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Influence of habitat connectivity and seasonality on the ichthyofauna structure of a riverine knickzone

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ABSTRACT. Knickzones are originated from basaltic outcroppings, present runs, riffles and pools and are highly influenced by flood pulses, which maintain their natural dynamic. However, the construction of hydroelectric power plants alters or eliminate the dynamism of this area and can affect the resident fauna that may be dependent on it. The aim of this study was to evaluate the organization of a knickzone's ichthyofauna considering the influence of seasonality and connectivity of habitats. The study was performed in a knickzone located in the Sapucaí-Mirim River, Southeast Brazil. We sampled four rocky pools connected to the river and three isolated pools, during rainy and dry conditions. The analysis of the two factors (connectivity and seasonality) and of their interaction showed a significant influence only for seasonality on ichthyofauna structure, with higher values of abundance in the rainy season. The species that most contributed to the high dissimilarity between seasons were *Knodus moenkhausii* (50% of contribution) and *Astyanax bockmanni* (21%). The former is the most abundant species in the rainy season and the later in the dry season. The alteration between low and high water level occurs frequently in knickzones, as it is a rocky shallow platform in the middle of a river, with floods occurring seasonally or in stochastic short-term periods. This hydrological seasonal dynamic, high limnological variability and complex interactions of different habitats (pools, runs and rapids) explain the particular ichthyofauna structure in such small area. Our results also indicate the potential importance of basaltic knickzones for regional fish diversity conservation, especially due to the imminent threat by intensive hydropower reservoir construction.

KEYWORDS. Basaltic substrate, conservation, rocky pool, Sapucaí-Mirim River, seasonal hydrologic pulses.

RESUMO. Influência da conectividade do habitat e sasonalidade na estrutura da ictiofauna de um pedral. Pedrais são originados de afloramentos basálticos, apresentando rápidos, corredeiras e poças e são altamente influenciados por pulsos de inundação que mantêm sua dinâmica natural. No entanto, a construção de usinas hidrelétricas altera ou elimina o dinamismo dessa área e pode afetar a fauna residente que pode ser dependente dela. O objetivo deste estudo foi avaliar a organização da ictiofauna de um pedral considerando a influência da sazonalidade e conectividade dos habitats. O estudo foi realizado em uma zona localizada no rio Sapucaí-Mirim, sudeste do Brasil. Foram amostradas quatro poças rochosas conectadas ao rio e três isoladas, em condições chuvosas e secas. A análise dos dois fatores (conectividade e sazonalidade) e de sua interação mostrou influência significativa apenas para a sazonalidade na estrutura da ictiofauna, com maiores valores de abundância na estação chuvosa. As espécies que mais contribuíram para a alta dissimilaridade entre as estações foram *Knodus moenkhausii* (50% de contribuição) e *Astyanax bockmanni* (21%). A primeira é a espécie mais abundante na estação chuvosa e a posterior na estação seca. A alteração entre baixo e alto nível de água ocorre com frequência em pedrais, pois é uma plataforma rochosa e rasa no meio de um rio, com inundações ocorrendo sazonalmente ou em períodos estocásticos de curto prazo. Esta dinâmica hidrológica sazonal, alta variabilidade limnológica e interações complexas de diferentes habitats (poças, rápidos e corredeiras) explicam a particular estrutura da ictiofauna em uma área tão pequena. Nossos resultados também indicam a importância potencial dos pedrais basálticos para a conservação regional da diversidade de peixes, especialmente devido à ameaça iminente da construção intensiva de reservatórios de hidrelétricas.

PALAVRAS-CHAVE. Substrato basáltico, conservação, poça rochosa, Rio Sapucaí-Mirim, pulsos hidrológicos sazonais

Seasonal hydrologic pulses strongly influence the ecology of tropical rivers (Correa & Winemiller, 2014; Fitzgerald *et al.*, 2017), introducing a temporal dynamic on the fish composition and structure in fluvial systems (Junk *et al.*, 1989; Driver & Hoeinghaus, 2016), particularly in environments with strong seasonal or annual flood and drought cycles (Poff & Ward, 1989; Larned *et al.*, 2010). The flood pulse increases the lateral connectivity among habitats (opportunity for dispersion), the physical space for colonizers, and the availability of shelter and food resources (Thomaz *et al.*, 2007). As water level decreases, some habitats become isolated and the effect of biological interactions on fish communities can be intensified (Fernandes *et al.*, 2009; Ferrareze & Nogueira, 2011), with harsh and variable abiotic conditions resulting in physiological stress upon the biota (Spranza & Stanley, 2000; Boulton, 2003).

Knickzones are river stretches often formed by changes in bed cover, channel geometry and erosion processes (Haykawa & Oguchi, 2009; Dibiase *et al.*, 2014). They are ecologically characterized by large rock outcrops forming a complex of habitats composed by riffles, runs and pools with distinct magnitudes and are highly influenced by flood pulses (Brambilla *et al.*, 2018). The immersed or exposed condition of the substrate of a knickzone is highly variable and differences are mainly seasonal (summer-rainy and winter-dry periods), but can also occur stochastically throughout the year, in short-term periods of storms and dry spell events (Brambilla *et al.*, 2018). The degree of connectivity of pools with the main river channel is also variable, with two connectivity conditions occurring during dry season: isolated pools with no connection with river flow and the connected ones with permanent connection with river flow. However, when the river water level is high, the entire substrate of the knickzone is fully immersed. After rainfall stops the water level quickly decreases and the degree of substrate exposed increases, consequently some pools quickly return to the isolated condition (Brambilla *et al.*, 2018).

These unique ecosystems are currently threat by the construction of hydroelectric power plants, fact evidenced by the controversial construction of the huge Brazilian hydroelectric plant of Belo Monte, in Xingu River (Amazon Basin; 11,233 MW) (Winemiller *et al.*, 2016). This threat is a worldwide scenario, considering the existence of 8,600 dams primarily designed for electric generation (Zarfl *et al.*, 2015). Furthermore, studies about freshwater communities of knickzones are scarce (Muehlbauer & Doyle, 2012). For macroinvertebrates, it is known that knickzones support a high diversity and a unique filterer-dominated community not found elsewhere in stream reaches (Muehlbauer & Doyle, 2012). However, there are no studies about fish communities inhabiting knickzones (Muehlbauer & Doyle, 2012).

Therefore, the aim of this study was to evaluate the organization of the ichthyofauna in a Brazilian knickzone, considering the influence of seasonality and connectivity of the knickzone's pools with the main river channel. Our hypothesis is that the structure of this ichthyofauna is influenced by these two factors, exhibiting differences between rainy and dry season and between connected and isolated pools, with lower values of abundance in dry season and isolated pools because of the longtime of disconnection with the main river channel.

MATERIAL AND METHODS

Study area. The study area is located in Sapucaí-Mirim River, a tributary of Grande River basin, between São Paulo and Minas Gerais States, Brazil. Currently, five small hydropower plants (SHP) are operating in this river basin, generating 70 MW, and another six potential sites were inventoried for future constructions (ANEEL, 2018). Based on recent satellite images, at least eight knickzones can be recognized in this river. The selected knickzone (20°34'34.1"S, 47°47'06.5"W) has an area of 0.03 km², representing 0.00032% of the Sapucaí-Mirim basin, and was chosen for the study because it presents a naturally dynamic river flow (it is located in the upstream zone of Palmeiras SHP, but beyond its operational influence). In this knickzone, we selected four pools connected and three isolated from the river flow to study the ichthyofauna structure (See Brambilla et al., 2018 for more details and photos of sampling area).

Sampling. Samplings were performed during one day of a dry season month (June/2014) and one day of a rainy season month (December/2014) (Fig. 1). The dry season sampling was performed approximately two months after the water level of the river starts decreasing (Fig. 1). In December, the outflow reached a peak of 90 $m^3 s^{-1}$ when, according to Brambilla *et al.* (2018), this knickzone become fully immersed. However, the rainy season sampling occurred two days after this high outflow peak when the water had already started to decrease and the river outflow reached 58 $m^3 s^{-1}$, with runs, riffles and pools already exposed (rainy condition). The pools sampled differed in relation to some characteristics, such as the presence of marginal herbaceous vegetation in contact with water, the amount of filamentous algae (estimated visually) and the volume of water (measured with graduated tape and ruler and calculated with the volume formula of the most similar geometric figure) (Tab. I).

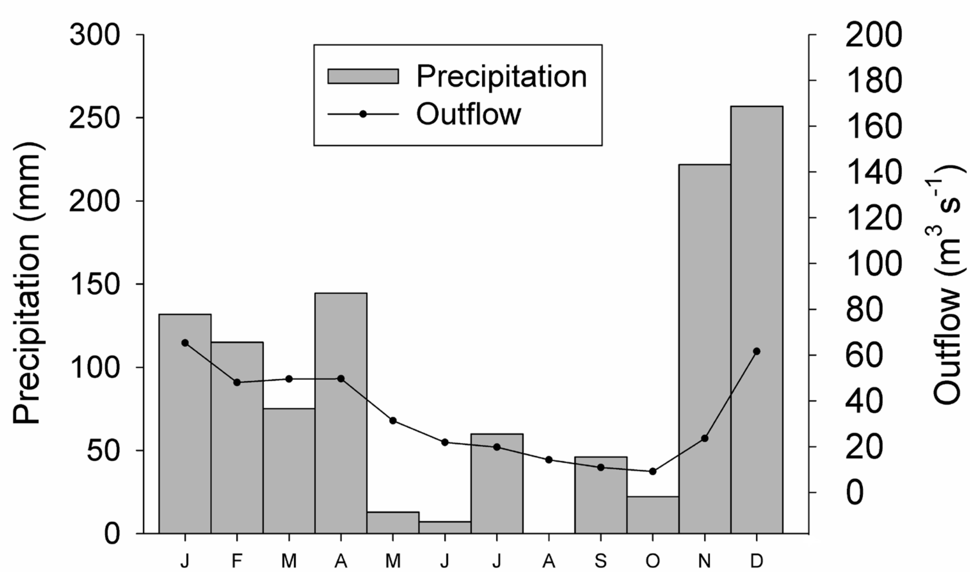

Fig. 1. Monthly rain precipitation in Sapucaí-Mirim River basin, Southeast Brazil during 2014.

Tab. I. Physical characteristics of the pools studied in a basaltic knickzone of the Sapucai-Mirim River, sampled in a dry and rainy season. C- connected pool, I- isolated pool.

Pools	Marginal vegetation		Amount of algae		Volume of water (m^3)		Degree of connection	
	Dry	Rainy	Dry	Rainy	Dry	Rainy	Dry	Rainy
C1	yes	yes	medium	-	50-100	>100	medium	high
C2	no	yes	medium	-	<50	50-100	medium	high
C3	no	no	medium	-	>100	>100	high	high
C4	no	no	high	-	50-100	>100	low	medium
I1	no	no	-	-	<50	<50	-	-
I2	no	no	medium	-	>100	>100	-	-
I3	no	no	-	-	<50	<50	-	-

In each pool, several sampling methods were used, including seine, sieve (mesh size 0.5 cm) and electrofishing, in order to obtain a representative sample of the ichthyofauna. The sampling effort was five passes of seine and sieve and 30 minutes of electrofishing on each pool (during each season). Sampled fish were immediately euthanized in a hyper concentrated solution of eugenol, fixed in formalin 10%, and subsequently transferred to 70% ethanol.

In laboratory, fish were identified according to morphological and meristic features (Castro *et al*., 2004; Graça & Pavanelli, 2007; Langeani & Rego, 2014). The identifications were checked through scientific collections and confirmed by specialists (Dr. Francisco Langeani Neto from the State University of São Paulo - Campus São José do Rio Preto and Dr. Cláudio Zawadzki from the State University of Maringá). The specimens were deposited in two collections (LBP - Laboratório de Biologia e Genética de Peixes, UNESP, Botucatu; NUP –Núcleo de Pesquisas em Limnologia, Ictiologia e Aqüicultura, UEM, Maringá).

The specimens that presented standard length values lower than the first sexual maturation size reported in literature for the species (Nakatami *et al*., 2001; Graça & Pavanelli, 2007; Langeani & Rego, 2014) were considered juveniles, development period characterized by whole formation of fins and scales until sexual maturation (Nakatami *et al*., 2001).

Analyses. In order to discriminate the fish assemblage structure considering connectivity and seasonality, it was used a Non-Metric Multidimensional Scaling (NMDS) (Legendre & Legendre, 2012). The ordination analysis was applied to a Bray-Curtis similarity matrix derived from fish abundance data transformed in log (x+1). A Permutation Multivariate Analysis of Variance (PERMANOVA) (Anderson, 2001) based on the Bray-Curtis similarity matrix, derived from fish abundance data transformed in log (x+1), was used to test for differences in fish assemblage between seasons (rainy and dry), connectivity (isolated and connected) and the interaction between both factors. When the PERMANOVA pseudo-F is significant ($p < 0.01$), a Permutation Analysis of Multivariate Dispersions (PERMDISP) is applied to the same data set to confirm if the differences found are really related to the factors analyzed (pseudo-F not significant in the PERMDISP results; $p > 0.01$) or only related to the dispersion or heterogeneity of samples (in this case with a pseudo-F significant, $p < 0.01$) (Anderson, 2006; Warton *et al*., 2012). A Similarity Percentage Routine (SIMPER) was used to determine the contribution of individual taxa to the average dissimilarity (typifying species) (Clarke & Warwick, 2001). Analyses were performed in PRIMER v6.0 software.

RESULTS

The ichthyofauna of the studied knickzone of Sapucaí-Mirim River was composed by 23 species, distributed in 11 families (Tab. II). The most frequent order was Characiformes (5 families, 11 species), followed by Siluriformes (3 families, 6 species) and Perciformes (1 family, 4 species). The orders Cyprinodontiformes and Gymnotiformes appeared with only one family and one species each.

The rainy season presented 447 specimens of 20 species, the dry season 161 specimens of 12 species. Connected pools harbored 399 specimens of 22 species and isolated pools 209 specimens of 9 species. Most species (82%) were small in size (smaller than 20 cm of standard length), representing 98% of total abundance, and the remaining were medium-sized (between 20-50 cm of standard length). The most abundant species were *Knodus moenkhausii* (Eigenmann & Kennedy, 1903) and *Astyanax bockmanni* Vari & Castro, 2007 during both the rainy and dry seasons (Tab. II). Juveniles of *Astyanax bockmanni, Knodus moenkhausii,* and *Geophagus brasiliensis* (Quoy & Gaimard, 1824) were collected in both seasons and juveniles of *Schizodon nasutus* Kner, 1858, *Astyanax lacustris* (Lütken, 1875), *Steindachnerina insculpta* (Fernández-Yépez, 1948), *Hoplias malabaricus* (Bloch, 1794) and *Poecilia reticulata* Peters, 1859 were collected only in the rainy season.

The ordination analysis (NMDS), applied to fish abundance data, suggested a separation of the ichthyofauna assemblage between dry and rainy seasons and not between condition of connectivity, with rainy-season samples more aggregate than dry-season ones (Fig. 2). Supporting NMDS results, the PERMANOVA indicated differences in fish structure only for the factor seasonality (pseudo-F = 3.94, $p = 0.008$), but neither for connectivity (pseudo-F = 1.25, $p = 0.278$) nor for the interaction of the two factors (pseudo-F = 0.51, $p = 0.845$). The not-significant results of the PERMDISP (pseudo-F = 10.04, $p = 0.02$) confirmed that the seasonal difference was really related to the factor

Tab. II. Taxonomic list and abundance of the fish species sampled in connected (C) and isolated (I) pools, during a dry (D) and rainy (R) season, in a basaltic knickzone of the Sapucaí-Mirim River. Voucher number of specimens deposited in two collections (LBP, Laboratório de Biologia e Genética de Peixes, UNESP, Botucatu; NUP, Núcleo de Pesquisas em Limnologia, Ictiologia e Aqüicultura, UEM, Maringá). * Non-native species. Taxonomic list based on ESCHMEYER *et al.* (2018).

FAMILY	SPECIES	CD	ID	CR	IR	TOTAL	VOUCHER
Anostomidae	*Schizodon nasutus* Kner, 1858	-	-	5	-	5	LBP 18825
Characidae	*Astyanax bockmanni* Vari & Castro, 2007	40	49	40	54	183	LBP 18793
	Astyanax lacustris (Lütken, 1875)	-	-	7	-	7	LBP 18794
	Bryconamericus turiuba Langeani, Lucena, Pedrini & Tarelho-Pereira, 2005	-	8	-	-	8	LBP 21923
	Knodus moenkhausii (Eigenmann & Kennedy, 1903)	12	11	185	54	262	LBP 21918
	Piabarchus stramineus (Eigenmann, 1908)	-	-	1	-	1	LBP 18797
	Piabina argentea Reinhardt, 1867	-	3	11	9	23	LBP 18817
	Planaltina britskii Menezes, Weitzman & Burns,2003	-	-	2	-	2	LBP 21919
Curimatidae	*Steindachnerina insculpta* (Fernández-Yépez, 1948)	-	-	3	2	5	LBP 18827
Erythrinidae	*Hoplias malabaricus* (Bloch, 1794)	-	-	6	-	6	LBP 18807
Paradontidae	*Apareiodon* **cf.** *piracicabae* (Eigenmann, 1907)	-	3	25	10	38	LBP 21917
Poeciliidae	*Poecilia reticulata* Peters, 1859*	-	-	6	-	6	LBP 21922
Gymnotidae	*Gymnotus sylvius* Albert & Fernandes-Matioli, 1999	1	-	1	-	2	LBP 18805
Cichlidae	*Coptodon rendalli* (Boulenger, 1897)*	-	-	1	-	1	LBP 18829
	Geophagus brasiliensis (Quoy & Gaimard, 1824)	3	1	14	1	19	LBP 18804
	Laetacara araguaiae Ottoni & Costa, 2009	-	-	2	-	2	LBP 21920
	Oreochromis niloticus (Linnaeus, 1758)*	-	-	1	-	1	LBP 18815
Heptapteridae	*Imparfinis mirini* Haseman, 1911	1	-	-	-	1	LBP 21924
	Rhamdia quelen (Quoy & Gaimard, 1824)	1	-	-	-	1	LBP 18822
Loricariidae	*Hypostomus ancistroides* (Ihering, 1911)	4	1	-	2	7	LBP 21925
	Hypostomus fluviatilis (Schubart, 1964)	7	-	1	-	8	NUP 15003
	Hypostomus nigromaculatus (Schubart, 1964)	15	1	3	-	19	LBP 21926
Trichomycteridae	*Pseudostegophilus paulensis* Miranda Ribeiro, 1918	-	-	1	-	1	LBP 21921
		84	77	315	132	608	

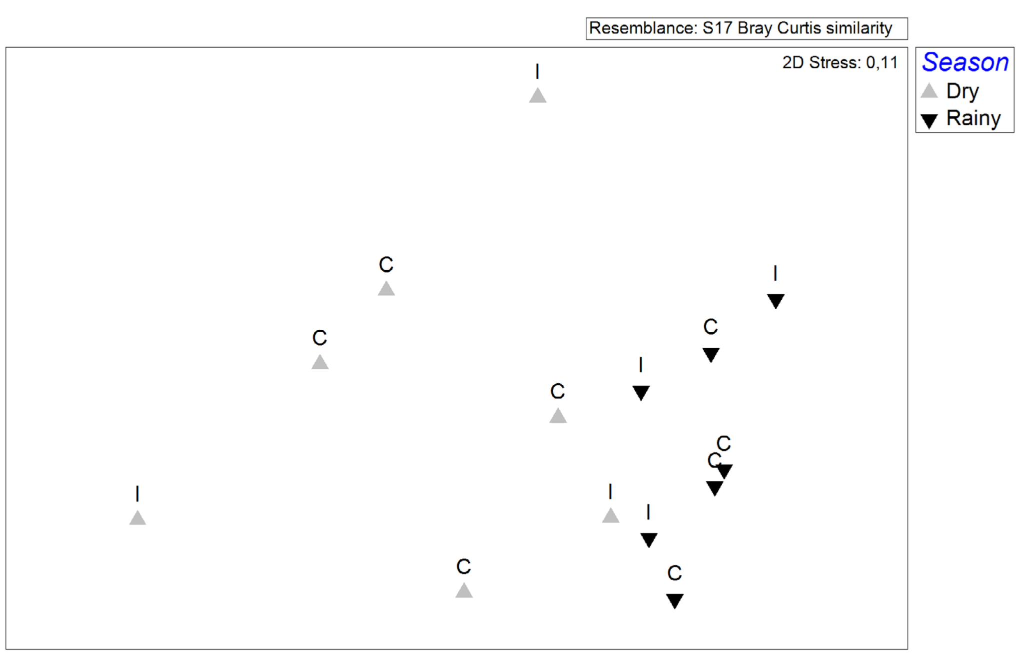

Fig. 2. Non-metric multidimensional plots of the abundance of fish assemblage sampled in isolated (I) and connected (C) pools during the rainy and dry season in the Sapucaí-Mirim River knickzone, Southeast Brazil.

analyzed and not for data dispersion or heterogeneity of samples. The dissimilarity between seasons was of 81.6%, according to SIMPER analysis, which also evidences the difference between dry and rainy seasons. The species that most contribute to this dissimilarity were *Knodus moenkhausii* (50% of contribution) and *Astyanax bockmanni* (21%), the former being the most abundant species sampled in the rainy season and the later the most abundant sampled in the dry season (Tab. II). The SIMPER analysis also showed a higher average similarity percentage between pools during the rainy (44.7%) than during the dry season (18.8%), what agree with the NMDS results of more aggregation of rainy season samples (Fig. 2).

DISCUSSION

The orders Characiformes and Siluriformes were the most representative in the studied knickzone. This is the common pattern for the Upper Paraná basin (Lowe-McConnell, 1975; Agostinho & Júlio Jr., 1999; Langeani *et al*., 2007), which is also recurrent in the Sapucai-Grande basin (Castro *et al*., 2004; Oliveira *et al*., 2016).

The ichthyofauna structure of the studied knickzone differs from that reported in other stretches of Sapucaí-Mirim River (Castro *et al*., 2004; Oliveira *et al*., 2016). In this knickzone, it was sampled 23% of the total fish species richness known for this river and five new species records were reported (*Bryconamericus turiuba* Langeani, Lucena, Pedrini & Tarelho-Pereira, 2005, *Knodus moenkhausii, Planaltina britskii* Menezes, Weitzman & Burns, 2003*, Hypostomus fluviatilis* (Schubart, 1964) and *Pseudostegophilus paulensis* Miranda Ribeiro, 1918). As the sample methodologies used in this study were the same of the other studies, probably those new records are related to the particular physical and limnological characteristics of this habitat (Brambilla *et al*., 2018), which may support specific ecological requirements such as food resources, shelters and reproduction sites. Additionally, the presence of juveniles of some species reinforces the importance of this macrohabitat, indicating that they can be used for complete life cycle of these species. The knickzone contains plentiful shelters, reducing pressure from predators (Schlosser, 1987) and providing suitable conditions for rearing grounds (Bain *et al.*, 1989; Gore *et al*., 1989; Flebbe & Dolloff, 1995).

The initial hypothesis of this study was corroborated only in part, since only the seasonality, was proven to have influence on the structure of the fish assemblage in the studied knickzone. The effect of seasonal hydrologic pulses was evident in all analyses, with a separation between dry and rainy periods, the second with higher values of abundance. A similar temporal pattern was also observed in Neotropical floodplains (Ortega *et al.*, 2015, Siqueira-Souza *et al.*, 2016), Tropical marginal lakes (Ferrareze & Nogueira, 2011) and Amazonian rapids (Fitzgerald *et al*., 2017). In the studied knickzone the factor seasonality (dry and rainy seasons) clearly influenced the ichthyofauna structure, both composition and abundance.

The dry period starts with the decrease of rains and, consequently, with water retraction (low hydrometric level). In this hydrological phase, areas located in higher elevations or more distant from the river channel become disconnected and aquatic organisms can remain confined within these habitats for a variable period of time (Humphries & Baldwin, 2003; Lake, 2003). During this isolation, stressful abiotic conditions intensify progressively until the following flood (Tockner *et al*., 2000). At the same time, biotic interactions, such as competition and predation, are expected to become more intense, mainly among individuals restricted to habitats of small proportions like lagoons and pools. Therefore, non-random patterns of species co-occurrence (aggregation/segregation) are expected between these natural disturbance events, due to harsh abiotic/biotic conditions that lead some species to local extinctions (Arrington *et al*., 2005).

When the rainy period starts, it is expected that communities shift from structured patterns in low-water periods to random patterns in high-water periods. Fish assemblages can display a progressive increase in organization following hydrometric variations (Arrington *et al*., 2005; Fernandes *et al*., 2009). The increase in water level expands the area available for dispersal and provides the connection between isolated sites and the main channels of rivers, consequently resetting the organizational process of assemblages (Ortega *et al*., 2015). In this situation, a reduction of competition and predation occurs, which can play a major role in maintaining high fish diversity over a larger scale (Fitzgerald *et al*., 2017). Additionally, increased input of terrestrial resources during the rainy season together with decreased species density should enhance fitness via greater supply of energy for growth, reproduction and migration (Fitzgerald *et al*., 2017).

This alteration between low and high water levels occurs frequently in knickzones. Floods in such rocky shallow platform in the middle of the river occur even seasonally or in stochastically, in short-term periods. This hydrological dynamic results in a high limnological variability and complex interactions among the different habitats (pools, runs and rapids), in terms of depth, area, volume, different rocky substrates, presence of marginal vegetation and connectivity with the river flow (Brambilla *et al*., 2018). Certainly, all this temporal and spatial interactions in a relatively small area corresponding to the knickzones, contribute to explain the particular ichthyofauna structure and high species richness observed in our study.

Although the results did not point for the influence of connectivity on the ichthyofauna structure, Brambilla *et al*. (2018) found influence of this factor on limnological parameters. The connection of each pool with the river flow promotes a water renovation, which decrease harsh abiotic situations, increasing the dissolved oxygen concentration and reducing extreme values of pH and temperature. However, this connection may not be strong enough like flood events to reset the organizational process of assemblages and, consequently, alter the structure of the ichthyofauna in knickzones, evidence also found in lakes of Pantanal wetland

(Penha *et al*., 2017) and in upper Parana River floodplain (Vasconcelos *et al*., 2014).

This study shows the importance of knickzone as a different environment for the river ichthyofauna. We observed a high fish richness and abundance considering the proportionally small area of the knickzone and even the presence of species exclusive to this macrohabitat if compared to the Sapucaí-Mirim River fish assemblage. There were also evidences that this rocky habitat is a nursery and growth area for some species. Additionally, these characteristics indicate the knickzones have a high importance to fish conservation, mainly in a context of threats to river biodiversity by the construction of hydroelectric power plants. It is difficult to avoid the construction of dams, but if this kind of macrohabitat could be preserved when a dam construction occurs, an extinction or decrease of some fish species can be avoided. Besides that, it would be important to preserve the natural flood and dry cycles of river (the most influential factor in fish structure of knickzones). Sabo *et al*. (2017) showed that maintaining flow regimes would improve fisheries, but can also benefit other fish species besides those commercially exploited. Thus, knickzones should be considered as strategic environments in the regional planning for biodiversity conservation, especially due to their eminent threat by intensive hydropower reservoir construction.

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