

Effects of a small natural barrier on the spatial distribution of the fish assemblage in the Verde River, Upper Paraná River Basin, Brazil

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Abstract

Geographical barriers influence species distribution and play an important role in the segregation of fish assemblages. The present study aims to test the influence of a small natural barrier on the spatial distribution of fish species in the Verde River, Upper Paraná River Basin, Brazil, considering two biotopes: upstream and downstream of the Branca Waterfall. We observed the highest species richness downstream of the Branca Waterfall, which also had the highest number of exclusive species. Richness, evenness, and abundance varied significantly among biotopes. The composition and structure of the fish assemblage differed between biotopes, which were characterized by different indicator species, mainly downstream of the Branca Waterfall. Physical and chemical variables and geographical distance between sites were not responsible for the differences observed. Hence, the present study shows that small barriers can also be crucial in structuring fish fauna and play a key role in the segregation of fish assemblages.

Keywords: community ecology, fish fauna, segregation, spatial distribution, waterfalls.

Efeitos de uma pequena barreira natural sobre a distribuição espacial da assembleia de peixes no rio Verde, bacia do alto rio Paraná, Brasil

Resumo

As barreiras geográficas influenciam a distribuição das espécies e desempenham um papel importante na segregação das assembleias de peixes. Dessa forma, o objetivo deste estudo foi avaliar mudanças espaciais na assembleia de peixes do rio Verde, sob a influência de uma pequena barreira geográfica natural, bacia do alto rio Paraná, Mato Grosso do Sul, Brasil. Para isso, seis locais foram amostrados e agrupados em dois biótopos: montante e jusante da cachoeira Branca. Maior riqueza e número de espécies exclusivas foram observadas a jusante da cachoeira Branca. A riqueza, equitabilidade e abundância diferiram significativamente entre os biótopos. Além disso, a composição e a estrutura da assembleia de peixes também diferiram entre os biótopos, os quais foram caracterizados por distintas espécies indicadoras, especialmente a jusante da cachoeira Branca. As variáveis físicas e químicas da água e as distâncias geográficas, entre os locais, não foram responsáveis pelas diferenças observadas. Dessa forma, este estudo demonstrou que pequenas barreiras geográficas podem ser cruciais na estruturação da ictiofauna e desempenhar um papel-chave na segregação de assembleias de peixes.

Palavras-chave: ecologia de comunidades, ictiofauna, segregação, distribuição espacial, corredeiras.

1. Introduction

Understanding species distribution is one of the main challenges in ecology. In most situations, species have their distribution determined by a series of historical and environmental factors. The knowledge of how these factors affect species distribution is important to build predictive models (Jackson et al., 2001; Teixeira et al., 2005; Suárez

and Petrere Junior, 2007) and to understand spatial and temporal organization patterns of fish assemblages. Fish assemblages are expected to change along stretches of the same river, as a result of evolutionary processes and adaptations of each species. These processes and adaptations are modulated by habitat heterogeneity, environmental

influences, and human activities (e.g., removal of riparian vegetation, construction of dams, canalization, and pollution; Meador and Goldstein, 2003).

Several factors that operate at different spatial and temporal scales determine which species can colonize and persist in specific habitats (Hoinghaus et al., 2007; Rahel, 2007). Hence, regional characteristics may influence the composition and diversity of local fish assemblages (Angermeier and Winston, 1998). These characteristics act as a series of ecological screens or filters (Jackson and Harvey, 1989; Poff, 1997; Quist et al., 2005; Hugueny et al., 2010), such as food resource availability (Uieda and Pinto, 2011), habitat complexity (Alexandre and Almeida, 2010; Felipe and Suárez, 2010), and natural barriers (Robinson and Rand, 2005; Torrente-Vilara et al., 2011; Dias et al., 2013). Cascades, rapids, and waterfalls are potential geographical barriers for the dispersion of aquatic organisms, through the decrease of habitat connectivity; thus, they are crucial in determining species distribution (Rahel, 2007).

Differences in freshwater assemblages among sites may be determined by connectivity (Miranda and Raborn, 2000; Rahel, 2007; Cote et al., 2009) or isolation of the aquatic systems (Torrente-Vilara et al., 2011). Connectivity is one of the main forces that shapes fish population dynamics and leads to changes in the community (Olden et al., 2001; Petry et al., 2003). According to the serial discontinuity concept of lotic ecosystems (Ward and Stanford, 1983; Stanford and Ward, 2001), artificial barriers disrupt the longitudinal gradient of the river. Artificial barriers alter the river biotic and abiotic conditions and lead to variations in the composition and structure of the fish assemblage between upstream and downstream stretches. Likewise, natural barriers may cause faunal discontinuities and increase dissimilarities in the ichthyofauna, as changes in landscape characteristics cause habitat alterations and increase species turnover along the longitudinal gradient (Balon and Stewart, 1983; Rahel and Hubert, 1991).

This study aims at accessing the spatial distribution of fish species in two biotopes: upstream and downstream of the Branca Waterfall, Verde River, Upper Paraná River Basin, Brazil. We assessed the effect of a small natural barrier on the spatial distribution of fish. We expected most of the differences between fish assemblages to be better explained by the small natural barrier than by local environmental conditions. Therefore, we aimed at answering the following questions: (i) Are fish assemblage structure and composition different upstream and downstream of the waterfall?; (ii) Are those differences in composition and structure related to the presence of a small natural barrier?; (iii) Do the composition and structure of fish assemblages in the area influenced by physical and chemical variables of the water?

2. Material and Methods

2.1. Study area

The Verde River Water Basin is located in the Brazilian Cerrado, the second largest biome in the country and one of the world's biodiversity hotspots (Klink and Machado, 2005; Abell et al., 2008). It comprises the northeastern part of the state of Mato Grosso do Sul, with the municipalities

of Camapuã, Costa Rica, Água Clara, Ribas do Rio Pardo, Brasilândia, and Três Lagoas. Its mouth is located in the Paraná River, in the reservoir of the Engenheiro Sérgio Motta Hydropower Plant (locally known as Porto Primavera Dam), state of São Paulo.

The Branca Waterfall is located in the middle stretch of the Verde River close to Água Clara. It is a small obstacle, with approximately 1.5 m in height, characterized by a gradient of intense flow, with several cascades, turbulent waters, and extensive rapids. In this stretch, the substrate is rocky and the waterfall surroundings are composed of marginal native shrubby vegetation and rocks.

2.2. Sampling

We sampled fish species in six sites along the Verde River (Figure 1). In the spatial variation analysis, aiming at identifying the effects of the natural barrier on fish dispersal, we grouped the sites into two biotopes: upstream (1-3; Figure 1) and downstream of the Branca Waterfall (4-6; Figure 1). The physical characteristics of each biotope are described in Table 1.

Sampling was carried out monthly during the fish reproductive season (from November 2010 to March 2011 and from October 2011 to February 2012) and quarterly from May to August 2011, summing up 12 samples. We used as fishing devices gillnets (mesh sizes of 2.4, 3, 4, 5, 6, 7, 8, 9, 10, 12, 14, and 16 cm between opposite knots) and trammel nets (with inner mesh sizes of 6, 7 and 8 cm between opposite knots), locally known as *feiticeiras*, with 1.5 m in height and 20 m in length. We let nets set for 24 h and checked them at every 8 h. After capturing fish specimens, we anesthetized them with a benzocaine solution (250 mg/l) following AVMA (2001), fixed them in plastic bags containing formaldehyde 10% and placed them in polyethylene containers. In the laboratory, we identified the fish following Graça and Pavanelli (2007), measured (total and standard length in cm), and weighed them (g). We preserved vouchers of each species in alcohol 70% and deposited them in the fish collection of Nupélia (Núcleo de Pesquisas em Limnologia, Ictiologia e Aquicultura) at Universidade Estadual de Maringá (available at <http://peixe.nupelia.uem.br>).

2.3. Environmental variables

Concomitantly with fish sampling, we measured water physical and chemical variables, such as temperature (°C; mercury bulb thermometer), electrical conductivity (µS/cm; portable conductivity meter Digimed® DM-3P; Digimed – Analytical Instrumentation – Santo Amaro, São Paulo State, Brazil), dissolved oxygen (mg/L; portable oxymeter YSI 550A), pH (portable phmeter Digimed® DM-2P), turbidity (NTU, Turbidimeter LaMotte® 2020e), and transparency (Secchi disk), to describe the environmental conditions.

2.4. Data analysis

2.4.1. Assemblage attributes

We estimated species abundance based on catch per unit effort (CPUE) in terms of number of individuals (individuals/1,000 m² of net/day) and biomass (kg/1,000 m² of net/day), following King (1995).

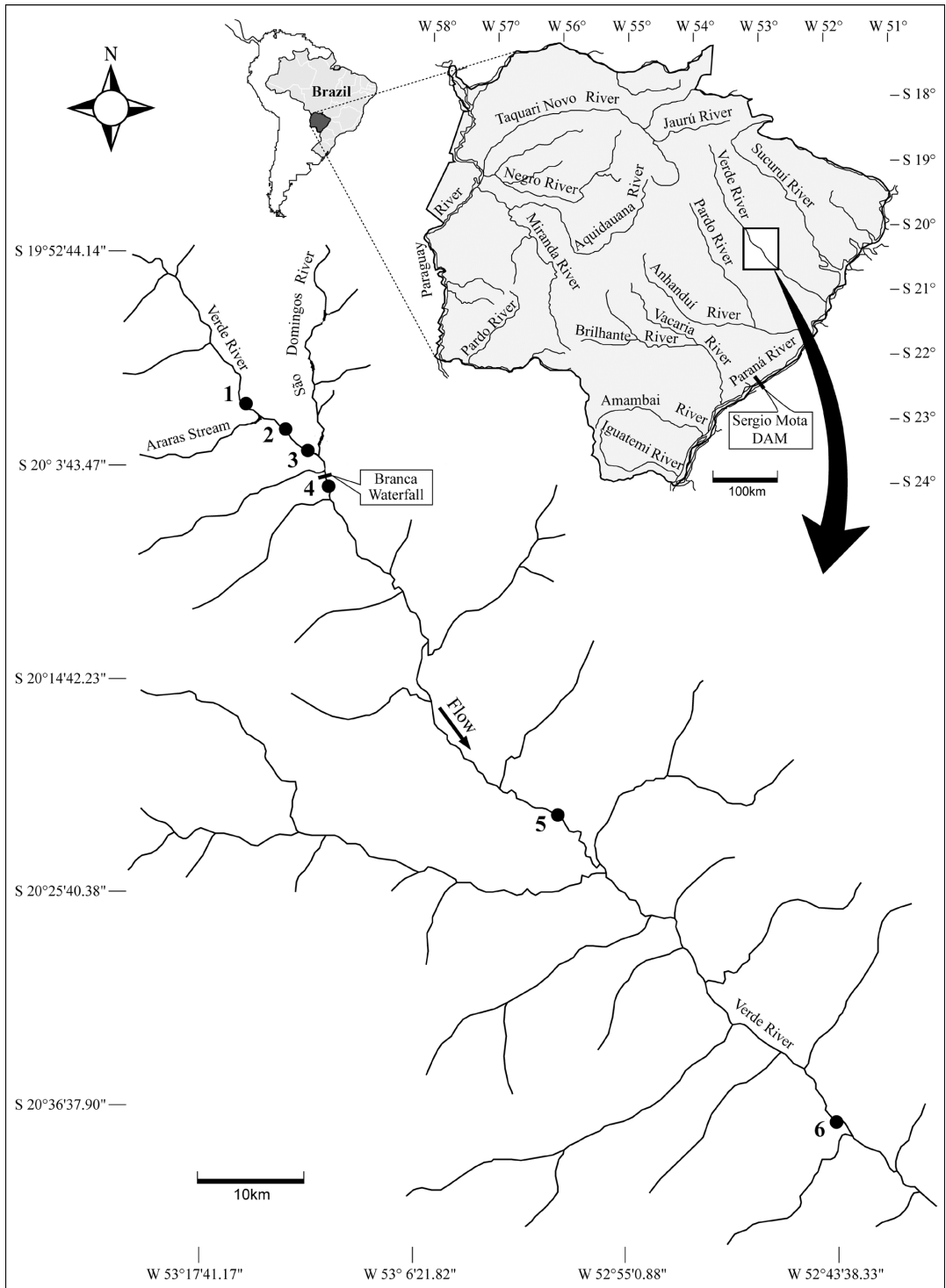


Figure 1. Spatial location of sampling sites in the Verde River, Upper Paraná River Basin, state of Mato Grosso do Sul, Brazil. Sampling sites were grouped according two biotopes: upstream (1-3) and downstream (4-6) of the Branca Waterfall.

For each month and site (per sample), we calculated species richness (number of fish species), Shannon diversity index ($H' = -\sum_{i=1}^s p_i \times \ln(p_i)$, where: s = number of species and p_i = proportion of species i), and evenness

($E = H'/\ln S$, where: H' = Shannon diversity index and S = species richness) (Magurran, 1988).

We used a t-test for independent samples to evaluate spatial differences between biotopes relative to species

Table 1. Physical characteristics of the sampling sites in the Verde River, Upper Paraná River Basin, state of Mato Grosso do Sul, mid-western Brazil.

Site	Biotope	Predominant substrate	Riparian vegetation	Channel physiography	Surrounding
1, 2 and 3	Upstream of the Branca Waterfall	Rocky/sandy	Preserved region with native riparian vegetation (shrubby) with 20 to 30 m in width on both margins.	Width between 40 and 150 m, with fast and turbulent waters, few backwater, and shelter sites. Some marginal lagoons and floodplain areas.	Extensive livestock farming and eucalyptus plantation.
4, 5 and 6	Downstream of the Branca Waterfall	Rocky/sandy	Native riparian vegetation (shrubby) with 10 m in width, on average.	Width between 40 and 60 m, with fast and turbulent waters, backwater areas, shelters on the margins, and large floodplain regions.	Extensive livestock farming and reforestation.

richness, Shannon diversity index, evenness, CPUE (number and biomass), and environmental variables.

2.4.2. Fish assemblage distribution patterns

To summarize composition and structure of the fish assemblage, we applied a nonmetric multidimensional scaling (NMDS; Kruskal, 1964). We computed Bray-Curtis distances and we followed the general NMDS procedure outlined by McCune and Grace (2002). We used random starting configurations, the number of runs with the real data was 100, and the stability criterion was standard deviations ≤ 0.005 in stress over 100 iterations. This analysis was performed using the CPUE data matrix in number (square root transformed to remove the effect of high values) in different months and sampling sites (by sample).

We assessed the variation in assemblage composition and structure in relation to position of sites relative to Branca Waterfall (biotopes; “a” component), geographic distances between sites (“b” component), and environmental variables (“c” component) using variation partitioning routine (Vrpart; Peres-Neto et al., 2006). We chose the Vrpart routine because it divides the variation of a response matrix into two, three, or four explanatory matrices and assesses the individual contributions of each one, and its interactions. We used Hellinger transformation (Legendre and Gallagher, 2001) on CPUE data (in number of each species) of assemblage structure to preserve Euclidian metric distances. The matrix of geographic distances was composed of site coordinates in UTM and was included in the analysis because close sites probably have more similar assemblages than distant ones (Tobler, 1970; Nekola and White, 1999). So, vrpart partitioning out this variation to test the effects of other matrices. We applied significance tests for each contribution matrix with redundancy analysis (RDA function), followed by an analysis of

variance (ANOVA with 999 permutations), as suggested by Oksanen et al. (2015).

We used the indicator value analysis (IndVal; Dufrêne and Legendre, 1997) to detect how strongly each species contributed to the differences between biotopes. To test the significance of the indicator value we used a Monte Carlo procedure with 1,000 permutations.

Assemblage attributes (species richness, Shannon diversity index, and evenness), NMDS, and IndVal were all calculated in the software PC-Ord® 5.0 (McCune and Mefford, 2006). The t-test was calculated in the software Statistica™ 7.0 and the Vrpart in the software R (R DEVELOPMENT CORE TEAM, 2012) with the Vegan package (Oksanen et al., 2015). The level of significance used in all analyses was $p < 0.05$.

3. Results

3.1. Ichthyofauna survey

We caught 5,964 fishes of 82 species, 21 families, and five orders (Appendix A). The orders Characiformes (38 species) and Siluriformes (34 species) comprised 88% of all species collected. In addition, we collected specimens of the orders Gymnotiformes (six species), Perciformes (three species), and Myliobatiformes (one specie).

The species with highest abundance in number (CPUE) upstream of the Branca Waterfall were *Leporinus friderici*, *Astyanax altiparanae*, *Astyanax* aff. *fasciatus*, and *Leporinus obtusidens*. The most abundant species downstream of the Branca Waterfall were *Schizodon borellii*, *L. friderici*, *A. altiparanae*, and *L. obtusidens*. In addition, this biotope also showed the largest number of long-distance migratory species (13). Among the migratory species, the most abundant and frequent was *L. obtusidens*, captured in the three downstream sites (Appendix A). Five fish species recorded

(*Myloplus tiete*, *Brycon orbignyana*, *Pseudoplatystoma corruscans*, *Salminus hilarii*, and *Salminus brasiliensis*) are on the list of endangered or vulnerable species (IUCN, 2014). In the present study these species showed expressive frequencies in both biotopes.

3.2. Assemblage attributes

Total abundance (CPUE) differed significantly between biotopes, both in number ($t = -2.56$; $p = 0.01$) and biomass ($t = -6.06$; $p < 0.01$) (Figure 2a and b, respectively). Higher mean values of CPUE, in number and weight, were registered downstream of Branca Waterfall (216.73 individuals and 78.00 kg. 1000m⁻² of nets in 24h, respectively). We recorded the highest species richness downstream of the Branca Waterfall (70 species). Among those, 32 species were exclusive of this site (Appendix A), including some large-bodied (see Vazzoler, 1996) Siluriformes: *Auchenipterus oostemystax*, *Hemisorubim platyrhynchos*, *Megalonema platanum*, *Pterodoras granulosus*, *Pimelodus ornatus* and *Sorubim lima*. Upstream of the Branca Waterfall, we recorded 50 species, including 12 exclusive species (Appendix A). We observed significant differences in species richness

($t = -3.61$; $p < 0.01$) and evenness ($t = 2.06$; $p < 0.05$; Figure 2c and d, respectively).

3.3. Fish assemblage distribution patterns

The NMDS showed that the composition and structure of the fish assemblage segregated between biotopes. In this analysis, we reached a final stress of 0.23 (Monte Carlo test; $p < 0.01$) for a two dimensional solution. The spatial variability was evidenced by the axis 1, showing that the composition and structure of the fish assemblage are strongly influenced by changes along the longitudinal gradient (Figure 3).

As pointed out by the IndVal, the two biotopes were characterized by different sets of indicator species. We identified fourteen species as indicators downstream of the Branca Waterfall, including mainly large migratory species (five; as mentioned by Vazzoler, 1996). Four species were considered indicators upstream of the Branca Waterfall (Table 2).

Concerning environmental variables, we found significant spatial differences between biotopes, only in electrical conductivity ($t = -2.10$; $p < 0.05$) and turbidity

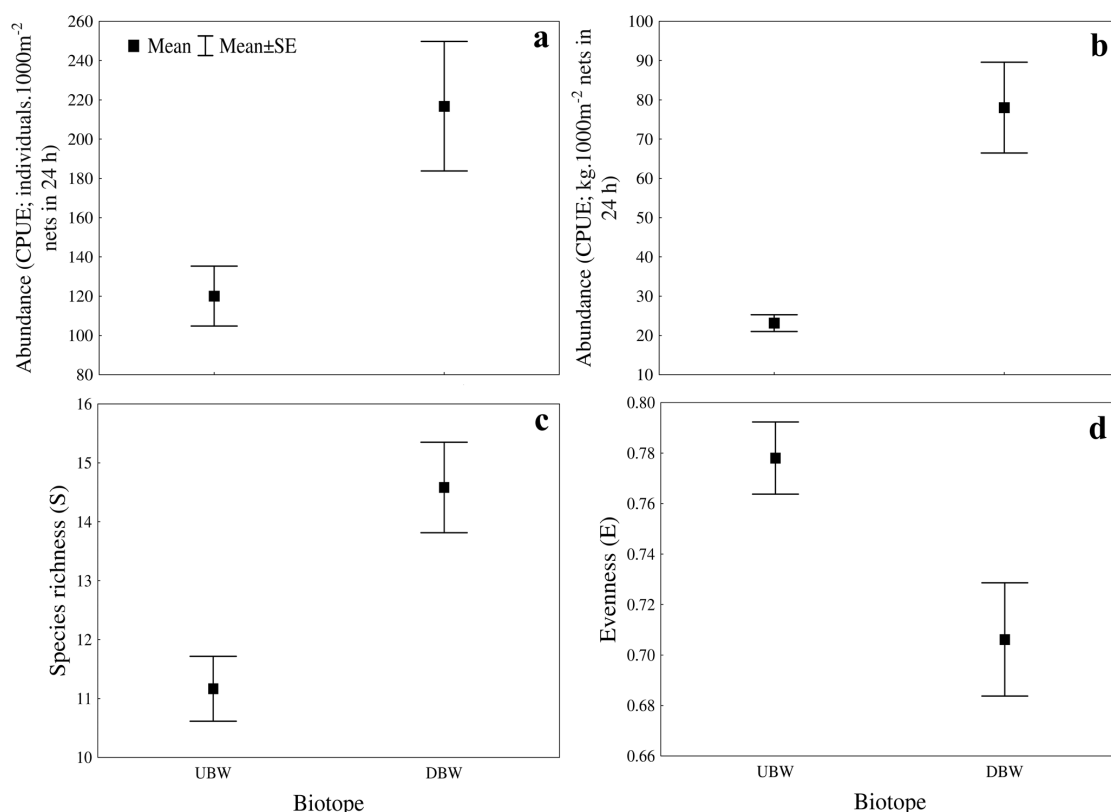


Figure 2. Results of t-test for independent samples comparing the abundance in number (a) and weight (b) of individuals (catch per unit of effort; CPUE), species richness (c) and evenness (d) between two biotopes: upstream (UBW) and downstream (DBW) of the Branca Waterfall in the Verde River, Upper Paraná River Basin, Brazil, from November 2010 to February 2012. Average values of abundance, species richness and evenness for each biotope and their standard errors are displayed in each boxes.

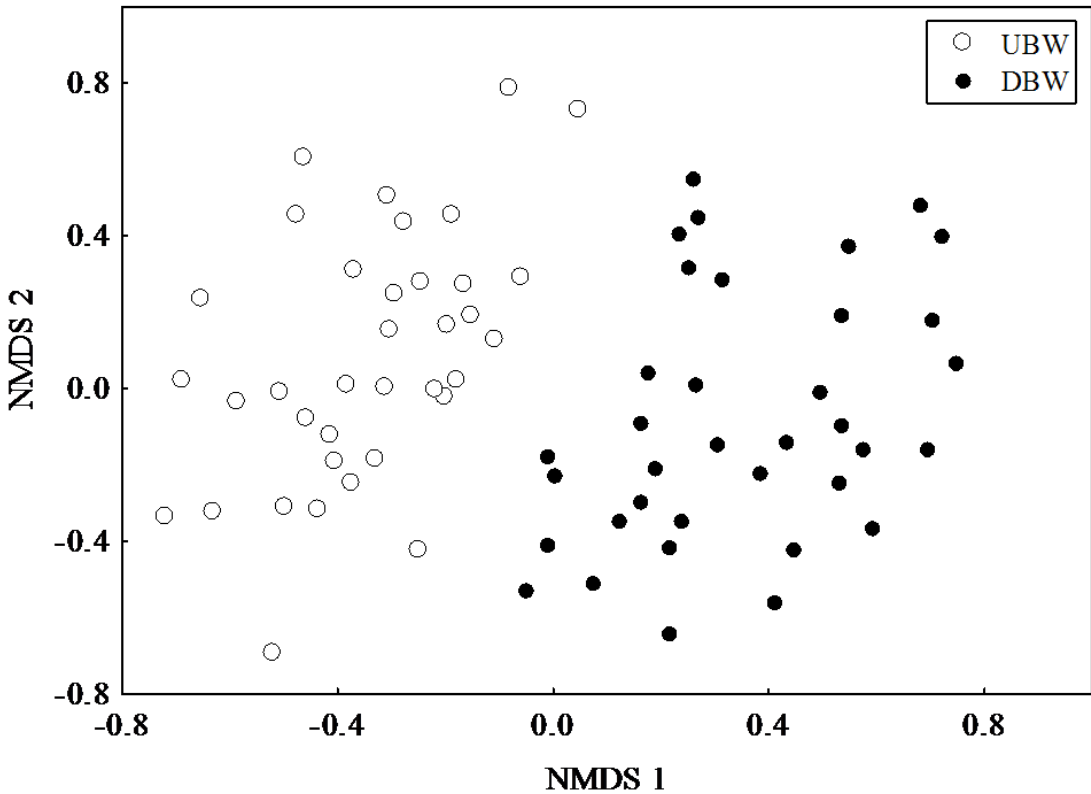


Figure 3. Scores of the axes (two dimensional solution: axis 1 and axis 2) of the nonmetric multidimensional scaling (NMDS) used for the analysis of spatial patterns, ordered by biotope: upstream (UBW) and downstream (DBW) of the Branca Waterfall, Verde River, Upper Paraná River Basin, Brazil, from November 2010 to February 2012.

Table 2. Analysis of species indicator value, showing relative abundance (RA%), relative frequency (RF%), and indicator value (IndVal) of each species in each biotope: upstream (UBW) and downstream of the Branca Waterfall (DBW), in the Verde River, Upper Paraná River Basin, Brazil, from November 2010 to February 2012. Only the species with $p < 0.05$ in the Monte Carlo test are listed.

Biotope	Specie	RA%	RF%	IndVal	p
UBW	<i>A. aff. fasciatus</i>	80	92	73	0.00
	<i>A. lacustris</i>	71	53	37	0.03
	<i>E. trilineata</i>	86	39	33	0.00
	<i>M. tiete</i>	95	69	66	0.00
DBW	<i>A. osteomystax*</i>	100	44	44	0.00
	<i>G. knerii</i>	98	83	81	0.00
	<i>H. cf. cochliodon</i>	100	47	47	0.00
	<i>H. orthonops</i>	100	69	69	0.00
	<i>H. platyrhynchos*</i>	100	53	53	0.00
	<i>M. platanum*</i>	100	17	17	0.02
	<i>P. corruscans*</i>	94	25	24	0.01
	<i>P. galeatus</i>	100	22	22	0.00
	<i>P. gracilis</i>	90	36	33	0.00
	<i>R. descalvadensis</i>	100	19	19	0.00
	<i>R. vulpinus*</i>	100	39	39	0.00
	<i>S. borellii</i>	100	83	83	0.00
	<i>S. maculatus</i>	100	19	19	0.01
<i>S. marginatus</i>	100	22	22	0.00	

*Migratory species.

($t = -2.58$; $p < 0.05$; Table 3). We found higher mean values of electrical conductivity upstream of the Branca Waterfall. On the other hand, we recorded higher mean values of turbidity downstream of the waterfall.

Composition and structure of fish assemblages was weakly, but significantly associated with biotopes, spatial distances and environmental variables (varpart individual contributions of “a” component: adjusted $R^2 = 0.06$, $p < 0.01$; “b” component: adjusted $R^2 = 0.04$, $p < 0.01$; and “c” component: adjusted $R^2 = 0.03$, $p < 0.01$, respectively).

4. Discussion

A small natural geographical barrier led to marked differences in the fish assemblages between biotopes. According to Robinson and Rand (2005), who studied changes in the fish assemblage along an altitudinal gradient in a southern Appalachian watershed in the U.S., fish assemblages in areas with barriers to dispersal should differ from those in areas with no barriers. In addition, local differences in abundance and richness may indicate that potential barriers limit fish dispersal (Nislow et al., 2011).

The spatial structure of the ichthyofauna pointed to marked differences between downstream and upstream stretches of the Branca Waterfall. The downstream biotope has a particular species composition, which may be explained by the influence of the natural barrier. The role of biogeographic barriers, such as waterfalls, cascades, and large rapids, in the isolation of freshwater fish is well documented (Robinson and Rand, 2005; Rahel, 2007; Júlio Júnior et al., 2009; Olden et al., 2010; Torrente-Vilara et al., 2011; Vitule et al., 2012; Dias et al., 2013), but this is not the case for small natural barriers. Barriers constitute a determining factor in the composition of regional faunas and ichthyofauna dissimilarity. The Branca Waterfall causes a disruption in the longitudinal gradient of the river. It possibly acts as an ecological filter that limits the ascendant and descendant movement of fish between the sites located upstream and downstream of the waterfall.

The absence of migratory species upstream of barriers is attributed to geographic isolation, as barriers impede the dispersal needed to complete the life cycle of fish (Britto and Sirol, 2005). In the present study, the small natural barrier has apparently isolated not only the small-sized species with low dispersal capacity, but also large migratory Siluriformes (as mentioned in Vazzoler, 1996), which were considered indicator species downstream of the Branca Waterfall. However, records of species in the upper stretches also suggest bidirectional movements, as some long-distance migratory species were recorded in both biotopes. Most of these species belong to the order Characiformes, such as *L. elongatus*, *S. brasiliensis*, and *S. hilarii*. Our data suggest that these species transpose the Branca Waterfall and possibly use upstream areas for their reproductive activities. In order to migrate upstream of a river, a fish should swim faster than the water velocity, which requires a large amount of energy. As Characiformes are thought to be more efficient swimmers than the Siluriformes

Table 3. Environmental variables (mean \pm standard deviation) for the two biotopes: upstream (UBW) and downstream of the Branca Waterfall (DBW), in the Verde River, Upper Paraná River Basin, Brazil, from November 2010 to February 2012.

Environmental variable/Biotope	UBW	DBW
Water temperature (°C)	26.20 \pm 2.08	26.6 \pm 1.84
Dissolved oxygen (mg/l)	7.81 \pm 0.73	7.69 \pm 0.68
pH	6.50 \pm 1.25	6.80 \pm 0.52
Electrical conductivity (μ S/cm)	26.47 \pm 12.36	22.41 \pm 13.56
Turbidity (NTU)	21.09 \pm 13.29	33.42 \pm 35.55
Water transparency (cm)	70.55 \pm 40.52	79.70 \pm 41.04

(Santos et al., 2007; Makrakis et al., 2010), they would have better capacity to transpose barriers. These results indicate that the Branca Waterfall is not a completely unbridgeable barrier (a small barrier), especially in periods of flood. However, the Verde River’s barrier plays a selective role in the passage of fish upstream.

As previously reported, Verde River has its mouth in the reservoir of Porto Primavera. According to Agostinho et al. (2007, 2008), there is a high reduction in diversity and productivity in reservoirs, which compels species to search for alternative sites for survival and reproduction. Therefore, the Verde River is an important alternative route for migratory species. The importance of the maintenance of free stretches in tributaries upstream reservoirs it is well documented in the literature (Hoffmann et al., 2005; Agostinho et al., 2008; Gubiani et al., 2010). In addition, according to Olden et al. (2010), biogeographic processes that increase habitat isolation and limit dispersal resulted in high diversity of freshwater fish. Hence, the high diversity, mainly of migratory species, observed downstream of the Branca Waterfall suggests that the ichthyofauna is under the influence of both the Porto Primavera reservoir and the waterfall itself, and is highly isolated and diverse.

Physical and chemical factors are pointed as important for determining the distribution and composition of fish assemblages (Matthews, 1998; Jackson et al., 2001; Oberdorff et al., 2001; Barros et al., 2013). However, in the present study we observed a weak correlation between selected environmental variables and geographical distance with the spatial structure of the ichthyofauna. In addition to the abiotic factors and geographical distance, several other factors may influence the structuring of fish assemblages, such as biotic factors (e.g. predation and competition), regional factors (e.g. climatic variables) (Jackson et al., 2001). It is clear, though, that dispersal barriers, such as the small barrier of Branca Waterfall, played an important role promoting spatial variations in fish assemblages.

Therefore, small barriers should be assessed in detail not only in the Verde River, but also in other rivers.

There is no consensus on the waterfall height that would constitute a threshold to prevent freshwater fish from dispersing upstream (i.e., an insurmountable barrier, sensu Dias et al., 2013). However, our study showed that small barriers may be crucial in structuring fish assemblages. The Branca Waterfall has a strong influence on the spatial distribution of the fish fauna of the Verde River. It plays a key role in the segregation of assemblages, and provides the stretch downstream of Branca Waterfall with a rich and diverse fauna. In conclusion, conservation and management strategies of aquatic organisms should consider that even small barriers may cause differences in community structure or even isolate communities (Rahel, 2007; Júlio Júnior et al., 2009; Torrente-Vilara et al., 2011; and results reported herein).

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Appendix A. Taxonomic nomenclature following Reis et al. (2003) and Graça and Pavanelli (2007) and abundance in number (CPUE) for the species collected in each biotope: upstream (UBW) and downstream of the Branca Waterfall (DBW), in the Verde River, Upper Paraná River Basin, Brazil, from November 2010 to February 2012.

	Voucher NUP	Abundance - number of individuals (CPUE) by Biotope	
		UBW	DBW
Class Chondrichthyes			
ORDER MYLIOBATIFORMES			
Family Potamotrygonidae			
<i>Potamotrygon</i> cf. <i>falkneri</i> Castex & Maciel, 1963	10918		0.05*
Class Osteichthyes			
ORDER CHARACIFORMES			
Family Paradontidae			
<i>Apareiodon affinis</i> (Steindachner, 1879)	14457	0.11	0.16
<i>Parodon nasus</i> Kner, 1859	6194	0.85	0.53
Family Curimatidae			
<i>Steindachnerina insculpta</i> (Fernández-Yápez, 1948)	1424		0.11*
<i>Steindachnerina brevipinna</i> (Eigenmann & Eigenmann, 1889)	2372		0.05*
Family Prochilodontidae			
<i>Prochilodus lineatus</i> (Valenciennes, 1836)	6151	1.06	2.07
Family Anostomidae			
<i>Leporinus</i> sp.		0.05*	
<i>Leporellus vittatus</i> (Valenciennes, 1850)	1902	1.06	0.64
<i>Leporinus amblyrhynchus</i> Garavello & Britski, 1987	14468	0.21*	
<i>Leporinus obtusidens</i> (Valenciennes, 1836)	277	10.7	15.2
<i>Leporinus friderici</i> (Bloch, 1794)	1180	27.59	41.36
<i>Leporinus lacustris</i> Campos, 1945	3308	0.11*	
<i>Leporinus piavussu</i> Britski, Birindelli & Garavello, 2012	14070	0.11	0.37
<i>Leporinus octofasciatus</i> Steindachner, 1915	11867	1.22	0.37
<i>Leporinus striatus</i> Kner, 1858	3810		0.16*
<i>Schizodon altoparanae</i> Garavello & Britski, 1990	2020		0.48*
<i>Schizodon borellii</i> (Boulenger, 1900)	1925	0.05	78.54
<i>Schizodon nasutus</i> Kner, 1858	2495		0.21*
Family Characidae			
<i>Astyanax</i> aff. <i>fasciatus</i> (Cuvier, 1819)	32	17	4.34
<i>Astyanax</i> aff. <i>paranae</i> Eigenmann, 1914	133	0.37*	
<i>Astyanax altiparanae</i> Garutti & Britski, 2000	6149	20.87	16.21
<i>Moenkhausia</i> aff. <i>intermedia</i> Eigenmann, 1908	3208		0.11*
<i>Moenkhausia</i> aff. <i>sanctaefilomenae</i> (Steindachner, 1907)	371	0.58	0.05
<i>Piabina argentea</i> Reinhardt, 1867	6209	0.05*	
Subfamily Salmininae			
<i>Salminus brasiliensis</i> (Cuvier, 1816)	1865	3.23	1.85
<i>Salminus hilarii</i> Valenciennes, 1850	1893	0.69	0.26
Subfamily Bryconinae			
<i>Brycon orbignyanus</i> (Valenciennes, 1850)	12174	0.32	0.37
Subfamily Serrasalminae			
<i>Myloplus tiete</i> (Eigenmann & Norris, 1900)	2484	2.81	0.16
<i>Serrasalmus maculatus</i> Kner, 1858	396		0.42*
<i>Serrasalmus marginatus</i> Valenciennes, 1837	439		0.42*
Subfamily Characinae			
<i>Galeocharax knerii</i> (Steindachner, 1879)	263	0.16	6.94
<i>Roeboides descalvadensis</i> Fowler, 1932	13601		0.53*

*Species exclusive of each biotope.

Appendix A. Continued...

	Voucher NUP	Abundance - number of individuals (CPUE) by Biotope	
		UBW	DBW
Family Acestrorhynchidae			
<i>Acestrorhynchus lacustris</i> (Lütken, 1875)	14483	3.18	1.32
Family Cynodontidae			
<i>Rhaphiodon vulpinus</i> Spix & Agassiz, 1829	11153		1.17*
Family Erythrinidae			
<i>Erythrinus Erythrinus</i> (Bloch & Schneider, 1801)	11197	0.11*	
<i>Hoplias</i> sp. 1	292	2.38	1.54
<i>Hoplias</i> sp. 2	3457	0.53	0.21
<i>Hoplias</i> sp. 3	3458	0.16*	
Family Hemiodontidae			
<i>Hemiodus orthonops</i> Eigenmann & Kennedy, 1903	10609		12.18*
ORDER SILURIFORMES			
Family Callichthyidae			
<i>Callichthys callichthys</i> (Linnaeus, 1758)	1722	0.05*	
Family Cetopsidae			
<i>Cetopsis gobioides</i> Kner, 1858	2476		0.11*
Family Loricariidae			
Subfamily Ancistrinae			
<i>Megalancistrus parananus</i> (Peters, 1881)	9111		0.05*
Subfamily Loricariinae			
<i>Loricariichthys platymetopon</i> Isbrücker & Nijssen, 1979	13632		0.26*
<i>Loricariichthys rostratus</i> Reis & Pereira, 2000	4730		0.11*
<i>Rineloricaria latirostris</i> (Boulenger, 1900)	13669	0.11	0.05
<i>Rineloricaria</i> sp.		0.05	0.05
Subfamily Hypostominae			
<i>Hypostomus ancistroides</i> (Ihering, 1911)	332	0.05*	
<i>Hypostomus</i> cf. <i>cochliodon</i> Kner, 1854	2556		2.86*
<i>Hypostomus margaritifer</i> (Regan, 1908)	1766	0.05*	
<i>Hypostomus microstomus</i> Weber, 1987	1725	0.53	0.05
<i>Hypostomus</i> cf. <i>nigromaculatus</i> (Schubart, 1967)	12462	0.58	0.05
<i>Hypostomus</i> cf. <i>regani</i> (Ihering, 1905)	2286	1.85	0.37
<i>Hypostomus</i> cf. <i>strigaticeps</i> (Regan, 1908)	3190	2.54	0.95
<i>Pterygoplichthys anisitsi</i> Eigenmann & Kennedy, 1903	1529		0.16*
Family Heptapteridae			
<i>Pimelodella avanhandavae</i> Eigenmann, 1917	3455		0.05*
<i>Pimelodella gracilis</i> (Valenciennes, 1835)	3118	0.16	1.48
<i>Pimelodella</i> sp.			0.11*
<i>Rhamdia quelen</i> (Quoy & Gaimard, 1824)	2501		0.05*
Family Pimelodidae			
<i>Hemisorubim platyrhynchos</i> (Valenciennes, 1840)	2506		3.23*
<i>Iheringichthys labrosus</i> (Lütken, 1874)	671	0.42	0.64
<i>Megalonema platanum</i> (Günther, 1880)	1729		0.42*
<i>Pimelodus</i> cf. <i>argenteus</i> Perugia, 1891	3230		0.11*
<i>Pimelodus maculatus</i> La Cèpède, 1803	420	0.05	0.32
<i>Pimelodus microstoma</i> Steindachner, 1877	14465	2.44	1.75
<i>Pimelodus ornatus</i> Kner, 1858	2492		0.16*
<i>Pseudoplatystoma corruscans</i> (Spix & Agassiz, 1829)	523	0.05	0.9

*Species exclusive of each biotope.

Appendix A. Continued...

	Voucher NUP	Abundance - number of individuals (CPUE) by Biotope	
		UBW	DBW
<i>Sorubim lima</i> (Bloch & Schneider, 1801)	2494		0.26*
Family Doradidae			
<i>Pterodoras granulosus</i> (Valenciennes, 1821)	4722		0.21*
<i>Rhinodoras dorbignyi</i> (Kner, 1855)	11151	0.32	0.11
<i>Trachydoras paraguayensis</i> (Eignmann & Ward, 1907)	9185		0.48*
Family Auchenipteridae			
<i>Auchenipterus osteomystax</i> (Miranda-Ribeiro, 1918)	2627		1.80*
<i>Tatia neivai</i> (Ihering, 1930)	2080	0.69	0.05
<i>Parauchenipterus galeatus</i> (Linnaeus, 1766)	3302		1.32*
ORDER GYMNOTIFORMES			
Family Gymnotidae			
<i>Gymnotus inaequilabiatus</i> (Valenciennes, 1839)	14327		0.05*
<i>Gymnotus sylvius</i> Albert & Fernandes-Matioli, 1999	13301	0.16	0.11
Family Sternopygidae			
<i>Eigenmannia trilineata</i> López & Castello, 1966	14372	1.59	0.26
<i>Eigenmannia virescens</i> (Valenciennes, 1847)	14466	0.21	0.16
Family Aptereronotidae			
<i>Sternopygus macrurus</i> (Bloch & Schneider, 1801)	2096	0.21	0.16
<i>Porotergus ellisi</i> Arámburu, 1957	2092		0.21*
ORDER PERCIFORMES			
Family Cichlidae			
<i>Cichla kelberi</i> Kullander & Ferreira, 2006	1746	0.11	0.05
<i>Crenicichla britskii</i> Kullander, 1982	14329	0.11*	
<i>Cichla piquiti</i> Kullander & Ferreira, 2006	3379	0.05*	
Species richness		50	70

*Species exclusive of each biotope.

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