BOLETIM DO INSTITUTO DE PESCA

ISSN 1678-2305 online version

Scientific Article



# EFFECTS OF FLOOD PULSE ON THE COMMUNITY OF LORICARIIDAE (PISCES, SILURIFORMES) IN OXBOW LAKES OF THE PANTANAL, BRAZIL

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Received: July 20, 2017
Approved: October 21, 2017

## ABSTRACT

Seasonal variations can promote environmental changes, and consecutively, influence the structure of the fish assemblage. The aims of this study were: i) to investigate the effect of flood pulse and lateral connectivity on Loricariidae assemblages in oxbow lakes; and ii) to determine the environmental factors driving the local structure of these species in the northern portion of the Pantanal. For this purpose, the fish community was sampled in two oxbow lakes between September 2005 and August 2007. The assemblages were mainly affected by seasonal fluctuations and were spatially unstructured, demonstrating that the flood pulse has a predominant role in the structuring of Loricariidae. In addition, the homogeneity of the assemblages between the lakes pointed to a frequent movement of the fish among the different subsystems, suggesting a high level of interaction and mixing between the habitats along the floodplain. The flood pulse was also responsible for significant changes in depth, dissolved oxygen and turbidity along the seasons, factors driving the structure of the fish assemblages. It was evident that seasonal environmental changes and connectivity are significant in the structure of Loricariidae assemblages in the Pantanal, sustaining high diversity and abundance.

**Key words:** fish; lateral connectivity; flood pulse; Pantanal.

## EFEITOS DO PULSO DE INUNDAÇÃO SOBRE A COMUNIDADE DE LORICARIIDAE (PISCES, SILURIFORMES) EM LAGOAS DO PANTANAL, BRASIL

## RESUMO

Variações sazonais podem promover alterações ambientais, e consecutivamente, influenciar a estrutura da assembleia de peixes. Os objetivos desse estudo foram i) investigar o efeito do pulso de inundação e conectividade lateral sobre a assembleia de Loricariídeos em lagoas marginais; e ii) determinar os fatores ambientais que controlam estrutura local dessas espécies no Pantanal Matogrossense. Para isso foi amostrado a comunidade íctica de duas lagoas marginais, entre setembro de 2005 e agosto de 2007. As assembleias foram afetadas sobretudo por flutuações sazonais e pouco estruturada espacialmente, demonstrando que o pulso de inundação tem papel preponderante na estruturação de Loricariidae. Além disso, a homogeneidade das assembleias entre as lagoas apontou um frequente movimento dos peixes entre os diferentes subsistemas, o que sugere um alto nível de interação e mistura entre os habitats ao longo da planície de inundação. O pulso de inundação também se manifestou em mudanças significativas na profundidade, oxigênio dissolvido e turbidez ao longo do período de estudo, determinantes para a estrutura das assembleias. Assim, ficou evidente que mudanças ambientais sazonais e a conectividade são fatores determinantes da estrutura das assembleias de Loricariidae nas lagoas marginais no Pantanal, sustentando elevada diversidade e abundância.

**Palavras-chave:** peixes; conectividade lateral; pulso de inundação; Pantanal.

## INTRODUCTION

The floodplains are considered transition zones between terrestrial and aquatic ecosystems (JUNK *et al.*, 1989; WARD *et al.*, 1999). In this sense, these ecosystems connect the rivers channels to the adjacent water bodies promoting the flow of water, nutrients and organisms between the subsystems and, thus, keeping them in a dynamic equilibrium in space and time (JUNK *et al*., 1989; TOCKNER *et al*., 2000). In this sense, the Flood Pulse Concept (FPC; JUNK *et al*., 1989) was the first conceptual model to define the seasonal hydrology as the main force in maintaining the biotic integrity of flood plains in tropical regions (FERNANDES *et al*., 2009; THOMAZ *et al*., 2007). The FPC assumes the seasonal oscillations in the hydrological level of the rivers as the key factor to the functioning of the ecosystem, conditioning the productivity of the biological assemblages in a predictable way, as well as the abiotic factors of the river and marginal lakes (RODRÍGUEZ and LEWIS JUNIOR, 1997; SILVA *et al*., 2009; TEJERINA-GARRO *et al*., 1998; TOCKNER *et al*., 2000; WANTZEN and JUNK, 2006).

The association of fish assemblages with the flood pulse is closely related to the connectivity of water bodies and, consequently, their effects on local environmental conditions (ARRINGTON and WINEMILLER, 2004; FERNANDES *et al*., 2009; JUNK *et al*., 1989). The connectivity between subsystems (marginal lakes, rivers and streams) is determined by the increase in the hydrometric level of the rivers, with consequent extravasation of the marginal dikes and flood of the lower portions in the period of flooding (SILVA *et al.*, 2001; HARRIS *et al*., 2005), a process that is well described in the literature as an ichthyofauna dispersion way (ARRINGTON and WINEMILLER, 2004; JUNK *et al*., 1989). This lateral connectivity also allows flows between different environments in the landscape, as well influences the processing and distribution of particulate organic matter (POM) and dissolved organic matter (DOM) between the river and floodplain compartments (RESENDE, 2008).

For fish assemblages, the lateral connectivity of the rivers with the flood plain also allows the lateral migration of species, a behavior associated mainly with the process of reproduction and maintenance of the populations (PETRY *et al*., 2003a; 2003b). The ichthyofauna is also favored by the increase of shelters against predators, i.e., ideal places for feeding and development of fingerlings (PETRY *et al*., 2003a; POUILLY and RODRÍGUEZ, 2004; POUILLY *et al*., 2004). This allows the environments to have a spatially or temporally limited connection (e.g., marginal lakes) ecosystems essential for the maintenance of species (WANTZEN and JUNK, 2006), sustaining high biodiversity (HOEINGHAUS *et al*., 2003; POUILLY and RODRÍGUEZ, 2004; WANTZEN and JUNK, 2006). However, although well documented for species of greatest economic potential, the lateral migration of species between the main channel of the river and the floodplain is still poor studied.

Loricariidae is the fifth richest family of neotropical vertebrates (> 800 species described; FERRARIS, 2007; LUJAN *et al*., 2015). This taxon contemplates species with bottom feeding behavior and little interspecific variation in their diet (GERMAN and BITTONG, 2009; GERMAN *et al*., 2010). They still show widespread consumption of debris and algae, on which their physiology is highly specialized (GERMAN and BITTONG, 2009; GERMAN *et al*., 2010). Loricariidae is widely distributed due to its adapted morphology and ability to utilize benthic resources. Its species inhabit a wide range of aquatic habitats, from torrential rivers or groundwater, to brackish water ecosystems. In the Pantanal, Loricariidae inhabits from streams to river channels, but are most commonly found in pools and ponds in the floodplain due to their resistance to low oxygen concentrations in water (BRITSKI *et al.*, 2007; SOARES *et al*., 2006) and the high food availability in these environments (WANTZEN and JUNK, 2006). Studies on Loricariidae in the Pantanal floodplain are still incipient, especially regarding the effects of environmental heterogeneity on its distribution in the landscape. Thus, the aim of this study was to evaluate the effect of flood pulse and lateral connectivity on the Loricariidae assemblages in oxbow lakes in the northern portion of the Pantanal, in addition to determining the factors that control the species richness and local abundance. In this sense, we hypothesized that the abiotic conditions and the assemblages of Loricariidae in marginal lakes are regulated mainly by the flood pulse and changes in the river-lakes connectivity.

## METHODS

### Study area

This study was carried out in the Caiçara Basin System (16°05'-16°06' S; 57°44-57°45' O), in two marginal oxbow lakes of the Paraguay River in the municipality of Cáceres, state of Mato Grosso, northern portion of Pantanal (Figure 1). The two portions were named Upper Caiçara (UC) and Bottom Caiçara (BC). These lakes are characteristically lentic in the low waters and semi-lotic during periods of rain and high waters, when the lateral water connection with the Paraguay river channel is reestablished (SILVA *et al*., 2009). BC maintains its connection with the Paraguay River channel throughout the year by a small flow of water, while UC loses its connection in low water periods. In each pond, three random sampling points were selected, representing their lower, median and upper portions.

### Environmental variables

In order to distinguish the seasonal periods, the daily variations between 1996 and 2007 in the hydrometric level of the Paraguay River near the River Agency of the Brazilian Navy in the city of Cáceres – MT, were taken as basis. From this information, it was possible to determine the periods of low (between August and October), rising (November to January), high (February to April) and falling water (May to July) in that portion of the Pantanal (Figure 2).

The abiotic parameters of the water were recorded bimonthly, along with the fish catch, between September 2005 and August 2007, representing two complete hydrological cycles. Dissolved oxygem (DO, mg $L^{-1}$; oximeter YSI 550-A), water temperature (°C), electrical conductivity (μS $cm^{-3}$; condutivimeter WTW LF-340), pH (portable pHmeter Tecnal TC-2P), Secchi transparency ($cm^{-1}$) and total depth ($cm^{-1}$) were recorded at all sampling points.

### Fish assemblages

The fish catch (SISBIO authorization number 10376) was made in consecutive triplicates using nylon fishing net in a rectangular metallic frame (3 $mm^{-1}$ between adjacent nodes,

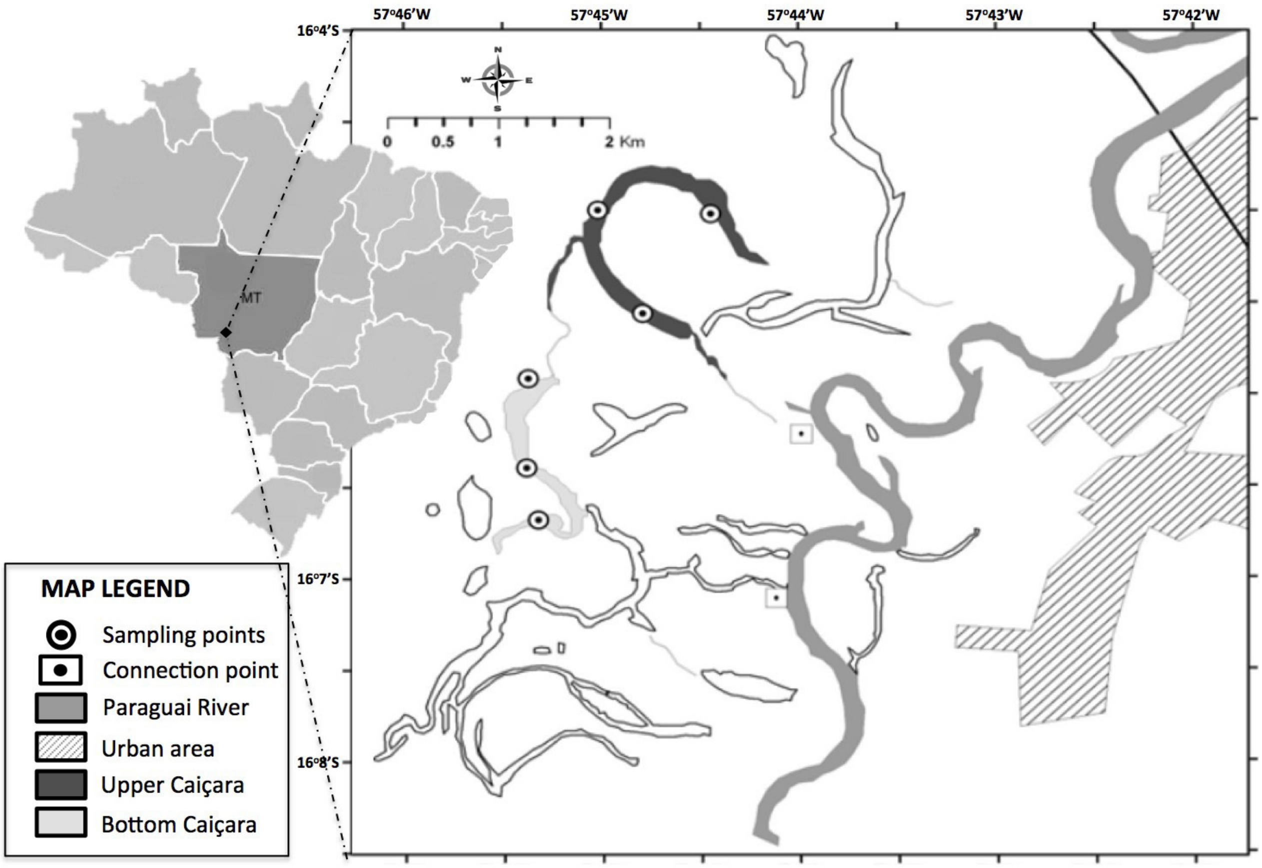


**Figure 1.** Location of the Caiçara basin system and sampled points. Northern portion of the Pantanal, state of Mato Grosso (MT), Brazil.

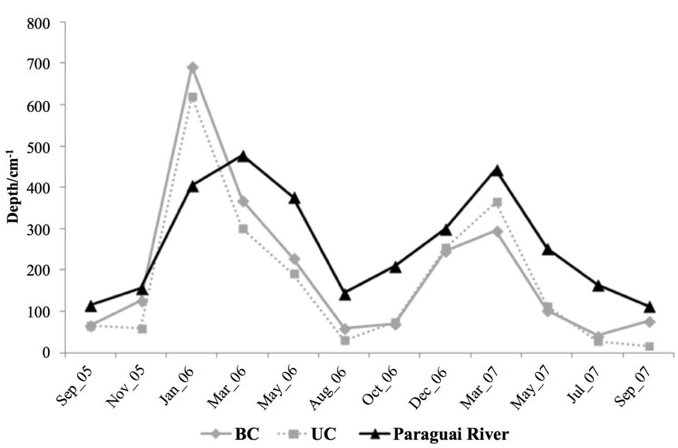


**Figure 2.** Variation of the average depth of the two studied lakes (UC and BC, light gray) and the Paraguay River (black) over time.

105 cm$^{-1}$ width, 205 cm$^{-1}$ length), seines (5 mm$^{-1}$ between adjacent nodes, 25 m$^{-1}$ length and 4 m high), cast nets of different mesh sizes and heights, and five sets of waiting nets of different meshes: 20, 30, 40, 50, 60 mm$^{-1}$ between adjacent nodes, 30 m$^{-1}$ length and 1,7 m$^{-1}$ high. The nets were placed for 24 hours per sampling point, and every 8 hours a survey was carried out to collect the captured specimens. The collected fish were fixed in 10% formalin and transported to the Laboratory of Zoology of the Mato Grosso State University for identification, using fish identification manuals, regional keys (BRITSKI *et al.*, 2007) and species description articles.

## Data analyses

Data normality was assessed using the Kolmogorov-Smirnov test, homogeneity of the variance was tested according to Levene and when necessary the data were log-transformed ($\log_{10}$ X+1). A Principal Component Analysis (PCA) based on a covariance matrix was used to evaluate the relationship between the abiotic variables of the ponds and seasonal periods (low, rising, high and falling water). The significance of the axes was measured according to the Broken-Stick model (LEGENDRE and LEGENDRE, 2012). An Analysis of Similarity (ANOSIM) was used to test the formation of different groups using the Gower index corrected by Bonferroni (HAMMER *et al.*, 2001). Abiotic and biotic variables (richness and total abundance) were compared separately between lakes and seasonal periods using an Analysis of Variance (One-way ANOVA) followed by Tukey tests to discriminate the categorical variables (ZAR, 1996).

To analyze the overall structure of the Loricariidae assemblage between the lakes and seasonal periods based on the frequency and relative abundance of the species, we performed a Multivariate Analysis of Variance (MANOVA/index-Pillai Trace; SCHEINER, 2001), followed by contrast analysis to discriminate the categorical variables corrected by Bonferroni, adjusting the multiple comparisons (RICE, 1989). Finally, a Spearman correlation (ρ) analysis was used to determine the association of physical variables with the richness and abundance of Loricariidae, taking into account $p < 0,05$. The Spearman coefficient ρ varies between -1 and 1, where values between 0.7 and 1 indicate a strong correlation, from 0.3 to 0.7 indicate moderate correlation and from 0 to 0.3 a weak correlation (PRESS *et al.*, 1992).

# RESULTS

## Environmental Variables

Principal Components Analysis (PCA) separated the sample units into three distinct groups: low water, transition (rising and falling water) and high water (Figure 3). The first two axes of the PCA together explained 73.44% of the variation of the abiotic parameters. The first axis of the PCA explained 52.98% of the variation, and was negatively correlated with dissolved oxygen, pH, turbidity, and electrical conductivity and positively with temperature, transparency and depth (of the Paraguay River and points). The second axis explained 20.46% of the variation, and had a positive relation with all the parameters. The first axis (4.23) differed when compared to the Broken-Stick model, unlike the second axis (1.63), which did not present a difference (2.23 and 1.96 in Broken-Stick model for first and second axes, respectively) allows us to consider only the first axis. The analysis of similarity (ANOSIM) was significant for the groups formed by the PCA, where the low and high water were different. The transition period did not differ from the other groups ($p<0,001$).

The pH values ($F_{(3, 212)}=41.1$; $p<0.01$), dissolved oxygen ($F_{(3, 212)}=130.8$; $p<0.01$), turbidity ($F_{(3, 212)}=120.1$; $p<0.01$), electrical conductivity ($F_{(3, 212)}=19.1$; $p<0.01$) were significantly different between the periods, with the highest values observed in the low water. While the highest temperature values ($F_{(3, 212)}=6.3$; $p<0.01$) were observed in the period of rising. Water transparency ($F_{(3, 212)}=352.2$; $p<0.01$), average depth of point ($F_{(3, 212)}=173.5$; $p<0.01$) and river ($F_{(3, 212)}=615.6$; $p<0.01$) during high water. Only temperature differed between the two lakes ($F_{(1, 214)}=15.1$; $p<0.01$), with the highest values recorded in BC.

## Fish assemblages

A total of 3986 individuals belonging to the Loricariidae family, divided into 8 genera and 14 species, were captured in the Upper (N = 1688) and Lower Caiçara (N = 2298; Table 1). The most abundant species in UC and BC was *Hypoptopoma inexspectatum* (Holmberg, 1893) (809 and 1145 respectively). There were no significant differences in richness ($F_{(1, 70)}= 0.4$; $p=0.51$; Figure 4A) and abundance ($F_{(1, 70)}=1.4$; $p=0.23$; Figure 4B) between lakes. On the other hand, the assemblages (frequency and abundance combined) differed between the lakes (Pillai Trace=0.53; $F=3.4_{(28,110)}$; $p<0.01$).

The Loricariidae assemblages differed significantly between studied periods both in richness ($F_{(3, 68)}=25.4$; $p<0.01$) and abundance of species ($F_{(3, 68)}=14.9$; $p<0.01$), with higher values found in the low waters and lower in the periods of high water (Tukey < 0.05; Figure 4C, D), also leading to changes in the structure of the Loricariidae community over the seasonal periods (Pillai Trace=0.24; $F=4.0_{(28,110)}$; $p<0.01$). The structure of the Loricariidae assemblage changed between periods of high and rising water (Contrast analysis = 0.55) and subsequently between falling and rising water (Contrast analysis = 0.12). The other combinations showed no significant difference.

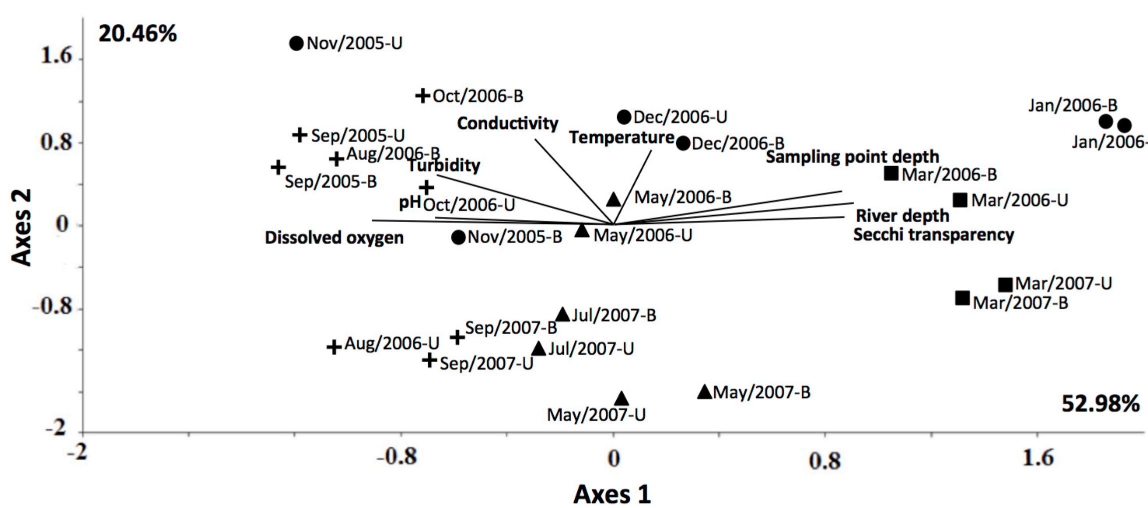


**Figure 3.** Results of the PCA based on the physical and chemical variables of the water, between the seasonal periods of high (square), falling (triangle), low (cross) and rising water (circle) throughout the sample period.

**Table 1.** List of species of Loricariids collected in two sites of the Caiçara basin system (UC and BC). Number of individuals collected (N), relative abundance and standard error (RA-SE). The classification of the higher taxonomic categories followed ESCHMEYER (1998), while families and subfamilies are presented in accordance with REIS *et al*. (2003) and MIRANDE (2010).

| Subfamily/Species | UC | | BC | |
|---|---|---|---|---|
| | N | RA-SE | N | RA-SE |
| **Hypoptomatinae** | | | | |
| *Hypoptopoma inexspectatum* (Holmberg, 1893) | 809 | 04.87 ± 0.94 | 1145 | 04.79 ± 0.88 |
| *Otocinclus vittatus* Regan, 1904 | 126 | 02.12 ± 0.21 | 159 | 02.18 ± 0.22 |
| **Loricariinae** | | | | |
| *Loricaria sp.* | 64 | 21.28 ± 3.99 | 71 | 20.31 ± 4.05 |
| *Loricariichthys labialis* (Boulenger, 1895) | 60 | 13.42 ± 3.44 | 23 | 13.87 ± 4.23 |
| *Loricariichthys platymetopon* Isbrücker & Nijssen, 1979 | 68 | 19.07 ± 4.72 | 55 | 14.37 ± 7.11 |
| *Rineloricaria* sp. | 0 | 0 | 1 | 21.70 ± 0.00 |
| *Rineloricaria parva* (Boulenger, 1895) | 221 | 06.36 ± 1.09 | 575 | 06.30 ± 1.25 |
| *Sturisoma barbatum* (Kner, 1853) | 1 | 17.00 ± 0.00 | 6 | 20.43 ± 3.50 |
| *Sturisoma robustum* (Regan, 1904) | 9 | 20.14 ± 3.14 | 21 | 21.53 ± 3.81 |
| **Hypostominae** | | | | |
| *Hypostomus sp.* | 0 | 0 | 1 | 01.20 ± 0.00 |
| *Hypostomus boulengeri* (Eigenmann and Kennedy, 1903) | 147 | 09.07 ± 7.43 | 150 | 09.91 ± 7.17 |
| *Hypostomus cochliodon* Kner, 1854 | 82 | 10.69 ± 7.54 | 38 | 15.32 ± 7.11 |
| *Hypostomus latifrons* Weber, 1986 | 5 | 02.64 ± 0.70 | 23 | 8.68 ± 9.13 |
| *Pterygoplichthys anisitsi* Eigenmann & Kennedy, 1903 | 96 | 28.52 ± 4.33 | 30 | 28.37 ± 4.04 |
| **Total** | **1688** | | **2298** | |

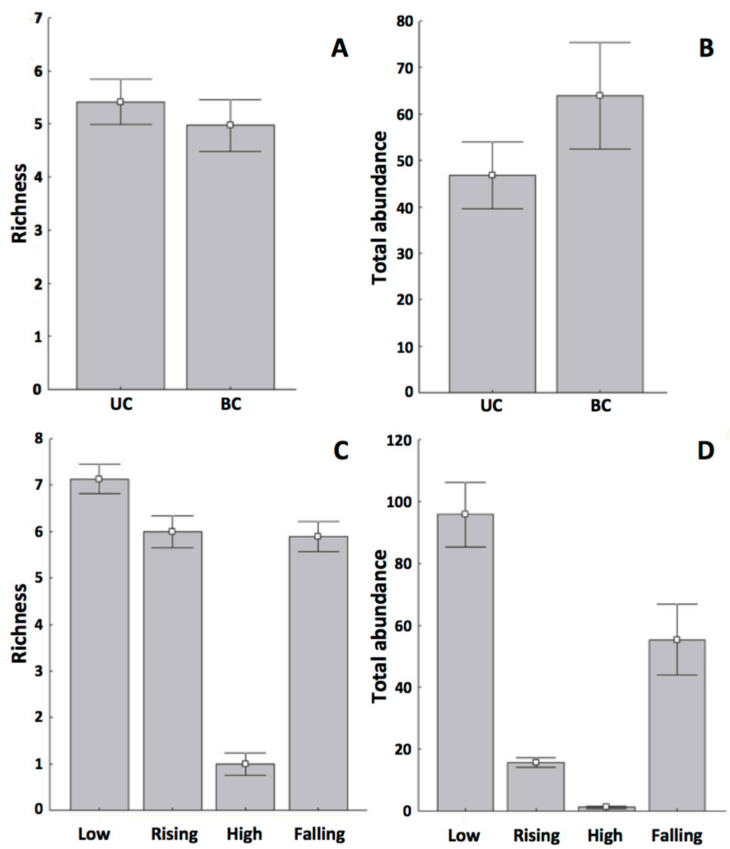


**Figure 4.** Number of species (A and C), total abundance (B and D) and standard error of the representatives of Loricariidae in the studied sites (A and B) and throughout the seasonal periods (C and D).

The richness of the Loricariidae community was negatively correlated with the mean depth of the river ($r = -0.72$, $p < 0.01$), mean depth of the point ($r = -0.59$, $p = 0.04$) and positively with water turbidity ($r = 0.59$, $p = 0.04$) and dissolved oxygen ($r = 0.79$; $p < 0.01$). However, there was no significant correlation between pH ($r = 0.50$, $p = 0.09$), temperature ($r = -0.11$, $p = 0.73$), transparency ($r = -0.52$; $p = 0.07$) and electrical conductivity ($r = 0.29$, $p = 0.35$). A similar pattern was observed for abundance of Loricariidae, negatively correlated with water transparency ($r = -0.91$; $p < 0.01$), mean depth of the river ($r = -0.84$; $p < 0.01$) and sample points ($r = -0.55$, $p < 0.01$), but presented a positive correlation with dissolved oxygen ($r = 0.7$, $p = 0.01$). However, there was no correlation with pH ($r = 0.45$, $p = 0.14$), turbidity ($r = 0.54$, $p = 0.06$), temperature ($r = -0.29$, $p = 0.34$) and electrical conductivity ($r = 0.15$, $p = 0.64$).

## DISCUSSION

Loricariidae accounted for about 8% of the richness and 38% of the abundance of the fish assemblage in the Caiçara basin system (MUNIZ, 2010). This reinforces that Loricariidae, within the Siluriformes order, is among the most representative taxonomic groups in ichthiofaunistic surveys (BRITSKI *et al.*, 2007; BUCKUP *et al.*, 2007; LOWE-MCCONNELL, 1999). The results also corroborate the diversity observed in previous studies in the Pantanal (FLORENTINO *et al.*, 2016; RESENDE *et al.*, 1998), evidencing that this system is essential for the conservation of a great number of continental species of fish, mainly holding a high diversity of Loricariidae and detritivorous fish (MUNIZ, 2010; POUILLY *et al.*, 2004). According to ROACH (2013), the Pantanal ensures unique conditions for the maintenance of many representatives of the fauna due to the high productivity of the great flood plains. Previous studies in Amazonian rivers show lower Loricariidae diversity than those observed in the Pantanal systems (FLORENTINO *et al.*, 2016; FREITAS and GARCEZ, 2004; SOUSA and FREITAS, 2008). This attests the need of conservation of the fluvial flood plains for the maintenance of the native ichthyofauna of the Pantanal.

Although connectivity in marginal lakes may play a regulatory role in biological communities (JUNK and WANTZEN, 2007; POUILLY *et al.*, 1999, 2004), the Loricariidae assemblages were mainly affected by seasonal fluctuations and were spatially unstructured, partially corroborating the hypothesis of this study. The homogeneity of the communities between the lakes indicates a frequent movement of the fish among the subsystems, which suggests a high level of interaction and mixing between the habitats along the floodplain (POUILLY *et al.*, 2004). According to CORREA *et al.* (2008), during high waters, fish have the possibility to freely move through the floodplain, flooded forests and river channels, allowing the possibility of rearrangement of the fish assemblage between the lakes. In this way, the presence of corridors between the subsystems allows the assemblages to be homogeneously distributed in the environment (THOMAZ *et al.*, 2007). On the other hand, seasonal hydrological oscillations may also reinforce differences in fish assemblages, as flooded forests may be a preferred habitat for many species. This indicates that changes in the hydrodynamics of these environments may affect the seasonal dynamics of the flood pulse and may endanger fish assemblages in the Pantanal.

The depth, as determinant of the connectivity, was one of the main factors affecting the structure of the ichthyofauna in the studied lakes. Previous studies have identified a similar effect, suggesting that the transparency and depth of water has a significant effect on the structure of the neotropical fish community (RODRÍGUEZ and LEWIS JUNIOR, 1997; SÚAREZ *et al.*, 2001; TEJERINA-GARRO *et al.*, 1998). In addition, during the flood, connectivity allows access of larvae and juveniles to lakes, where they find favorable conditions against predators and food (PETRY *et al.*, 2003a, 2003b). Similarly, the isolation of lakes ensures the survival of numerous species that feed on fish during dry periods (MUNIZ, 2010). This corroborates the importance of connectivity between river and marginal lakes for the reproductive maintenance of the fish assemblages of the Pantanal rivers.

Seasonal changes implied significant changes in abiotic parameters, with effects on the structure of the fish community. Previous studies have suggested that the precipitation regime and seasonal hydrometric variations have a direct influence on water characteristics (TAGLIANI *et al.*, 1992; SILVA *et al.*, 2001; SAINT-PAUL *et al.*, 2000; SILVA *et al.*, 2009). For example, on dissolved oxygen (SILVA *et al.*, 2009; SÚAREZ *et al.*, 2001; THORP and DELONG, 1994), water chemistry (HENDERSON and CRAMPTON, 1997; SAINT-PAUL *et al.*, 2000), transparency and depth (RODRÍGUEZ and LEWIS JUNIOR, 1997; TEJERINA-GARRO *et al.*, 1998), which are determinant in the structuring of the ichthyofauna.

Seasonal fluctuations in dissolved oxygen concentration as well as increased turbidity were features significantly related to variations in the structure of the Loricariidae community. These changes are evidenced in the PCA, are related to the increases of dissolved oxygen and turbidity in the studied lakes during low waters and has been also evidenced in previous studies (BISWAS and BORUAH, 2000; RODRÍGUEZ and LEWIS JUNIOR, 1997; SILVA *et al.*, 2009; TEJERINA-GARRO *et al.*, 1998; THOMAZ *et al.*, 2007; WINEMILLER and JEPSEN, 1998). The increase in dissolved oxygen can also lead to higher primary productivity in the system during periods of low water, which for many species, means availability of resources, explaining the high abundance and richness of Loricariidae in this period. On the other hand, during the period of high water many species living on shoals or river banks of the main river channel go into the flooded areas (ARRINGTON and WINEMILLER, 2004) searching for suitable habitats. This could explain the low abundance and richness during the rainy season in the floodplain of the Pantanal. However, the possible influence of the dilution effect, caused by the increase in the volume of water during the flood, on the capture efficiency of the equipment used cannot be ruled out. These aspects can be further investigated through specific and targeted experiments to meet this objective.

## CONCLUSIONS

In this study we evaluated how the environmental conditions can influence the structure of Loricariidae assemblages and collected data about their biological characteristics, helping in the conservation of this group. It was evident that seasonal hydrological changes are significant in the structure of the Loricariidae assemblages in the marginal lakes. Thus, it is expected changes in the natural morphology of the rivers, either by damming them, building waterways, or by the effect of climate changes (e.g., global warming), which may alter the seasonal flooding regimes, imperiling the native fish assemblages of the Pantanal. Also, the high diversity of the Loricariidae family in the Pantanal floodplain evidences the need to preserve this environment and also corroborates the importance of the connectivity between the river and marginal lakes in order to maintain the diversity of the ichthyofauna in the region.

## ACKNOWLEDGEMENTS

The first author thanks CAPES for the scholarship during his doctoral research in the Postgraduate Program in Ecology of the Universidade de Brasília (UnB). R.S. Rezende also thanks the Universidade Federal Rural do Semi-Árido (UFERSA) for logistical support and H.P. Silva thanks the Fundação de Amparo à Pesquisa do Estado do Mato Grosso (FAPEMAT). Finally, we would like to express our special gratitude to the whole group of Centro de Estudos em Limnologia, Biodiversidade e Etnoecologia do Pantanal (CELBE) for their constant support throughout the study and we also thank the two anonymous reviewers for their significant contributions.

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