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Original article

Seasonal and longitudinal variation in fish assemblage structure along an unregulated stretch of the Middle Uruguay River

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Diversity patterns and their causes remain important questions, especially for ecosystems that preserve natural conditions. This is the case of fish diversity in large Neotropical rivers. In this context, we investigated fish diversity patterns along an extensive unregulated river section (*ca*. 450 km) in the Middle Uruguay River Basin. Sampling was conducted seasonally between May 2017 and March 2018, at six sites (patches) with contrasting environmental conditions. We collected 3,008 individuals belonging to 90 species. Nine were migratory, which summed relevant biomass in local assemblages (20 to 60%). We observed spatial variation in assemblage structure, but weak seasonal effects. Overall, biomass was similar among sites, but richness tended to increase downstream. Migratory fishes showed opposed trends, with higher richness and biomass upstream, particularly catfishes (Siluriformes). Ordination analyses separated sites in three groups based on variations in composition and abundance, and revealed associations between these groups and specific hydro-geomorphic conditions (*i.e.*, flow, depth, channel width and the presence of riparian vegetation). Our study revealed that fish diversity distributes heterogeneously along the main channel, where hydro-geomorphic patches select for distinct assemblages along riverine gradients.

Keywords: Diversity, Floodplain, Migratory fish, Riparian vegetation, River channel.

Os padrões de diversidade e suas causas continuam sendo questões importantes, especialmente em ecossistemas que preservam condições naturais. Este é o caso da diversidade de peixes em grandes rios neotropicais. Neste contexto, investigamos padrões de diversidade de peixes ao longo de um extenso gradiente fluvial (*ca*. 450 km) no médio rio Uruguai. As amostragens ocorreram sazonalmente entre maio/2017 e março/2018 em seis locais com condições ambientais distintas. Coletamos 3.008 indivíduos pertencentes a 90 espécies. Nove eram migradoras, as quais somaram relevante biomassa nas assembleias locais (20 a 60%). Houve variação espacial na estrutura das assembleias, mas fraco efeito sazonal. No geral, a biomassa foi semelhante entre os locais, mas a riqueza tendeu a aumentar em direção a jusante. Peixes migradores apresentaram padrão inverso, com maior riqueza e biomassa a montante, especialmente bagres (Siluriformes). Análises de ordenação separaram os locais em três grupos de acordo com a variação na composição e na abundância, e revelaram correlação entre esses grupos e condições hidro-geomorfológicas específicas (*i.e.*, velocidade, profundidade, largura do canal e vegetação riparia). Nosso estudo revelou que a diversidade de peixes se distribui de maneira heterogênea ao longo do canal, onde características hidro-geomorfológicas selecionam assembleias distintas ao longo de gradientes fluviais.

Palavras-chave: Canal do rio, Diversidade, Peixes migradores, Planície aluvial, Vegetação Ripária.

Introduction

Understanding the main processes that affect the structure of fish communities remains an important challenge (Jackson *et al*., 2001; Costa, Freitas, 2015). In large river systems, fish diversity distributes heterogeneously across different spatiotemporal gradients, including longitudinal, lateral, altitudinal and seasonal dimensions (Humphries *et al*., 2014). The Patch Dynamics Concept applied to river ecosystems (Pringle *et al*., 1988; Winemiller *et al*., 2010), in particular, explains lotic environments as hierarchical and dynamic mosaics of interconnected patches (*i.e.*, habitats), where organisms disperse and colonize according to their niche attributes. At intermediate spatial scales (*i.e.*,

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hundreds of kilometers), the main channel of large rivers is heterogeneous and dynamic, formed by arrays of large hydro-geomorphic patches such as constricted, braided and floodplain channel areas, with relevant spatiotemporal variation in flow patterns, depth, sediment, connectivity and primary production (McCluney *et al*., 2014). Hydrological and geomorphological processes are key factors, because they create a mosaic-type riverscape with some longitudinal orientation (Ward, Tockner, 2001; Scarabotti *et al*., 2017). According to this view, fish diversity respond to this arrangement of fluvial patches (Hoeinghaus *et al*., 2004; Foubert *et al*., 2018), which provide habitats for different life-strategies (Altermatt, 2013) and work as dispersal routes for migratory fishes (Makrakis *et al*., 2012).

However, few aquatic ecosystems remain free from human disturbances. Anthropic activities modified the functioning of most large rivers, with detrimental effects on aquatic biodiversity (Naiman, Dudgeon, 2011; Ballesteros *et al*., 2017). The main disturbances include hydrological alterations, habitat loss, pollution, invasive species and overexploitation (Agostinho *et al*., 2005). These disturbances have affected fish diversity (Pelicice *et al*., 2017), especially when they induce changes in the structure and distribution of habitat patches along the river, causing species losses, population declines and strong shifts in composition and functional traits (Agostinho *et al*., 2016; Arantes *et al*., 2017). Migratory fishes, in particular, have been significantly affected by river regulation and other impacts, and populations are currently suppressed or extirpated from some stretches and basins (Hoeinghaus *et al*., 2009; Loures, Pompeu, 2018; Pelicice *et al*., 2018). In the Neotropical region, few large rivers preserve their fluvial pristine conditions. This is especially true for the La Plata Basin, the second main basin in South America, where human development is expressive (*e.g*., industry, urbanization, agriculture, hydropower) (Luz-Agostinho *et al*., 2008; Petesse, Petrere, 2012; Smith *et al*., 2018).

Notable exceptions are the Paraguay-Paraná axis (Quirós *et al*., 2007; Rabuffetti *et al*., 2016) and the Uruguay River Basin (Zaniboni-Filho, Schulz, 2003), which still preserve long unregulated sections. Both systems offers the possibility to understand how fish diversity distributes along large rivers in the La Plata Basin. The Uruguay, in particular, extends over 1,800 km from south Brazil to the La Plata River (Uruguay), near the Atlantic Ocean. This basin has three geomorphological domains (*i.e.*, Upper, Middle and Lower (Zaniboni-Filho, Schulz, 2003)), marked by the presence of natural physical barriers (*e.g.*, waterfalls) and different hydro-geomorphic patches (*e.g.*, constricted channels with rapids or deep pools) along its main course, a conformation that probably contributed to generate a high fish diversity [275 fish species; (Bertaco *et al.,* 2016)]. The Uruguay river is currently subjected to several disturbances (*e.g.*, dams, pollution, deforestation), but the middle reach still preserves significant lotic segments with riparian vegetation: a long fluvial stretch (*ca*. 900 km) is found between Foz do Chapecó and Salto Grande dams. The presence of this free-flowing section, which is formed by a mosaic of hydro-geomorphic patches, offers the opportunity to understand fish diversity patterns in lotic corridors of the La Plata Basin.

In this scenario, we investigated fish diversity (species richness, abundance and composition) along an extensive fluvial gradient (*ca.* 450 km) in the Middle Uruguay River. In particular, we analyzed the response of fish species to habitat variation along the river corridor, a section characterized by different hydro-geomorphological conditions and landscape structure, *i.e.*, the presence of constricted channels in the form of shallow rapids or deep pools, and floodplain areas. Variation in flow, depth, channel width and the presence of riparian vegetation, for example, must select for specific local assemblages. In this sense, based on the Patch Dynamics Concept applied to river ecosystems (Pringle *et al*., 1988; Winemiller *et al*., 2010), we predict spatial discontinuity in fish diversity patterns (*i.e.*, distinct local assemblages along the river corridor), where assemblage structure is associated with hydro-geomorphic patches (*e.g.*, constricted channels or floodplain areas). In this sense, we expect that macro-habitat conditions, particularly spatial (*e.g.*, location) and geomorphological factors (*e.g.*, depth, width), explain fish assemblage structure. In particular, we expect higher fish biomass and richness in floodplain patches, where conditions are more variable and habitat diversity is high (Junk *et al*., 1989). Moreover, we expect significant seasonal variation in fish diversity, considering that hydrological dynamics affect the structure of habitat patches (Humphries *et al*., 2014), inducing changes in local assemblages. Finally, considering that this river section is unregulated, we predict that migratory fishes are regular components of local assemblages, summing relevant fraction of fish biomass – contrasting with patterns observed in highly regulated basins, where migratory fishes are rare or absent (Loures, Pompeu, 2018; Pelicice *et al*., 2018).

Material and Methods

Study area. The Uruguay River is divided into three regions (Upper, Middle and Lower Uruguay), which are separated by physical barriers. Salto do Yucumã Fall, located inside the Turvo State Park (Brazil), is the division between the Upper and Middle Uruguay. The Salto Grande Dam, located in the border between Argentina and Uruguay, divides the Middle from the Lower Uruguay. Currently, large and small dams regulate the Upper Uruguay section.

The Middle Uruguay River is characterized by a long fluvial segment (approximately 900 km), with riparian forests in both margins (Brazil-Argentina border). This segment has two important protected areas, the Yaboti Biosphere Reserve (Argentina) and the Turvo State Park (Brazil); human activities, however, have induced some disturbances, including the loss of riparian vegetation, urbanization and overfishing. The middle Uruguay is characterized by a width ranging from 280 m in the most upstream stretch, to 2,000 m in the region near Salto Grande HPP. It has an average slope of 9 cm/km, which is more marked in the upper region, where the Atlantic Forest Biome predominates (Zaniboni-Filho, Schulz, 2003). The lower reach, downstream from the municipality of São Borja, contains a floodplain area and belongs to the Pampa Biome.

Sampling design. Samples were collected at six sites, to cover a spatial extent of 450 km (Fig. 1) and to encompass a long river gradient with different hydro-geomorphic patches: constricted channel with shallow rapids, constricted channel with deep pools, and a floodplain. The characterization of the sampling sites is shown in Tab. 1 and Tab. **S1** - Available only as supplementary file accessed with the online version of the article at http://www.scielo.br/ni.

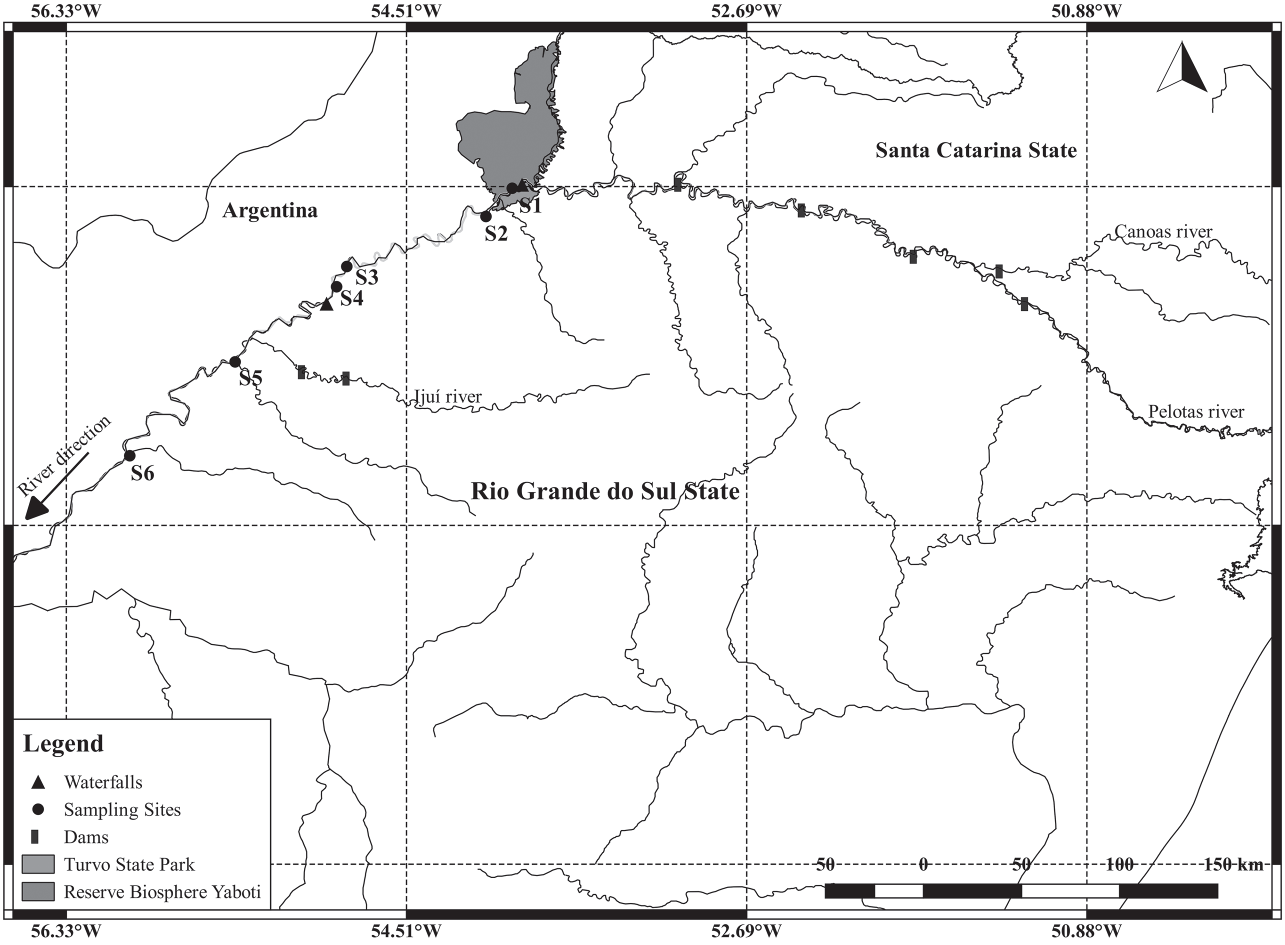

Fig. 1. Location of sampling sites along the Middle Uruguay River, RS, Brazil. Derrubadas (S1), Esperança do Sul (S2), Alecrim (S3), Porto Vera Cruz (S4), São Nicolau (S5) and São Borja (S6).

Tab. 1. Information about sampling sites along the Middle Uruguay River, Brazil. *Distance from the beginning of the Middle Uruguay River Basin. **Percentage of riparian forests covering a 10 km^2 long river section.

Sampling site (*)	Habitat description	Coordinates		Width (m)	Depth (m)	Altitude (m)	Riparian Vegetation (%)**	Municipality (RS, Brazil)
S1 (16 km)	Rapids and pools	27º10’64”S	53º54’31”W	280	3/12	135	98	Derrubadas
S2 (41 km)	Pools	27º18’.70”S	54º06’33”W	405	18	123	8	Esperança do Sul
S3 (175 km)	Pools	27º34’.26”S	54º49’55”W	840	14	96	15	Alecrim
S4 (217 km)	Rapids	27º42’.01”S	54º53’47”W	790	3	91	18	Porto Vera Cruz
S5 (332 km)	Rapids	28º04’.44”S	55º25’38”W	1230	4	69	19	São Nicolau
S6 (450 km)	Floodplain and pools	28º34’.15”S	56º0.9’51”W	1250	2/19	52	6	São Borja

Data collection. A total of 24 field trips were carried out seasonally between May 2017 and March 2018. Different fishing gears were employed to maximize fish capture, covering littoral, benthic and pelagic habitats. Fish were collected using a set of gillnets with different mesh sizes (20, 30, 40, 50, 80 mm between adjacent knots), 10 m long and 2.0 m high. Using a total of 20m^2 of net of each mesh. We also used two longlines, 100 m long, 30 hooks each (hooks 5/0 and 12/0), baited with small fish, corn and snail. All set of fishing gears remained deployed for 12 hours, mainly overnight. Gillnets were used to capture fish close to riverbanks, while the longline targeted pelagic and carnivorous fish. Additionally, we hauled a seine (0.8 cm mesh-size, 10m long and 2m high) over littoral areas, totaling three samples at each site per trip. To calculate Capture per Unit Effort (CPUE), we considered only fish captured by gill nets. Species captured with longlines and seines were used to evaluate assemblage composition and richness.

Specimens were fixed in 10% formalin and preserved in 70% ethanol. Species were identified according to Zaniboni-Filho *et al.* (2004), and voucher specimens will be deposited in the Fish Collection at the State University of Maringá, Paraná, Brazil. This study is part of project 534 entitled “Fish Ecology of the Middle Uruguay”, carried out under permits 55011-2 (ICMBio) and 104/2017 (Secretaria do Meio Ambiente e Infraestrutura do Estado do Rio Grande do Sul). This last permit allowed fish sampling in protected areas (Turvo State Park).

Habitat descriptors. We characterized habitat condition at each site by measuring limnological, land cover, spatial and geomorphological variables. The following limnological variables were recorded during each sampling occasion: pH, electrical conductivity (uS.cm^{-1}), dissolved oxygen (mg.l^{-1}), water temperature (°C), current velocity (m.s^{-1}), transparency (cm) and water level (m). These measurements were made at the surface using a multiparameter device and a flowmeter. Water transparency was measured with a Secchi disk, and water level with a level rule fixed at the shore. All limnological variables were measured simultaneously with fish sampling. For each site, we recorded the following geomorphological descriptors: river width, mean depth and altitude. Average depth was obtained from three measurements made at each sampling site. Width, distance and altitude were measured from georeferenced satellite images in Google Earth Pro (Google, Menlo Park, California). We also calculated the distance of each site to the beginning of the sub-basin (Middle Uruguay), as a proxy of spatial position along the river channel. Finally, we calculated the percentage of riparian vegetation covering each site. For this, an area of 10 km^2 (10 km long and 0.5 km of each river side) was considered at each margin of the sampling site. This calculation was performed using the program Fragstats package v.4.0.

Migratory species classification. Fish species were classified as migratory or non-migratory following specific literature (*e.g.*, Carosfeld *et al*., 2003; Agostinho *et al*., 2007; Reynalte-Tataje, Zaniboni-Filho, 2008; Makrakis *et al*., 2012). Migratory fishes have complex life cycles and migrate over long distances (> 100km) between feeding and spawning sites. Non-migratory fishes, on the other hand, include a variety of behaviors, *e.g.*, sedentary, short-distance displacements, rheophilic, limnophilic; reproductive dynamics differ from patterns observed for migratory species, since they demand smaller geographic ranges to complete their life cycles. All analyses focused on the entire community and migratory fishes.

Data analyses. Fish assemblage structure was described as abundance, species richness and composition. Abundance (individuals) and biomass (kilograms) were expressed as catch per unit effort (CPUEn = ind./100 m^2 of net; CPUEb = Kg/100 m^2 of net). Species richness is the number of species in each sample, and composition refers to the taxonomic identity of species.

We run nonparametric analysis of variance (Kruskall-Wallis) to evaluate differences in CPUEb and species richness among sites and seasons, followed by Dunn’s *a posteriori* test. We chose a non-parametric test because variance was not homogeneous. We conducted a Detrended Correspondence Analysis (DCA) to ordinate samples based on species abundance and composition. This analysis was conducted to depict variation in fish fauna structure among sites and seasons. A Multiple Response Permutation Procedure (MRPP) was carried out to verify the consistency, significance and homogeneity among groups (sites and seasons).

To investigate the importance of limnological, temporal and geo-spatial variables explaining fish assemblage structure, we conducted a variation partitioning approach. This procedure calculates pure and shared components of variation resulting from different sets of explanatory variables (Anderson, Gribble, 1998). We considered three sets of variables: 1) Limnological: pH, temperature, dissolved oxygen, electrical conductivity, water transparency, level and velocity; 2) Temporal (seasons): autumn, winter, spring and summer, included as four binary variables; 3) Geo-spatial: depth, altitude, width, riparian forest cover and distance from the beginning of the sub-basin. This analysis employs a two-step approach: (i) Canonical Correspondence Analyses (CCA) to select main variables from the different sets of explanatory variables (limnological, temporal and geo-spatial), and (ii) a partial CCA (pCCA) to investigate the correlation between assemblage structure and main variables selected (Borcard *et al*., 1992; Peres-Neto *et al*., 2006). This approach is valuable to reduce the number of possible predictors, simplifying the investigation and restricting analyses to main factors behind environmental variation. The selection of limnological variables, for example, is evidence that some local conditions (microhabitat) affect habitat selection by fishes. The selection of geo-spatial predictors, on the other hand, points to the existence of hydro-geomorphic patches that determine the distribution of fish diversity.

First, we run separate CCAs on each set of explanatory variables (limnological, temporal and geo-spatial). A Monte Carlo procedure (999 permutation) was applied to test the significance of each variable in the species-environment relationships. The forward selection procedure was used to reduce multicollinearity in the limonological and geo-spatial datasets. Second, combining all significant variables from each CCA, we run a pCCA to partition the variation explained by each variable on fish abundance. The variation explained was reported as percentage of total variation explained (TVE), calculated as the ratio between the sum of all canonical eigenvalues and total inertia. Statistical significance implied $p < 0.05$. All analyzes were carried out in PCORD version 5, Statistic version 7.1 and CANOCO version 5.

Results

Fish assemblage structure. We recorded 3,008 individuals belonging to 90 species, 27 families and 10 orders (Tab. **S2** - Available only as supplementary file accessed with the online version of the article at http://www.scielo.br/ni). Characiformes and Siluriformes were the most representative orders, with 42 (46.6%) and 32 (35.6%) species respectively. Most species belonged to the families Characidae (22), Loricariidae (13) and Pimelodidae (8). The most abundant species were *Iheringichthys labrosus* (11% of total abundance) and *Leporinus amae* (10%). Nine species were assigned as migratory (10% of total richness). We observed spatial and temporal variation in fish richness and biomass. Species richness tended to increase downstream, with higher values at site S6 (Fig. 2A); richness did not vary significantly among seasons (Fig. 2B). Fish biomass (CPUE) were similar among sites (Fig. 2C), but changed significantly among seasons, with higher values during the spring (Fig. 2D).

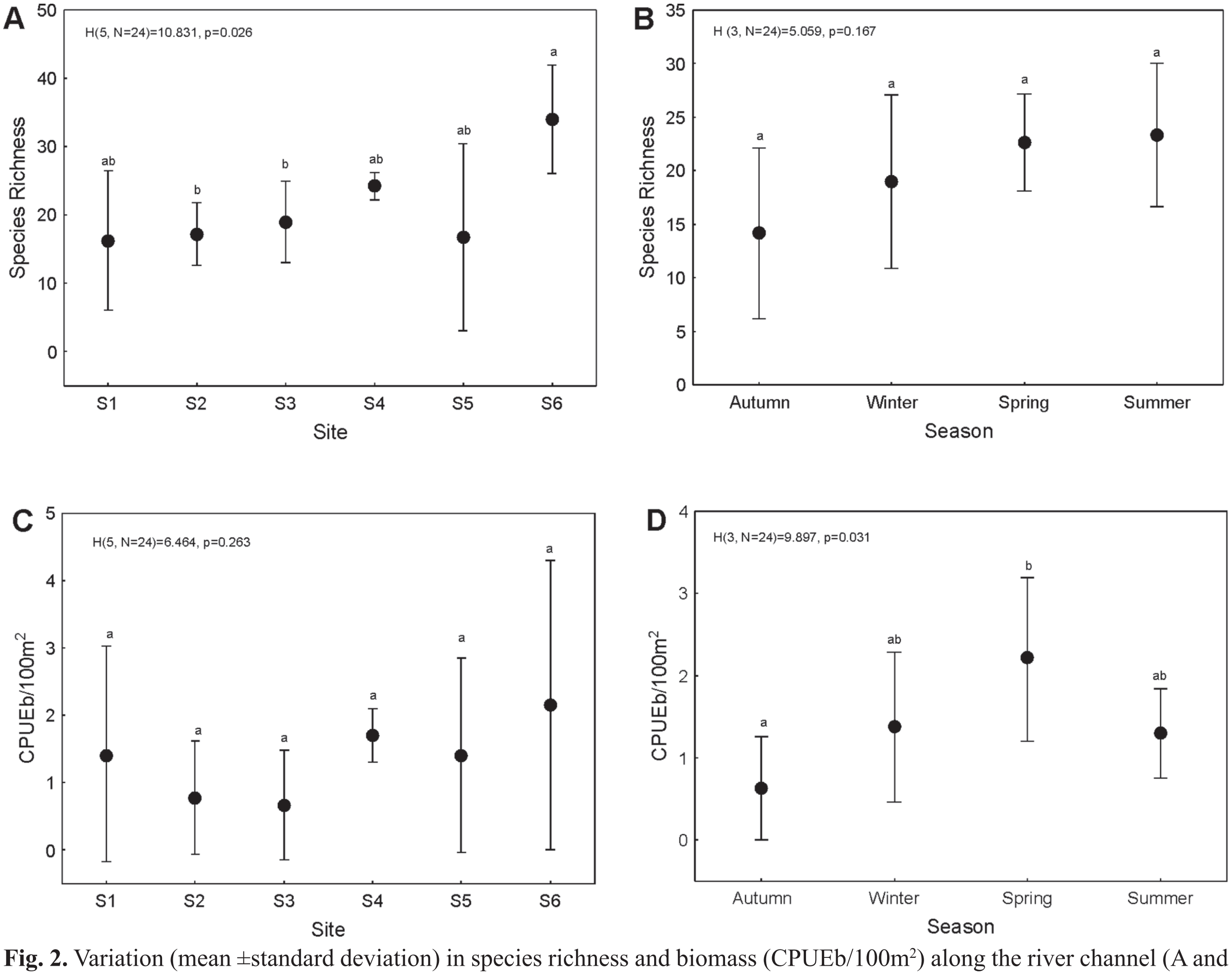

Fig. 2. Variation (mean ±standard deviation) in species richness and biomass (CPUEb/100m^2) along the river channel (A and C) and among seasons (B and D), in the Middle Uruguay River. Sites: S1 = upstream; S6 = downstream. Different letters indicate statistical difference ($p < 0.05$).

Considering migratory fishes, the number of species differed among sites, with higher values at site S1 (Fig. 3A); no temporal effect was observed (Fig. 3B). Fish biomass (CPUE) showed higher values at site S1 (Fig. 3C) and during the spring (Fig. 3D). The proportion (relative biomass) of migratory fishes at each site was variable, but they summed at least 20% of all biomass (Fig. 4A); higher fractions (> 50%) were observed at sites S1 and S5. Siluriformes were more abundant at sites upstream, while Characiformes tended to be widely distributed in the study area (Fig. 4B).

The DCA summarized spatial variation in fish composition and abundance (Fig. 5). The proportion of variance explained was 0.42 for Axis 1 and 0.22 for Axis 2. The ordination revealed three main groups: sites S2+S3, sites S1+S4+S5, and site S6. Axis 1 was affected primarily by *Prochilodus lineatus* (r = -0.49), *Salminus brasiliensis* (r = -0.54), *Steindachnerina brevipinna* (r = -0.52), *Astyanax lacustris* (r = -0.59), *Astyanax fasciatus* (r = -0.44), *Loricariichthys anus* (r = 0.42) and *Iheringichthys labrosus* (r = 0.40). Axis 2 was affected mainly by *Pachyurus bonariensis* (r = -0.46), *Iheringichthys labrosus* (r = -0.43), *Rhinodoras dorbignyi* (r = 0.69), *Pimelodus maculatus* (r = 0.48) and *Ageneiosus militaris* (r = 0.50). MRPP analysis confirmed the spatial pattern, revealing the same three groups: sites S1+S4+S5, sites S2+S3 and S6 (Tab. 2). The DCA showed no clear pattern concerning seasons (Fig. 5), and the MRPP confirmed no difference among seasons (T = -1.43; A = 0.04; p < 0.20).

Association with environmental variables. The forward selection method in each CCA selected three limnological variables (pH, temperature and velocity) and most geo-spatial variables (depth, width, riparian forest and distance). The pCCA run with these variables explained 30.2% (TVE) of the total variation in species abundance (Total inertia = 2.805). Geo-spatial variables explained 29.5% of total variation, limnological explained 18.7%, and temporal explained 16.7 % (Tab. 3). Geo-spatial variables explained the largest fraction of TVE, considering either non-overlapping components or components shared with other variable sets (co-variables).

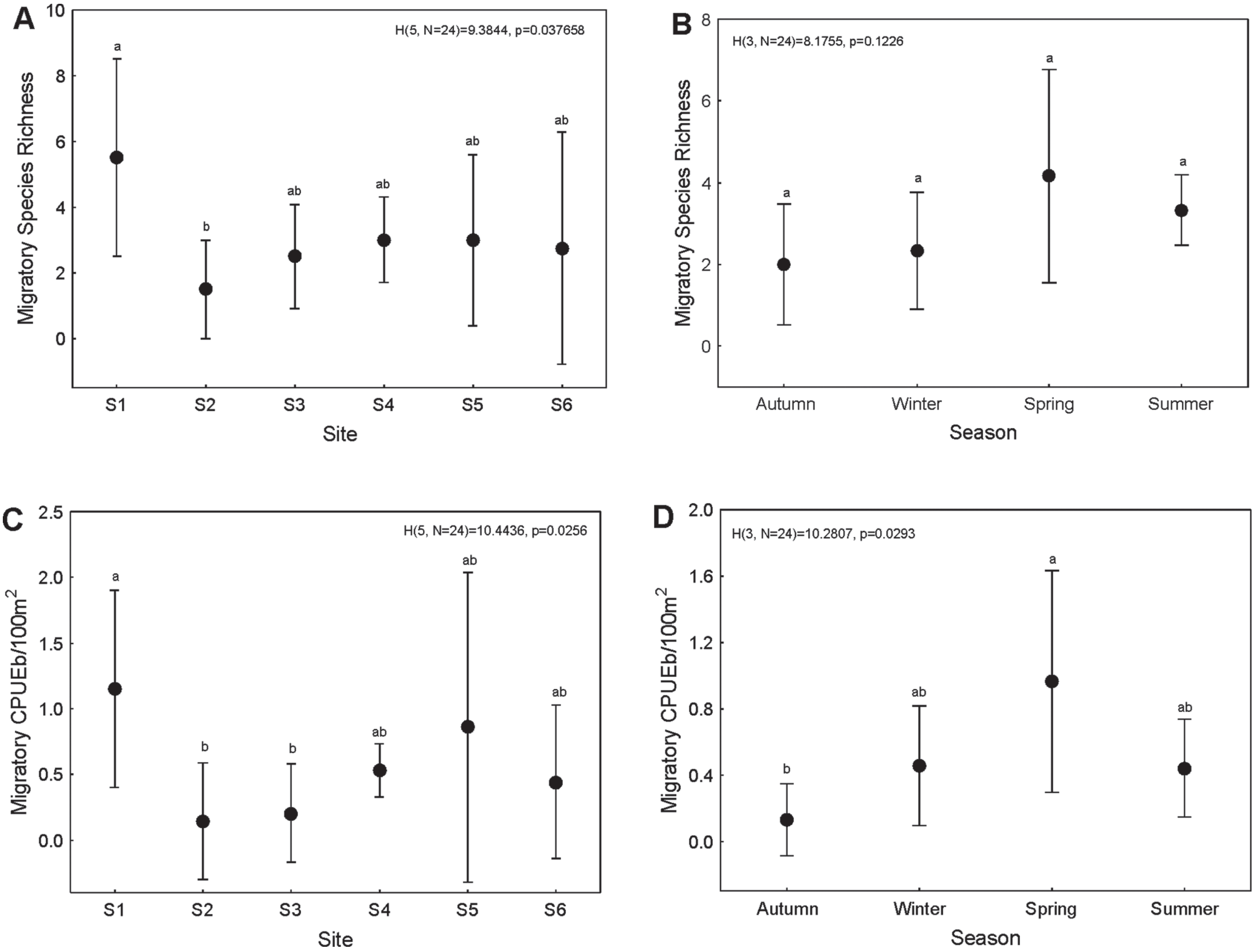

Fig. 3. Variation (mean ±standard deviation) in species richness and biomass (CPUEb/100m^2) of migratory fishes along the river channel (A and C) and among seasons (B and D), in the Middle Uruguay River. Sites: S1 = upstream; S6 = downstream. Different letters indicate statistical difference (p < 0.05).

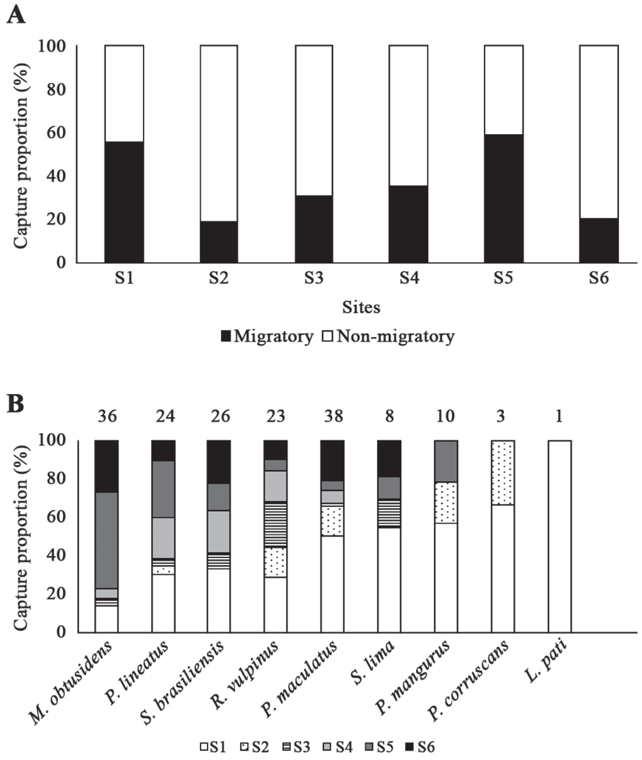

Fig. 4. Relative abundance (% biomass, CPUEb) of migratory fishes at each site (A), and spatial distribution of biomass considering each migratory species (B). The number of individuals captured is indicated above each bar. Characiformes: *Megaleporinus obtusidens, Prochilodus lineatus, Salminus brasiliensis* and *Rhaphiodon vulpinus*. Siluriformes: *Pimelodus maculatus, Sorubim lima, Pseudopimelodus mangurus, Pseudopplatystoma corruscans* and *Luciopimelodus pati*.

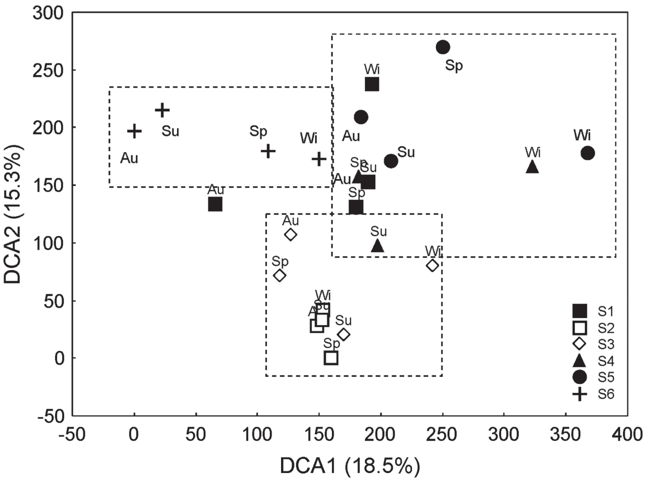

Fig. 5. Detrended Correspondence Analysis (DCA) applied to ordinate samples according to variations in fish composition and abundance along the Uruguay River. Rectangles depict groups confirmed by a Multiple Response Permutation Procedure (Tab. 2). Sites: S1 = upstream; S6 = downstream. Seasons: Au= Autumn; Sp= Spring; Su= Summer and Wi= Winter.

Tab. 2. Results of the MRPP analysis, which compared fish assemblage composition (CPUEn) between sites. Bold t-values indicate statistical differences ($p < 0.05$).

SITES	S1	S2	S3	S4	S5	S6
S1		**-1.45**	**-1.95**	-0.15	0.77	**-1.45**
S2			0.58	**-1.84**	**-1.54**	**-1.97**
S3				**-2.37**	**-1.51**	**-2.51**
S4					-0.89	**-1.42**
S5						0.47

Tab. 3. Results of the Partial Canonical Correspondence Analysis (pCCA) showing the total variation explained (TVE) for fish abundance data by each set of explanatory variables (L = Limnological, T= Temporal and GS= Geo-Spatial) and their corresponding non-overlapping components of variation. % TVE= percentage of total variation explained by each component.

Variables	Co-variables	%TVE
Set of variables		
L		18.7
T		16.7
GS		29.5
Non-overlapping components		
L	T*GS	9.4
T	L*GS	7.9
GS	T*L	19.1
L*T	GS	0.4
L*GS	T	3.2
T*GS	L	2.8
L*T*GS		0.3

The set of geo-spatial variables correlated significantly with species abundances (Monte Carlo test; $p < 0.05$). Limnological and temporal variables did not correlate. Considering only geo-spatial variables, the first two axis (Fig. 6) separated the same three groups observed in the DCA and MRPP. The distribution of sites along the first axis was influenced by river width ($r = -0.72$) and distance ($r = -0.98$), while the distribution along the second axis was affected mainly by depth ($r = 0.74$) and riparian vegetation ($r = -0.79$). Several species associated with positive and negative scores in each axis, but migratory species were placed in the lower right quadrant (Fig. 6); it indicates that migratory species are associated with sites S1, S4 and S5, correlating with moderate depth and width, riparian forest cover and the presence of rapids, *i.e.*, a constricted channel with the presence of rapids. The most distinct assemblages, however, occurred at site S6, where the river channel is wide, *i.e.*, a floodplain.

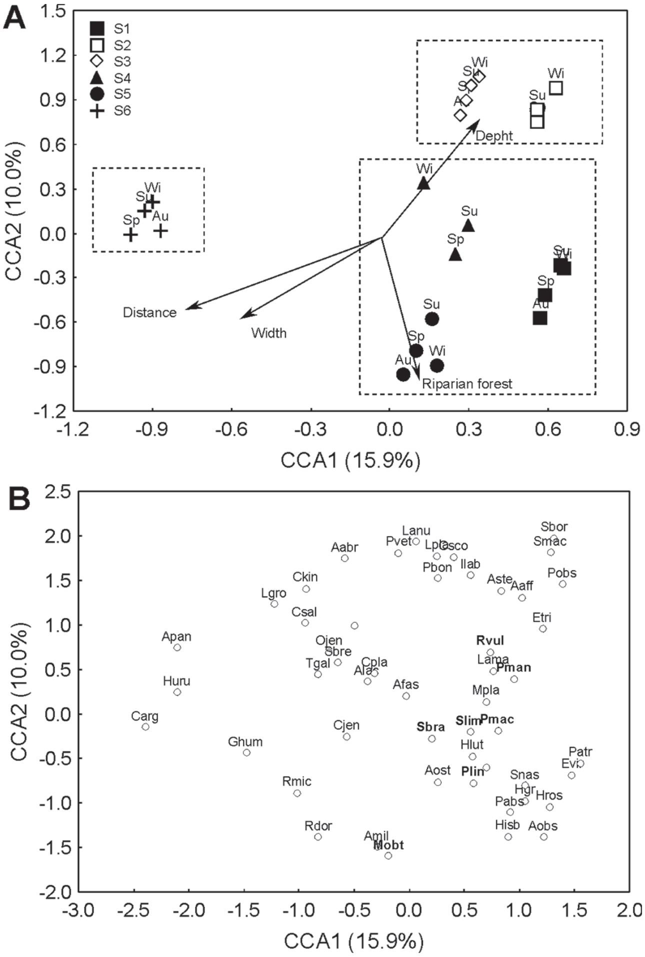

Fig. 6. Canonical Correspondence Analysis (CCA) applied to investigate the association between fish assemblage structure and environmental variables (spatial, geomorphology and landscape) along the Middle Uruguay River (A), and the influence of species on the ordination (B). Seasons: Au= Autumn; Sp = Spring; Su= Summer and Wi= Winter. Migratory species are marked in bold.

Discussion

The Middle Uruguay River has a long fluvial segment (*ca*. 900 km) free from dams. Our study, the first conducted in this region, covered a relevant river stretch (*ca*. 450 km) and included considerable variation in geomorphological conditions and landscape structure, *i.e*., the presence of constricted channels with shallow rapids or deep pools, and a floodplain. We assumed the Patch Dynamics Concept (Winemiller *et al*., 2010) as a theoretical background, and predicted spatial discontinuity in fish diversity patterns along the river corridor. Confirming this expectation, we observed significant spatial variation in assemblage structure (*i.e*., richness, abundance, biomass and composition). One important result is that macro-habitat features (*i.e*., geomorphology, spatial and landscape variables) explained most variation in species distribution, while limnological and seasonal factors exerted little influence. These results indicate that specific hydro-geomorphic conditions (patches) along riverine gradients select for distinct assemblages, supporting the prediction that spatial and hydro-geomorphological factors play a major role in determining the distribution of fish diversity. Another important finding was the prominence of migratory species in local assemblages, confirming the expectation that theses fishes are common and abundant in unregulated rivers. In general, our results indicate that the Patch Dynamics Concept, *i.e.*, lotic systems as mosaics of interconnected and variable patches, provides a valuable background to explain fish diversity patterns in fluvial corridors at intermediate spatial extents (*ca*. hundreds of kilometers).

Fish species distributed heterogeneously along the river, and correlated with hydro-geomorphic, spatial and landscape attributes, *i.e.*, channel width, depth, the presence of riparian forests and conditions related to flow and slope (presence of rapids, pools and floodplains). These factors determine macro-habitat conditions, which have strong effects on fish diversity (Torrente-Vilara *et al*., 2011; Carvajal-Quintero *et al*., 2015; Arantes *et al*., 2017; Foubert *et al*., 2018), and aquatic diversity in general (Ward, Tockner, 2001; Thorp *et al*., 2006). Ordination analyses (DCA, CCA) supported this view, because sites were combined in three groups with specific hydro-geomorphic conditions and fauna structure. Sites of the first group (S1, S4 and S5) were more canalized and shallow (*i.e*., rapids), surrounded by riparian vegetation, where migratory species predominated. In the second group (S2 and S3), riparian vegetation was rare, the channel was deeper and flow was slower (*i.e*., pools); the third group (S6) was a floodplain area. Therefore, these contrasting hydro-geomorphic conditions create habitat patches with specific environmental features, selecting for assemblages with different species composition. Dispersal between patches is probably another driver, because there is no strong physical barrier among sites, and fish species recorded have different dispersal modes and abilities. For example, rheophilic and migratory fishes move frequently along the river (Vitorino Júnior *et al*., 2016), while sedentary fishes may find some resistance (Hrbek *et al*., 2018). Results therefore support the view that large rivers are systems with multiple habitat patches linked by aquatic corridors (*i.e*., Patch Dynamics Concept), where fish species disperse and colonize according to their niches demands and dispersal abilities (Altermatt, 2013).

The importance of macro-habitat conditions was evident for the third group (S6), the only located in a floodplain area. This region has a distinct phytogeographic structure, because it belongs to the Pampa Biome, where riparian vegetation is naturally scarce and rice crops are common. At this site, we observed higher species richness (60 species in total). Floodplain areas tend to provide a diversity of microhabitats and food resources, allowing the coexistence of several species (Araújo, Tejerina-Garro, 2007; Súarez, 2008). In addition, due to the input of allochtonous material (*i.e*., flooding) and high aquatic productivity (*e.g*., macrophytes), floodplains provide adequate habitats for different life-strategies. For example, some small-sized species (*e.g.*, *Aphyocharax anisitsi* and *Roeboides affinis*) and juvenile of migratory fishes (*e.g.*, *Salminus brasiliensis* and *Megaleporinus obtusidens*; unpublished data) were captured only at this site. However, fish biomass was not as high as expected, although some samples showed high values. High fish biomass is typical in floodplains, but these ecosystems are also characterized by environmental variability, dictated by the hydrological regime (Junk *et al*., 1989). Moreover, migratory fishes, which are large-bodied, predominated in constricted channels, not in the floodplain area. Therefore, floodplain features likely determined the peculiar assemblage found in the downstream section of the study area.

We predicted seasonal variation in fish fauna structure, considering that hydrological dynamics have strong effects on environmental conditions in habitat patches (Humphries *et al*., 2014). In fact, studies have shown that fish diversity varies temporally in subtropical environments (Agostinho *et al*., 2007; Scarabotti *et al*., 2017). This prediction, however, was not confirmed. This trend is likely associated with the climatic condition of the studied year (*i.e.*, La Niña phenomenon), which experienced mild variations in water flow and temperature. Weak environmental variation may have affected seasonal processes that induce variation to community structure, such as migration, predation, resource availability and mortality (Winemiller, Jepsen, 1998; González-Bergonzoni *et al*., 2016; Fitzgerald *et al*., 2017). We also point out that the Uruguay river lacks a well-defined rainy season, since rains fall over the year (concentrated in spring and summer) and floods are swift and not intense (Zaniboni-Filho, Schulz, 2003). These features probably minimized seasonal variation in abiotic and biotic conditions. The exception was a weak but significant increase in fish biomass during the spring, a trend probably driven by the movement of migratory fishes, since their biomass also increased during this season. Migratory behavior is variable in the Uruguay river basin, but some species start their spawning migration during the spring (Zaniboni-Filho, Schulz, 2003), in response to spring rains, a climatic feature of the basin (Reynalte-Tataje *et al*., 2017).

Migratory species were important components of local assemblages, summing relevant biomass in lotic sites and confirming our prediction that these fishes are abundant in unregulated sections of the La Plata basin. It differs from impounded areas, where migratory fishes are numerically scant or absent (Agostinho *et al*., 2008; Petesse, Petrere, 2012; Reynalte-Tataje *et al*., 2012; Loures, Pompeu, 2018; Pelicice *et al*., 2018). The trend reported here, therefore, may resemble conditions found in more pristine environments, and serve as a baseline pattern for comparisons and impact assessment. However, migratory fishes distributed heterogeneously in the studied segment. Higher biomass and richness were observed in sites with lotic conditions, *i.e.*, constricted shallow channels, with the presence of rapids and riparian vegetation. In addition, fish orders showed different spatial distribution. While Siluriformes concentrated in upstream sites, particularly at S1, Characiformes were captured along the entire gradient, indicating that these fishes either disperse more easily along the river corridor or find suitable conditions at different patches. This differential distribution (Siluriformes *vs*. Characiformes) depicts a diversified behavior among migratory species – usually assigned as a single monotypic group. Other studies have shown a diversity of migratory patterns (Godinho, Kynard, 2008; Makrakis *et al*., 2012; Barthem *et al*., 2017; Lopes *et al*., 2018), and our data indicate that these fishes display specific preferences, choosing distinct patches along the fluvial corridor. We just highlight that fish migration (*i.e.*, stimuli and movement) might have been affected by limited rainfall and lower water levels during the study period, considering that the Yacumã Falls work as a natural barrier during dry periods (Zaniboni-Filho, Schulz, 2003); in fact, migratory fishes were more abundant at S1, 50 km downstream from this barrier.

The presence of migratory species in the region is important indication that the Middle Uruguay River is a hotspot of migratory diversity, with relevance for the whole La Plata Basin. This record is important because migratory fishes support commercial, recreational fisheries and ecossystem function (Hoienghaus *et al*., 2009; Días *et al*., 2019). Some populations seem to find suitable habitats for permanence and recruitment, especially because the area has critical habitats (long riverine segment, tributaries and floodplain). It includes protected areas, where relevant riparian forests remain, *i.e*., Turvo State Park and Yaboti Biosphere Reserve (Ribolli *et al*., 2018), and spawning grounds (Reynalte-Tataje *et al*., 2017). The absence of dams in this long river segment is the most relevant factor, but we note that large dams regulate the main channel of the Upper and Lower Uruguay. This condition may have negative effects on ecological dynamics in the Middle Uruguay, especially if these dams block migratory routes. In fact, three migratory species are listed as endangered in a regional red list (Rio Grande do Sul, 2014), namely *Brycon orbignyanus*, *Pseudoplatystoma corruscans* and *Salminus brasiliensis*. The present study recorded *S. brasiliensis* in all sites, but *P. corruscans* was rare (three individuals). *Salminus brasiliensis* is considered vulnerable in the Middle Uruguay, where fishing is banned since 2002; populations of *P. corruscans* are rarefied, reflecting its critical state in the basin. Habitat degradation, caused by the construction of dams, the loss of critical habitats, siltation and pollution, in addition to the increasing fishing pressure, may explain this situation.

Currently, the largest rivers in South America are regulated by cascades of dams (Pelicice *et al*., 2015; Agostinho *et al*., 2016). Dams modify hydro-geomorphic conditions along river channels, change the natural flow regime and decrease hydrological connectivity, causing significant disturbances to fish populations (Petrere Jr, 1996; Orsi, Britton, 2014; Lima *et al.,* 2016; Loures, Pompeu, 2018). The Middle Uruguay River is an important fluvial remnant in the La Plata Basin, but hydropower development is planned to occur in the region (*i.e.*, Garabi-Panambi Hydropower Complex). If it succeeds, we predict significant changes in fish diversity, with the proliferation of sedentary, generalists and/or opportunists species, and the decline ofmigratory species. In this sense, the maintenance of fluvial conditions, particularly the mosaic-type riverscape along the middle Uruguay River, including tributaries and protected areas, is crucial to preserve fish diversity in the region.

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