Winemiller, 1989).

The discharges of the aqueduct formed a lotic regime zone, and upon the influence of this artificial flow, the fish richness (S) and diversity (H ') were significantly lower compared with the other zones. This pattern differs from reservoirs built on the continuum of a river, where the lotic zone may exhibit the highest fish richness and diversity, as this is the main habitat for most species before damming (Agostinho et al., 2007; Affonso et al., 2016). In general, impoundment effects on fish diversity were more pronounced in lentic environments than lotic zones (Loures and Pompeu, 2019). The unnatural lotic zone of the Lajes Reservoir is intermittent in periods of low water and reduced flow and has a channel that prevents upstream migration of fish. This conjuncture of potential environmental stressors seems to be consistent with the lower richness and diversity observed in the lotic zone, which is regulated by artificial inflows.

Hypostomus luetkeni and *L. copelandii* were the only species that were exclusively typical of the lotic zone, associated with rocky substrate and turbid waters with comparatively low temperature. For *H. luetkeni*, the predominance of rocky substrate may be associated with periphyton, the main dietary item. The sucking mouth provided with expanded, suction-shaped lips allows strong adherence to the rocky substrate even under high flow conditions (Casatti et al., 2005). On the other hand, *L. copelandii*, a migratory species (Agostinho et al., 2007) may be using the lotic zone because of the flow.

The lentic zones occupy a large longitudinal extension of the Lajes Reservoir, reflecting the long retention time, dendritic morphology and the absence of large natural tributaries. In this zone, a longitudinal pattern can be observed in the abundance of species. We found the lowest fish abundance near the dam, whereas the highest abundance was recorded in the upper lentic zone. This pattern corroborates other (e.g., Sandhya et al., 2019), which reported lower fish abundances in lentic reservoir zones, especially in locations near dams, where the deep depth was a main driver limiting fish distribution (Fernando and Holčík, 1991). On the other hand, the largest abundances in the upper lentic zone are mainly due to the high local catches of L. castaneus in this compartment. This benthic and low mobility species is tolerant to hypoxia (Silva et al., 1997), and use the sandy substrate in low flow habitats, with greater depths (~ 8 m) (Costa et al., 2013), conditions that predominate in the upper reservoir zone. The impoundments facilitate the invasion, dispersal and establishment of Loricariichthys spp. (Casemiro et al., 2017), and the increased depth after reservoir formation expands this type of habitat, where this species is prone to occupy and reach high numerical abundance. In addition, L. castaneus had pronounced seasonality, being typical of the wet season. This pattern may be associated with the reservoir bed anoxic conditions in the wet season (Soares et al., 2008), consequently, the need for vertical displacement to obtain air oxygen (Silva et al., 1997), which would leave the species more exposed to capture.

In the transition zone, an ecotone between lotic conditions generated by artificial inflows and the lentic zone, the number of species (S) and diversity (H') were significantly higher than in other zones, meeting our expectation. Riverine-lacustrine ecotones in river-built reservoirs can support highly diverse assemblies because they provide physical, chemical, biological, and ecological connections between different environments (Buckmeier et al., 2013). Ecotones perform important functions in the spatiotemporal structuring of communities, with tendencies to increase biodiversity (Willis and Magnuson, 2000). The highest species richness in the river-reservoir transition zone was observed by Terra et al. (2010), Yang et al. (2012), Nobile et al. (2019) and Sandhya et al. (2019) and were associated to high environmental heterogeneity and the suitability of ecotones to temporarily promote coexistence between riverine and lacustrine species, or those tolerant of hydrological variations. In the transition zone of the Lajes Reservoir, macrophyte banks are found, increasing the

physical structure, complexity and heterogeneity of habitats, which could be associated with the presence of native species such as A. cf. *bimaculatus, C. gilbert* and *H. malabaricus* (Thomaz and Cunha, 2010; Costa et al., 2013). In the case of gradients promoted by artificial water discharges, the greatest richness found in the transition zone may be due to the stressful effects at the ends of the longitudinal gradient, generated by both the upstream aqueduct discharges, and the low number of pre-adapted species to the lentic environment near the dam.

Inter-basin water transfer projects affect both the donor and the recipient basins, with effects that include (but are not limited to) changes in flow dynamics and physicochemical conditions, as well as other deleterious effects such as habitat destruction, fishery collapse, spread of parasites, biological invasions, species extinction and water pollution (Zhuang 2016). In addition to these adverse effects, there are also those caused by dams, where native communities are already weakened by the physical, chemical and biological changes imposed by river fragmentation. Finally, fragmentation and interconnection of water bodies affect both abiotic and biotic environments, and the convergence of these impacts is complex and should be better understood in future studies.

5. Conclusions

Based on the finding of this study, we concluded that in the absence of the natural flow of a river, artificial discharges may promote longitudinal flow regime partitioning of reservoirs. The potential for water discharges to form longitudinal gradients in reservoirs may also be related to the location of the discharges, technical specifications of the hydraulic mechanism, as well as anthropogenic regulation in variables such as frequency, duration and magnitude of discharges. These should be better understood in later studies and taken into consideration when planning water diversion ventures.

Inter-basin water transfer connection areas in the reservoir exhibit lower fish richness and diversity, which may be associated with unstable and unnatural flow regime. On the other hand, the transition zone between an artificial lotic and lentic flow regime presents the highest fish species richness and diversity, which may be associated with greater environmental heterogeneity of this ecotone and to stressors at the ends of the longitudinal gradient, i.e., the upstream unnatural discharges and the downstream smaller number of species pre-adapted to the lentic environment.

Finally, our results corroborate the hypothesis that artificial flow regime, modulated by seasonality, influence environmental variables and have potential effect on the longitudinal distribution of the fish assemblages in an off-river reservoir.

CRediT authorship contribution statement

Gustavo Henrique Soares Guedes: Conceptualization, Investigation, Writing - original draft. **Tailan Moretti Mattos:** Investigation, Formal analysis. **Geysa da Silva Camilo**: Investigation. **Wagner Uehara:** Investigation, Formal analysis. **Débora Lisandra de Paiva Ferreira:** Investigation. **Francisco Gerson Araújo:** Conceptualization, Writing original draft.

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Compliance with ethical standards

Authors state that the research was conducted according to ethical standards.

Declaration of Competing Interest

The authors declare that they have no conflict of interest.

Availability of data

The data that support the findings of this study are available from the corresponding author upon reasonable request.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.ecohyd. 2020.02.002.

References

- Affonso, I.P., Gomes, L.C., Agostinho, A.A., Message, H.J., Latini, J.D., García-Berthou, E., 2016. Interacting effects of spatial gradients and fishing gears on characterization of fish assemblages in large reservoirs. Rev. Fish Biol. Fish. 26 (1), 71–81. doi:10.1007/s11160-015-9402-1.
- Agostinho, A.A., Gomes, L.C., Pelicice, F.M., 2007. Ecology and Management of Fishery Resources in Reservoirs in Brazil. EDUEM, Maringá (in portuguese).
- Agostinho, A.A., Gomes, L.C., Veríssimo, S., Okada, E.K., 2004. Flood regime, dam regulation and fish in the upper Paraná river: Effects on assemblage attributes, reproduction and recruitment. Rev. Fish Biol. Fish. 14 (1), 11–19. doi:10.1007/s11160-004-3551-y.
- Anderson, M., Gorley, R.N., Clarke, R.K., 2008. Permanova + For Primer: Guide to Software and Statistical Methods. PRIMER-E, Plymouth.
- Brazilian Committee of Dams, 2011. The History of Dams in Brazil, Centuries XIX, XX and XXI: Fifty Years of the Brazilian Committee of Dams. CBB, Rio de Janeiro (in portuguese).
- Brown, L.R., Bauer, M.L., 2010. Effects of hydrologic infrastructure on flow regimes of California's central valley rivers: Implications for fish populations. River Res. Appl. 26, 751–765. doi:10.1002/rra.1293.

- Buckmeier, D.L., Smith, N.G., Fleming, B.P., Bodine, K.A., 2013. Intra-annual variation in river-reservoir interface fish assemblages: implications in regulated rivers. River Res. Appl. 30 (6), 780–790. doi:10.1002/rra. 2667.
- Bunn, S.E., Arthington, A.H., 2002. Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. Environ. Manag. 30 (4), 492–507. doi:10.1007/s00267-002-2737-0.
- Casemiro, A.C.R., Garcia, D.A.Z., Costa, A.D.A., Britton, J.R., Orsi, M.L., 2017. Impoundments facilitate a biological invasion: dispersal and establishment of non-native armoured catish loricariichthys platymetopon (Isbrückler & Nijssen, 1979) in a neotropical river. Limnol. Ecol. Manag. Inland Waters 62, 34–37. doi:10.1016/j.limno.2016.11.001.
- Casatti, L., Rocha, F.C., Pereira, D.C., 2005. Habitat use by two species of hypostomus (Pisces, Loricariidae) in southeastern Brazilian streams. Biota Neotrop. 5, 157–165. doi:10.1590/S1676-06032005000300012.
- Costa, M.R., Mattos, T.M., Borges, J.L., Araújo, F.G., 2013. Habitat preferences of common native fishes in a tropical river in southeastern Brazil. Neotrop. Ichthyol. 11, 871–880. doi:10.1590/ S1679-62252013000400015.
- Dickson, K.E., Dzombak, D.A., 2017. Inventory of interbasin transfers in the United States. J. Am. Water Resour. Assoc. 53 (5), 1121–1132. doi:10. 1111/1752-1688.12561.
- Fernando, C.H., Holčík, J., 1991. Fish in reservoirs. Int. Rev. Der Gesamten Hydrobiol. Hydrogr. 76 (2), 149–167. doi:10.1002/iroh.19910760202.
- Fullerton, A.H., Burnett, K.M., Steel, E.A., Flitcroft, R.L., Pess, G.R., Feist, B.E., Torgersen, C.E., Miller, D.J., Sanderson, B.L., 2010. Hydrological connectivity for riverine fish: measurement challenges and research opportunities. Freshw. Biol. 55, 2215–2237. doi:10.1111/j.1365-2427.2010. 02448.x.
- Grill, G., Lehner, B., Thieme, M., Geenen, B., Tickner, D., Antonelli, F., Babu, S., Borrelli, P., Cheng, L., Crochetiere, H., Ehalt Macedo, H., Filgueiras, E., Goichot, M., Higgins, J., Hogan, Z., Lip, B., McClain, M.E., Meng, J., Mulligan, M., Nilsson, C., Olden, J.D., Opperman, J.J., Petry, P., Reidy Liermann, C., Sáenz, L., Salinas-Rodríguez, S., Schelle, P., Schmitt, R.J.P., Snider, J., Tan, F., Tockner, K., Valdujo, P.H., van Soesbergen, A., Zarfl, C., 2019. Mapping the world's free-flowing rivers. Nature 569, 215–221. doi:10.1038/s41586-019-1111-9.
- Junk, W.J., Bayley, P.B., Sparks, R.E., 1989. The flood pulse concept in river-floodplain systems. Can. Spec. Publ. Fish. Aquat. Sci. 106, 110–127.
- Kimmel, B.L., Lind, O.T., Paulson, L.J., 1990. Reservoir primary production. In: Thornton, K.W., Kimmel, B.L., Payne, F.E. (Eds.), Reservoir limnology: Ecological Perspectives. John Wiley & Sons, New York, pp. 133–193.
- Larsen, L.G., Choi, J., Nungesser, M.K., Harvey, J.W., 2012. Directional connectivity in hydrology and ecology. Ecol. Appl. 22, 2204–2220. doi:10. 1890/11-1948.1.
- Lakra, W.S., Sarkar, U.K., Dubey, V.K., Sani, R., Pandey, A., 2011. River inter linking in india: status, issues, prospects and implications on aquatic ecosystems and freshwater fish diversity. Rev. Fish Biol. Fish. 21 (3), 463–479. doi:10.1007/s11160-011-9199-5.
- Legendre, P., Anderson, M.J., 1999. Distance-based redundancy analysis: testing multispecies responses in multifactorial ecological experiments. Ecol. Monogr. 69 (1), 1–24 10.1890/0012-9615(1999)069[0001:DBRATM]2.0.CO;2.
- Liermann, C.R., Nilsson, C., Robertson, J., Ng, R.Y., 2012. Implications of dam obstruction for global freshwater fish diversity. Bioscience 62 (6), 539–548. doi:10.1525/bio.2012.62.6.5.
- Loures, R.C., Pompeu, P.S., 2019. Temporal changes in fish diversity in lotic and lentic environments along a reservoir cascade. Freshw. Biol. 64, 1806–1820. doi:10.1111/fwb.13372.
- Anderson, 2001. McArdle, B.H., M.J., Fitting multivarimodels to community data: a comment on disate redundancy analysis. Ecology tance-based 82, 290-297 10.1890/0012-9658(2001)082[0290:FMMTCD]2.0.CO;2.
- Mims, M.C., Olden, J.D., 2012. Life history theory predicts fish assemblage response to hydrologic regimes. Ecology 93, 35–45. doi:10.1890/ 11-0370.1.
- Mims, M.C., Olden, J.D., 2013. Fish assemblages respond to altered flow regimes via ecological filtering of life history strategies. Freshw. Biol. 58, 50–62. doi:10.1111/fwb.12037.
- Nilsson, C., Reidy, C.A., Dynesius, M., Revenga, C., 2005. Fragmentation and flow regulation of the world's large river systems. Science 308, 405– 408. doi:10.1126/science.1107887.

- Nobile, A.B., Freitas-Souza, D., Lima, F.P., Queiroz, J., Bayona-Perez, I.L., Carvalho, E.D., Ramos, I.P., 2019. Damming and seasonality as modulators of fish community structure in a small tributary. Ecol. Freshw. Fish doi:10.1111/eff.12475, (Early View, First published: 12 March 2019).
- Poff, N.L., Allan, J.D., Bain, M.B., Karr, J.R., Prestegaard, K.L., Richter, B.D., Sparks, R.E., Stromberg, J.C., 1997. The natural flow regime. Bioscience 47, 769–784. doi:10.2307/1313099.
- Poff, N.L., Zimmerman, J.K.H., 2010. Ecological responses to altered flow regimes: a literature review to inform the science and management of environmental flows. Freshw. Biol. 55 (1), 194–205. doi:10.1111/j. 1365-2427.2009.02272.x.
- Prchalová, M., Kubecka, J., Cech, M., Frouzová, J., Drastík, V., Hohausová, E., Juza, T., Kratochvíl, M., Matena, J., Peterka, J., Ríha, M., Tuser, M., Vasek, M., 2009. The effect of depth, distance from dam and habitat on spatial distribution of fish in an artificial reservoir. Ecol. Freshw. Fish 18, 247–260. doi:10.1111/j.1600-0633.2008.00342.x.
- Sandhya, K.M., Lianthuamluaia, L., Karnatak, G., Sarkar, U.K., Kumari, S., Mishal, Kumar, V., Panda, D., Ali, Y., Naskar, B.K., 2019. Fish assemblage structure and spatial gradients of diversity in a large tropical reservoir, Panchet in the Ganges basin, India. Environ. Sci. Pollut. Res. 26, 18804–18813. doi:10.1007/s11356-019-05314-8.
- Silva, J.M., Hernandez-Blazquez, F.J., Junior, H.F., 1997. A new acessory respiratory organ in fishes: morphology of the respiratory purses of loricariichthys platymetopon (Pisces, loricariidae). Ann. Sci. Nat. Zool. 18, 93–103.
- Soares, M.C.S., Marinho, M.M., Huszar, V.L.M., Branco, C.W.C., Azevedo, S.M.F.O., 2008. The effects of water retention time and watershed features on the limnology of two tropical reservoirs in Brazil. Lakes Reserv. Res. Manag. 13 (4), 257–269. doi:10.1111/j.1440-1770.2008.00379.x.
- Straškraba, M., Tundisi, J.G., 2013. Water Quality Management of Dams.. Oficina de Textos, São Paulo (in portuguese).
- Shumilova, O., Tockner, K., Thieme, M., Koska, A., Zarfl, C., 2018. Global water transfer megaprojects: a potential solution for the water-foodenergy nexus? Front. Environ. Sci. 6, 150–165. doi:10.3389/fenvs.2018. 00150.
- Terra, B.D.F., Santos, A.B.I., Araújo, F.G., 2010. Fish assemblage in a dammed tropical river: an analysis along the longitudinal and temporal gradients from river to reservoir. Neotrop. Ichthyol. 8 (3), 599–606. doi:10.1590/S1679-62252010000300004.
- Thornton, K.W., 1990. Perspectives on reservoir limnology. In: Thornton, K.W., Kimmel, B.L., Payne, F.E. (Eds.), Reservoir Limnology: Ecological Perspectives. John Wiley & Sons, New York, pp. 1–15.
- Thomaz, S.M., Cunha, R.E., 2010. The role of macrophytes in habitat structuring in aquatic ecosystems: methods of measurement, causes and consequences on animal assemblages composition and biodiversity. Acta Limnol. Bras. 22, 218–236. doi:10.4322/actalb.02202011.
- Vašek, M., Prchalová, M., Říha, M., Blabolil, P., Čech, M., Draštík, V., Frouzová, J., Jůza, T., Kratochvíl, M., Muška, M., Peterka, J., Sajdlová, Z., Šmejkal, M., Tušer, M., Vejřík, L., Znachor, P., Mrkvička, T., Seďa, J., Kubečka, J., 2016. Fish community response to the longitudinal environmental gradient in Czech deep-valley reservoirs: implications for ecological monitoring and management. Ecol. Indic. 63, 219–230. doi:10.1016/j.ecolind.2015.11.061.
- Willis, T.V., Magnuson, J.J., 2000. Patterns in fish species composition across the interface between streams and lakes. Can. J. Fish. Aquat.Sci. 57 (5), 1042–1052. doi:10.1139/f00-028.
- Winemiller, K.O., 1989. Patterns of variation in life history among south american fishes in seasonal environments. Oecologia 81, 225–241. doi:10.1007/BF00379810.
- Wu, H., Chen, J., Xu, J., Zeng, G., Sang, L., Liu, Q., Yin, Z., Dai, J., Yin, D., Liang, J., Ye, S., 2019. Effects of dam construction on biodiversity: a review. J. Clean. Prod. 221, 480–489. doi:10.1016/j.jclepro.2019.03.001.
- Yang, S., Gao, X., Li, M., Ma, B., Liu, H., 2012. Interannual variations of the fish assemblage in the transitional zone of the three gorges reservoir: persistence and stability. Environ. Biol. Fishes 93, 295–304. doi:10.1007/s10641-011-9936-6.
- Zhuang, W., 2016. Eco-environmental impact of inter-basin water transfer projects: a review. Environ. Sci. Pollut. Res. 23, 12867–12879. doi:10. 1007/s11356-016-6854-3.