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# Effect of waterfalls and the flood pulse on the structure of fish assemblages of the middle Xingu River in the eastern Amazon basin

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(With 3 figures)

## Abstract

The structure of fish assemblages in Neotropical rivers is influenced by a series of environmental, spatial and/or temporal factors, given that different species will occupy the habitats that present the most favourable conditions to their survival. The present study aims to identify the principal factors responsible for the structuring of the fish assemblages found in the middle Xingu River, examining the influence of environmental, spatial, and temporal factors, in addition to the presence of natural barriers (waterfalls). For this, data were collected every three months between July 2012 and April 2013, using gillnets of different sizes and meshes. In addition to biotic data, 17 environmental variables were measured. A total of 8,485 fish specimens were collected during the study, representing 188 species. Total dissolved solids, conductivity, total suspended matter, and dissolved oxygen concentrations were the variables that had the greatest influence on the characteristics of the fish fauna of the middle Xingu. Only the barriers and hydrological periods played a significant deterministic role, resulting in both longitudinal and lateral gradients. This emphasizes the role of the connectivity of the different habitats found within the study area in the structuring of its fish assemblages.

*Keywords:* natural barriers, connectivity, hydrological periods, community ecology, impacts of hydroelectric dams.

## Efeito das cachoeiras e do pulso de inundação na estrutura das assembleias de peixes do Médio Rio Xingu, Amazônia oriental

## Resumo

A estrutura da ictiofauna em rios neotropicais é constantemente influenciada por fatores ambientais, espaciais e/ou temporais, uma vez que as espécies tendem a ocupar ambientes com condições favoráveis à sua sobrevivência. Dessa forma, esta pesquisa tem como objetivo responder qual o principal fator responsável pela estruturação das assembleias de peixes no Médio Rio Xingu, testando a influência dos fatores ambientais, espaciais e temporais, além da presença de barreiras naturais (cachoeiras). Os dados foram coletados, trimestralmente, entre os meses de julho de 2012 e abril de 2013, utilizando redes de emalhe de tamanhos de malha variados. Foram mensuradas 17 variáveis ambientais. Foram coletados 8.485 indivíduos distribuídos em 188 espécies. Observou-se que sólidos dissolvidos totais, condutividade, material em suspensão total e oxigênio dissolvido foram as variáveis que mais influenciaram a ictiofauna do médio Rio Xingu. Observou-se que apenas as barreiras naturais e os períodos hidrológicos foram determinantes, ocorrendo tanto variação longitudinal quanto lateral, ficando claro que a conectividade entre os diferentes trechos do médio rio Xingu é de suma importância na estruturação das assembleias de peixes.

*Palavras-chave:* barreiras físicas naturais, conectividade, períodos hidrológicos, ecologia de comunidades, impactos de hidrelétricas.

## 1. Introduction

In natural riverine communities, the distribution of species, resources, and biological processes fluctuate in response to a range of processes that occur on different scales (Humphries et al., 2014). At the larger (regional) scale, climate, hydrology, and geomorphology are among the principal factors contributing to assemblage structure, while biotic and abiotic factors, such as inter-specific interactions and fluctuations in limnological variables, tend to function on more local scales (Hoeinghaus et al., 2007; Suarez and Petrere-Junior, 2007; Scarabotti et al., 2011). Variations in all these factors along the course of a river determine the distribution patterns of fish species, which tend to occupy the habitats that present the most favourable biotic and abiotic conditions for their survival and the maintenance of viable populations, as established in Hutchinson's (1957) theory of the ecological niche, and Southwood's (1977) habitat template. This variation in the composition of the fauna may be modified by different factors, such as the spatial configuration of environment and changes in local abiotic factors (Nekola and White, 1999), resources availability, among others.

The existence of barriers to dispersal, whether natural, such as rapids or waterfalls, or man-made, like dams, hampers species movements (Agostinho et al., 2008; Torrente-Vilara et al., 2011), separating the assemblages in each side of the barrier. In the absence of ostensible barriers, dissimilarities in the composition of assemblages would be expected to be related to the distance between them, considering the distinct dispersal capacities of the different component species (Hubbell, 2001; Morlon et al., 2008). Another factor that may also have a role in fish population structure is the response of each species to alterations in local abiotic factors, according to their environmental requirements, where each species will be present in an environment which presents a set of abiotic variables favourable to its existence (Hutchinson, 1957). Given all these aspects, the composition of aquatic assemblages would be expected to vary longitudinally along rivers, with more distant assemblages being less similar to one another than those located at shorter distances.

In addition to spatial variations, Neotropical floodplains areas are characterised by an annual change in water levels, which alternates between rainy and dry seasons, modifying the availability of habitats, and producing major fluctuations in the abundance and diversity of fish species (Goulding, 1980; Rodríguez and Lewis Junior, 1994). These fluctuations are characterised by an increase in connectivity in High Water period, with more similar assemblages due to higher dispersion, and greater isolation in Low Water period, with more dissimilar assemblages (Junk, 1980; Thomaz et al., 2007; Scarabotti et al., 2011). Changes in the hydrological cycle may alter local abiotic factors, such as limnological variables. During the High Water period, the river water carries a higher sediment load as a consequence of the pluvial runoff and the inundation of the floodplain, and the body of water becomes wider and deeper (e.g. Marques et al., 2003). This means that the temporal variation in Neotropical aquatic assemblages may be at least partly related to modifications in abiotic factors, and not only to changes in the connectivity of habitats.

Based on these considerations, the present study aimed to identify the principal determinant of the structure of fish assemblages in the middle Xingu River, Amazon Basin. Three predictions were tested: (i) the composition of assemblages located at shorter distances from one another will be more similar than that of more distant ones, given their enhanced potential for dispersal; (ii) given the distinct environmental requirements of species, the composition of assemblages among sites will be affected by modifications in local abiotic variables; (iii) as the hydrological cycle affects the availability of habitats, assemblages found at Low and High Water will have distinct compositions; (iv) as the presence of waterfalls and rapids may affect the connectivity of a river, distinct assemblages will be expected up- and down-stream of these features.

## 2. Material and Methods

### *2.1. Study area*

The Xingu River is a major right-bank tributary of the Amazon River, which originates in the Brazilian state of Mato Grosso, in the Serra do Roncador region, and discharges into the Amazon just downstream from the town of Porto de Moz, in Pará state. The river is 2,045 km long and flows predominantly in a south-north direction. Its principal tributary is the Iriri River, which originates approximately 100 km to the southwest of the town of Altamira, and other important tributaries of Xingu river are the Bacajá and Bacajaí rivers, on the Volta Grande do Xingu, downstream from Altamira (Eletronorte, 2001; Salomão et al., 2007; Eletrobras, 2009; Castilhos and Buckup, 2011).

The climate of this region is Am in the Köppen-Geiger classification, that is, tropical hot and humid (Peel et al., 2007). During the study period, monthly rainfall varied from 10.8 mm to 478.3 mm (INMET, 2014) and between 1971 and 2013, flow ranged from 1142.53 $m^3/s$ to 19518.23 $m^3/s$ on average, creating four distinct hydrological periods: Receding Water (June-August), Low Water (September-November), Flooding (December and February), and High Water (March-May). Because of this variation in river level, reaching on average 4.8 m in High Water period (Goulding et al., 2003), different environments become available during the year, including floodplains and flooded forests. In addition, some streams and lakes that connect with the river in High Water become isolated during the Low Water season.

The region is covered by typical lowland Amazon rainforest, with some enclaves of open vegetation. The waters of the Xingu are clear, with a transparency of 1 m to 5 m, light green in shallower parts, and dark green in the deeper environments (Castilhos and Buckup, 2011). The bottom is sandy or rocky, and rapids and waterfalls can be found in many areas, representing barriers to the dispersal of fish populations. The main waterfall is located in the region known as Volta Grande do Xingu at coordinates

03°23'24.9" S and 051°43'55.9" W; known as Jericoá, it presents a fairly sharp waterfall, where only large migratory fish can pass through. In addition, rapids in Bacajá River (a tributary of Xingu River) can be barriers too.

The present study focused on the middle Xingu, between the mouth of the Iriri River (20 km upstream of Altamira city) and the town of Senador José Porfírio (Figure 1). Data were collected tri-monthly between July 2012 and April 2013. In total, 36 sites were sampled, 9 in each hydrological period. Each sampling site was approximately 40 km, in fluvial distance, from each other.

### *2.2. Collection of biological samples and environmental data*

Fish specimens were collected using a sequential set of gillnets with meshes of different sizes, with each set being referred to as a "battery". Each battery was composed of seven, 20 m-long rectangular nets of 2 m in height made of monofilament nylon, with diagonal stretch meshes of 2, 4, 7, 10, 12, 15, and 18 cm. Each net had an area of 40 $m^2$, with a total area of 280 $m^2$ or 0.00028 $km^2$ per battery.

The flood period is characterised by the availability of new habitats, such as swamps and floodplain lakes. Due to the presence of these environments, sampling effort increased during this period, including one battery per swamp or floodplain lake sampled. Thus, the data were standardised using a Capture Per Unit Effort (CPUE), where the abundance of each species during a given month was divided by the area of the batteries set at the site in that month, providing a metric in the form of a number of individuals per $km^2$ of net per hour (ind./$km^2$/h). In other words, the CPUE was used as an index of species relative abundance, defined as the number of individuals captured per $km^2$ of gillnet per hour.

Three batteries were set at each site, with a distance of at least 5 km between each battery, in order to avoid problems of spatial autocorrelation. All the nets remained in the water for 15 hours, between 5 pm and 8 am of the following morning. The set of three batteries at each site was considered a single sample. Total sampling effort for each period of the hydrological cycle was 88.2 $km^2$ at High Water, 52.92 $km^2$ during the Receding Water, 52.92 $km^2$ at Low Water, and 48.51 $km^2$ during the Flooding period. The difference in sampling effort was due to amount of habitat, such as flooded forests, which are available only at High Water.

Once collected, the specimens were identified to the lowest possible taxonomic level (to species in most cases), fixed in 10% formaldehyde for 48 hours, and conserved in 70% ethanol. All specimens were deposited in the ichthyological collection at the Laboratório de Ictiologia de Altamira (LIA) of Universidade Federal do Pará (UFPA), as well as in the Museu Paraense Emílio Goeldi (MPEG) in Belém (Pará, Brazil).

In addition to the biological data, a number of environmental variables were obtained from the Norte Energia database, derived from samples collected by the International Ecology Institute (IIEGA). These data

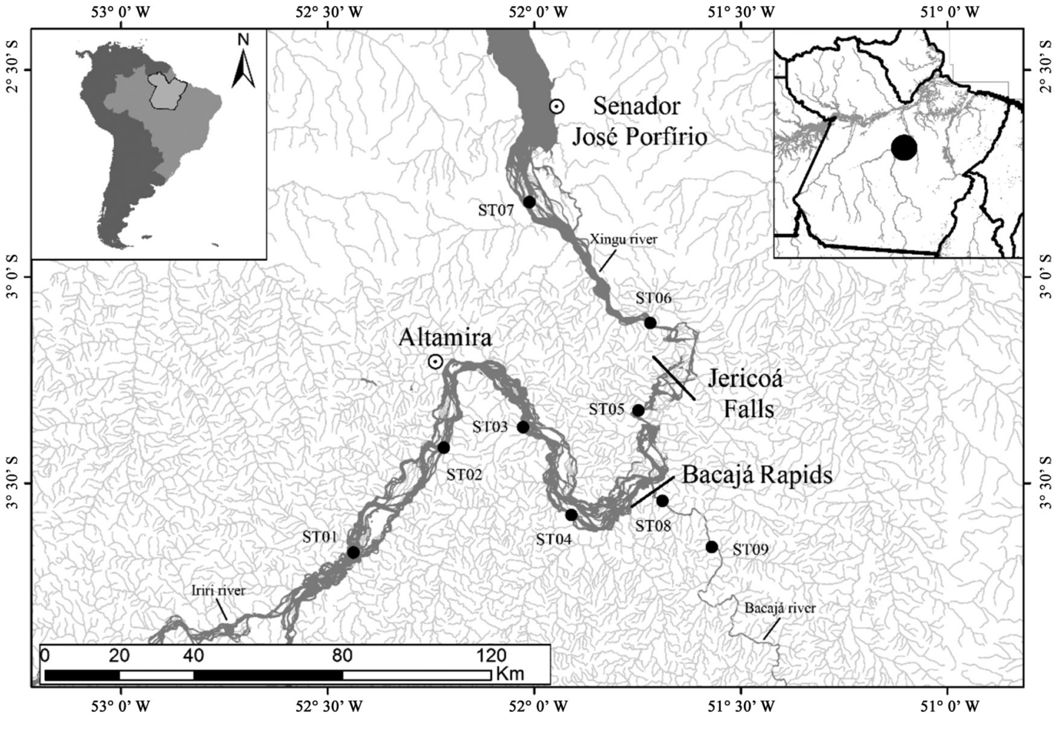

**Figure 1.** Sites visited during the present study for the collection of data on the local fish fauna of the middle Xingu River between July, 2012, and April, 2013. The points are represented by black circles, and the black bars show waterfalls.

were collected near the sites of fish sampling. A total of 17 variables were analysed: alkalinity (acronym: Alk, unit: mg-CaCO3/L), total carbon (C, mg/g sed), chlorophyll *a* (cloa, µg/L), conductivity (cond, mS/cm), Biochemical Demand for Oxygen (BDO, mg/L), suspended organic matter (SOM, mg/L), suspended inorganic matter (SIM, mg/L), total suspended matter (TSM, mg/L), total nitrogen (N, mg/L), dissolved oxygen (DO, mg/L), pH, redox potential (redox, mV), depth (depth, m), total dissolved solids (DisSol, mg/L), temperature (temp, °C), transparency (transp, m), and turbidity (turb, UNT).

### *2.3. Data analysis*

A Pearson Correlation Analysis was used to examine multicollinearity between variables, excluding those with correlation above a threshold of 0.8. A Principal Components Analysis (PCA) was used to determine which environmental variables were important in the differentiation of sites (Jongman, 1995). The axes were selected using the Broken Stick criterion. The environmental variables selected through this method were used for subsequent analyses. Prior to these analyses, the environmental variables were standardised by subtracting each value from the mean and then dividing it by the standard deviation in order to remove the effects of the different scales of measurement.

The pairwise distance between sites was measured following the course of the river, using 1:100,000 scale shape files of the local hydrography. To evaluate longitudinal variation in fish assemblage composition, the CPUE data (ind/km$^2$/h) from each site were ordinated distances (Clarke and Warwick, 2001). After NMDS, data were tested using a Permutational Analysis of Variance (PERMANOVA) with sums of squares type III (partial), permutation of residuals under a reduced model and 999 permutations. The PERMANOVA was based on the null hypothesis that the composition of the fish assemblages did not vary significantly among hydrological periods and spatially. Lastly, an Indicator Species Analysis (IndVal) was run to investigate which species were responsible for the differences among sites and/or hydrological periods (Clarke and Warwick, 2001).

We used Mantel analysis to evaluate the correlation of four matrices with fish assemblage composition (environmental variables, hydrological periods, presence of waterfalls/rapids, and fluvial distance between points), based on Pearson's correlation coefficient. We also tested the correlation among these four matrices with Mantel. When it was significant, we used partial Mantel to control the effect of each explanatory matrix on fish assemblages. Partial Mantel determines the partial correlation of two distance matrices, while controlling the effect of a third matrix (Legendre and Legendre, 2012), which allows us to see the individual effect of each matrix on the response matrix.

The matrix for the analysis of the hydrological periods was based on the pairwise comparison of sites by sample period. A score of zero was applied to pairs of samples from the same period (e.g., Flooding-Flooding), 1 for adjacent periods (e.g., Flooding-High Water), and 2 for alternate periods (e.g., Flooding-Receding Water). The matrix for the presence of waterfalls or rapids was also based on pairs of sites, which were scored zero for the absence of barriers and 1 when a barrier existed between them.

All statistical analyses were run in the R program (R Development Core Team, 2011) using the Vegan (Oksanen et al., 2011) and Ecodist packages (Goslee and Urban, 2007). All tests considered a 5% significance level.

## 3. Results

### *3.1. Environmental variables*

The High Water period was characterised by the highest alkalinity, BDO, depth, and redox potential. The highest temperatures and dissolved oxygen concentrations were recorded at Low Water. The highest values for all other variables were recorded during the transitional periods, that is, the Flooding and Receding Water cycles (see Appendix 1).

The variables total dissolved solids and turbidity were excluded of the analysis because presented large correlation with conductivity. The same occurred with suspended inorganic matter that was correlated to total suspended matter. The first PCA axis explained 28.35% of the variation, and the second, 19.92%, with a total of 48.28% for the first two ordination axes (Table 1). The most important variables of the first axis (loading > 0.7) were conductivity and total suspended matter, both negatively associated with the first Principal Component. Dissolved oxygen was the variable that contributed most to the

**Table 1.** Results of the Principal Components Analysis (PCA) for the nine sample points surveyed on the middle Xingu River between April, 2012 and April, 2013.

| Variable | Axis 1 | Axis 2 |
|---|---|---|
| Alk | –0.111 | 0.451 |
| C | –0.612 | 0.207 |
| Cloa | 0.12 | –0.594 |
| Cond | **–0.774** | –0.152 |
| BDO | –0.486 | –0.57 |
| SOM | –0.518 | –0.364 |
| TSM | **–0.804** | –0.229 |
| N | 0.57 | 0.001 |
| DO | 0.348 | **–0.817** |
| pH | 0.661 | –0.218 |
| Depth | 0.088 | 0.296 |
| Redox | 0.355 | 0.67 |
| Temp | 0.644 | –0.631 |
| Transp | 0.622 | 0.083 |
| Eigenvalue | 3.97 | 2.79 |
| % explanation | 28.35 | 19.92 |
| % accumulated explanation | 28.35 | 48.28 |
| Broken Stick | 3.25 | 2.25 |

The loading values for each environmental variable are shown for each axis, with those in bold type being characterised by a strong (> 0.7) correlation between axes. The acronyms are defined in Appendix 1.

formation of axis 2 (Table 1), with a negative association. The plot (Figure 2) shows a clear grouping of the Receding Water and Low Water periods, characterised by increased dissolved oxygen and reduced conductivity and total suspended matter. The Flooding and High Water periods presented the opposite values, with increased values of conductivity and total suspended matter and reduced dissolved oxygen. The points showed no spatial pattern, meaning that environmental variables did not group per sampling site.

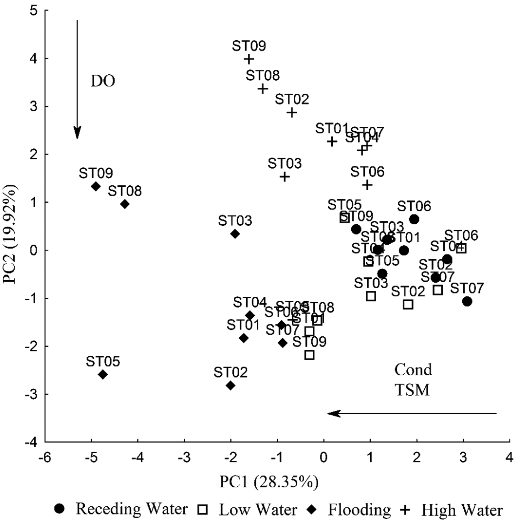

**Figure 2.** Plot of the PCA for the hydrological periods and sample sites surveyed on the middle Xingu River between July, 2012, and April, 2013.

### 3.2. Fish assemblages

A total of 8,485 fish specimens were collected during the present study, representing 188 species belonging to 33 families in nine orders (See Appendix 2). The most abundant order was Characiformes (5,765 specimens; 1,354.44 ind/km$^2$/h of net), followed by Siluriformes (2,803; 678.65 ind/km$^2$/h), and Perciformes (444; 104.91 ind/km$^2$/h). The most abundant family was Hemiodontidae (1,424; 333.48 ind/km$^2$/h), followed by Curimatidae (1,095; 261.97 ind/km$^2$/h), and Characidae (1,144; 254.97 ind/km$^2$/h). The most common species was *Hemiodus unimaculatus* (Bloch, 1794) (780; 185.87 ind/km$^2$/h), then *Ageneiosus ucayalensis* Castelnau, 1855 (396; 70.56 ind/km$^2$/h), and *Tocantinsia piresi* (Miranda Ribeiro, 1920) (387; 56.69 ind/km$^2$/h).

The PERMANOVA indicated significant temporal variation in the characteristics of the fish fauna (pseudo-F = 3.45; d.f. = 3; p = 0.001), despite a certain degree of overlap between the Flooding and High Water period, as shown in the NMDS plot (Figure 3). Significant spatial differentiation was also observed (pseudo-F = 2.32; d.f. = 8; p = 0.001). After the PERMANOVA, it was possible to realize the formation of three groups, the first encompassing sites 8 and 9 (group 1), the second, sites 1 through 5 (group 2), and the third by sites 6 and 7, forming group 3 (Figure 3). Groups 1 and 2 were separated by the Bacajá rapids and groups 2 and 3 were separated by the Jericoá falls.

Different species contributed to the formation of the spatial groups and to the differentiation among hydrological periods (Table 2). The IndVal test selected 31 species with

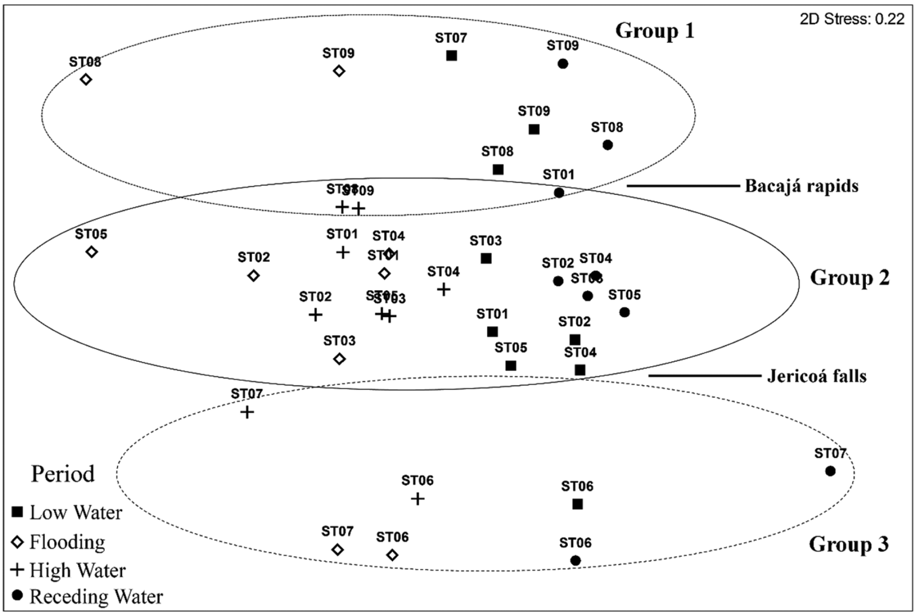

**Figure 3.** Results of the Non-Metric Multidimensional Scaling (NMDS) analysis of the data collected on the fish fauna of the middle Xingu River by sampling site and hydrological period between July, 2012, and April, 2013. The ellipses correspond to the three groups formed by the influence of Jericoá falls and Bacajá rapids.

**Table 2.** Results of Indicator Species Analysis per hydrologic period (a) and per sampling site (b) of the fish assemblages on the middle Xingu River.

**(a) Periods**

| Period | Species | IndVal | p |
|---|---|---|---|
| Receding Water | *Cyphocharax gouldingi* | 0.812 | 0.01 |
| Receding Water | *Triportheus rotundatus* | 0.73 | 0.015 |
| Receding Water | *Poptella brevispina* | 0.571 | 0.02 |
| Flooding | *Cyphocharax festivus* | 0.733 | 0.02 |
| Flooding | *Oxydoras niger* | 0.629 | 0.05 |
| High Water | *Triportheus albus* | 0.836 | 0.005 |
| Receding Water + Low Water | *Baryancistrus* aff. *niveatus* | 0.9 | 0.005 |
| Receding Water + High Water | *Myloplus arnoldi* | 0.749 | 0.01 |
| Low Water + High Water | *Limatulichthys griseus* | 0.758 | 0.01 |
| Low Water + High Water | *Brycon falcatus* | 0.684 | 0.035 |
| Low Water + High Water | *Brycon* aff. *pesu* “adiposa preta” | 0.667 | 0.02 |
| Flooding + High Water | *Ageneiosus ucayalensis* | 0.923 | 0.005 |
| Flooding + High Water | *Auchenipterichthys longimanus* | 0.892 | 0.005 |
| Flooding + High Water | *Auchenipterus nuchalis* | 0.861 | 0.005 |
| Flooding + High Water | *Myloplus rubripinnis* | 0.848 | 0.005 |
| Flooding + High Water | *Tocantinsia piresii* | 0.782 | 0.005 |
| Flooding + High Water | *Hypoptopoma inexpectatum* | 0.763 | 0.02 |
| Flooding + High Water | *Curimatella immaculata* | 0.745 | 0.015 |
| Flooding + High Water | *Chilodus punctatus* | 0.699 | 0.02 |
| Receding Water + Low Water + High Water | *Hemiodus sp.* “xingu” | 0.804 | 0.035 |
| Receding Water + Low Water + High Water | *Pimelodella cristata* | 0.72 | 0.015 |
| Low Water + Flooding + High Water | *Hydrolycus armatus* | 0.917 | 0.005 |
| Low Water + Flooding + High Water | *Boulengerella cuvieri* | 0.856 | 0.005 |
| Low Water + Flooding + High Water | *Geophagus altifrons* | 0.787 | 0.04 |

**(b) Sites**

| Sites | Species | IndVal | p |
|---|---|---|---|
| IC07 | *Hemiodontichthys acipenserinus* | 0.707 | 0.045 |
| IC09 | *Acestrorhynchus falcatus* | 1 | 0.005 |
| IC09 | *Moenkhausia intermedia* | 0.932 | 0.005 |
| IC09 | *Pterygoplichthys xinguensis* | 0.877 | 0.005 |
| IC09 | *Pristobrycon striolatus* | 0.866 | 0.01 |
| IC09 | *Ctenobrycon spilurus* | 0.824 | 0.02 |
| IC09 | *Poptella compressa* | 0.812 | 0.015 |
| IC01 + IC03 | *Agoniates halecinus* | 0.872 | 0.01 |
| IC01 + IC03 | *Bivibranchia velox* | 0.799 | 0.01 |
| IC06 + IC07 | *Ilisha amazonica* | 0.935 | 0.005 |
| IC06 + IC07 | *Pseudoloricaria laeviuscula* | 0.935 | 0.005 |
| IC06 + IC07 | *Hassar orestis* | 0.791 | 0.01 |
| IC06 + IC07 | *Pseudotylosurus microps* | 0.791 | 0.005 |
| IC07 + IC09 | *Hypoptopoma inexpectatum* | 0.83 | 0.03 |
| IC08 + IC09 | *Cynopotamus xinguano* | 0.782 | 0.005 |
| IC01 + IC02 + IC09 | *Hypostomus hemicochliodon* | 0.772 | 0.025 |
| IC02 + IC03 + IC04 | *Geophagus argyrostictus* | 0.828 | 0.015 |
| IC01 + IC02 + IC03 + IC04 | *Hemiodus vorderwinckleri* | 0.91 | 0.005 |
| IC02 + IC03 + IC07 + IC09 | *Leporinus friderici* | 0.848 | 0.015 |
| IC01 + IC02 + IC03 + IC04 + IC05 | *Leporinus maculatus* | 0.858 | 0.02 |
| IC01 + IC02 + IC03 + IC04 + IC06 | *Chilodus punctatus* | 0.753 | 0.045 |
| IC01 + IC02 + IC07 + IC08 + IC09 | *Hassar gabiru* | 0.874 | 0.005 |
| IC01 + IC02 + IC03 + IC04 + IC05 + IC06 | *Caenotropus labyrinthicus* | 0.885 | 0.05 |
| IC01 + IC02 + IC03 + IC04 + IC05 + IC06 | *Serrasalmus manueli* | 0.883 | 0.035 |
| IC01 + IC02 + IC03 + IC04 + IC05 + IC09 | *Acnodon normani* | 0.764 | 0.035 |
| IC01 + IC02 + IC03 + IC04 + IC06 + IC09 | *Pimelodus blochii* | 0.927 | 0.01 |
| IC01 + IC02 + IC03 + IC04 + IC08 + IC09 | *Loricaria birindellii* | 0.854 | 0.02 |
| IC01 + IC03 + IC04 + IC07 + IC08 + IC09 | *Acestrorhynchus microlepis* | 0.879 | 0.02 |
| IC01 + IC02 + IC03 + IC04 + IC05 + IC06 + IC09 | *Pachyurus junkii* | 0.92 | 0.045 |
| IC01 + IC02 + IC03 + IC04 + IC05 + IC08 + IC09 | *Squaliforma* aff. *emarginata* | 0.91 | 0.04 |
| IC01 + IC02 + IC03 + IC04 + IC05 + IC08 + IC09 | *Hemiodus sp.* “xingu” | 0.845 | 0.035 |

occurrence linked to the sampling sites, while 24 species were related to hydrological periods.

### *3.3. Factors that affect the distribution of fish species*

The Mantel analysis between the four explanatory matrices indicated a very weak correlation between the environmental variables and the hydrological periods, so this correlation was not considered in this study, although it was statistically significant (Table 3). On the other hand, there was a strong correlation between the presence of barriers and the fluvial distance. The effect of each matrix was then analysed separately to see their effects on fish assemblages.

The Mantel analysis indicated that the explanatory variables were responsible for 62% of the variation in the data (Table 3). Only the hydrological period and the presence of barriers (waterfalls or rapids) affected the distribution of the fish fauna, with the latter (barriers) being the most important. There was no influence of distance between sample points neither of environmental variables on fish assemblages.

## 4. Discussion

The hydrological cycle (temporal effect) and the presence of waterfalls (structural effect) are the main determinants of the fish species distribution in the middle Xingu River, confirming predictions iii and iv. Habitat connectivity among hydrologic periods is the main factor regulating the dispersal of individuals to new areas and to access new resources. In the case of lotic ecosystems, connectivity is observed longitudinally in relation to the course of the river, and laterally in relation to the influence of the hydrological cycle (Kondolf et al., 2006), with the formation of a vast flood plain.

Rivers and streams are dynamic and complex systems with a unidirectional flow of matter and energy. These processes modify gradually environmental conditions and the distribution of resources exploited by fishes, these variations being explained by the River Wave Theory (Humphries et al., 2014). This results in variations in the structure of fish assemblages along a longitudinal gradient, although the continuity of this gradient, the autochthonous production or allochthonous inputs. These factors may be interrupted abruptly and modified by the presence of physical barriers, such as waterfalls and rapids, resulting in distinct assemblages on either side of the barrier (Agostinho et al., 2008; Torrente-Vilara et al., 2011). Our study confirms this, since we observed the formation of groups between the waterfalls.

The characteristics of Neotropical fish assemblages also vary considerably in relation to the fluctuations caused by the seasonal flood pulse (Goulding, 1980; Junk et al., 1989; Scarabotti et al., 2011; Silva et al., 2013; Humphries et al., 2014). This process results in the inundation of the floodplain swamps, expanding the availability of resources (food and refuges, for example) and increasing the connectivity among habitats, resulting in a random redistribution of the fish fauna and reducing spatial variability (Thomaz et al., 2007). As the water drains back into the main channel, nutrients are washed out, while fish density and biotic interactions increase, some environments being isolated (Goulding, 1980; Junk et al., 1989). In the present study, the composition of the assemblages was affected by hydrologic periods, varying significantly among seasons, as recorded in a number of previous studies in the Neotropical region (Scarabotti et al., 2011; Silva et al., 2013). However, the effects of the Jericoá falls and Bacajá rapids were more pronounced than those of the flood pulse, and represent a major factor in the structuring of the fish assemblages of the middle Xingu. A similar pattern has been recorded in a number of previous studies of the effects of natural barriers on the abundance and distribution of fish species (Ingênito and Buckup, 2007; Torrente-Vilara et al., 2011).

Given the importance of physical barriers such as waterfalls and the habitat connectivity caused by the annual flood pulse, the construction of hydroelectric dams may have a significant impact on the composition of fish assemblages. In the specific case of the Belo Monte project on the Xingu River, which is being constructed in the middle of the study area, there is a predicted reduction in river discharge on the stretch that includes the Jericoá falls (Eletronorte, 2001; Norte Energia, 2010). This would result in the permanent loss of connectivity between the fish assemblages located up- and down-stream of these falls, as well as a marked change in the types of habitat available for the different species, which would affect species composition, as well as reproductive patterns and the recruitment processes of the majority of taxa (Agostinho et al., 2004). The impacts of the construction of hydroelectric dams are well documented (Junk and Mello, 1990; Agostinho et al., 2008; Mims and Olden, 2013; Sakaris, 2013; Freedman et al., 2014) and are related primarily to processes such as the loss and homogenization of habitats, and the replacement of species. This emphasizes the need for the systematic collection of data on the characteristics of local fish assemblages prior

**Table 3.** Results of the Mantel analysis between the four explanatory matrices–environmental variables, hydrological periods, the presence of barriers (waterfalls or rapids), and fluvial distance between points –and their effects on the composition of the fish assemblages on the middle Xingu River.

| | R | p |
|---|---|---|
| Environment x Period | **0.07** | 0.01 |
| Environment x Waterfall | –0.05 | 0.78 |
| Environment x Fluvial distance | –0.10 | 0.91 |
| Period x Waterfall | –0.05 | 1 |
| Period x Fluvial distance | –0.06 | 1 |
| Waterfall x Fluvial distance | **0.43** | <0.01 |
| Fish assemblages x Environment | –0.25 | 0.99 |
| Fish assemblages x Period | **0.23** | <0.01 |
| Fish assemblages x Waterfall* | **0.39** | <0.01 |
| Fish assemblages x Fluvial distance* | 0.01 | 0.41 |

The values in bold type are significant ($P < 0.05$). Marked (*) analysis were performed with partial Mantel.

to the flooding of reservoirs, in order to provide a sound database for the development of effective management strategies. However, little is known about the effect of the construction of reduced flow hydroelectric dams and this knowledge is nil when it comes to Amazon. Thus, this study is important because it allows the understanding of the structure of fish populations in the Middle Xingu River, forming bases for possible conservation measures.

The results of the present study indicated that the presence of waterfalls and the fluctuations of the flood pulse were the primary factors determining the distribution of fish species within the study area, creating both longitudinal and lateral gradients. This supports two of the operational hypotheses tested in the study, but rejects those on the possible effects of local environmental variables or the distance between sites. The difference in the composition of the assemblies due to hydrological periods and physical barriers are clearly the most important determinants of the structure of ichthyofauna in the study area, and is also one of the characteristics that may be most impacted by the construction of the Belo Monte hydroelectric dam. This re-emphasizes the need for the consideration of the region's unique characteristics in the planning of future management strategies.

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**Appendix 1.** Values recorded for the different environmental variables at the nine sampling sites on the middle Xingu River during each of the four principal hydrological periods (ebb, low water, flood, and high water) between July, 2012, and April, 2013. Alk = Alkalinity (mg-CaCO3/L), C = Total carbon (mg/g sed), Cloa = Chlorophyll a (µg/L), Cond = Condutivity (mS/cm), BDO = Biochemical Demand for Oxygen (mg/L), SIM = Suspended Inorganic Matter (mg/L), SOM = Suspended Organic Matter (mg/L), TSM = Total Suspended Matter (mg/L), N = Total nitrogen (mg/L), DO = Dissolved oxygen (mg/L), pH, Depth = depth (m), Redox = Redox potential (mV), SolDiss = Total Dissolved Solids (mg/L), Temp = Temperature (°C), Transp = Transparency (m), and Turb = Turbidity (UNT).

| Period | Alk | C | Cloa | Cond | BDO | SIM | SOM | TSM | N | DO | pH | Depth | Redox | SolDiss | Temp | Transp | Turb |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Receding Water | 6.59± 3.16 | 0.27± 0.16 | 12.92± 5.82 | 0.02± 0.001 | 0.67± 0.28 | 3.82± 2.34 | 2.31± 0.55 | 6.13± 2.71 | 2.76± 5.74 | 7.12± 0.26 | 7.98± 0.30 | 3.16± 5.21 | 117.23± 14.09 | 0.01± 0.01 | 29.85± 0.68 | 1.06± 0.32 | 4.60± 2.44 |
| Low water | 7.36± 5.73 | 6.96± 5.96 | 4.87± 3.18 | 0.02± 0.02 | 1.05± 0.60 | 4.57± 6.21 | 2.58± 1.60 | 7.14± 7.70 | 0.87± 0.50 | 7.54± 0.22 | 7.47± 0.60 | 2.02± 4.28 | 77.94± 28.04 | 0.01± 0.01 | 30.85± 0.61 | 0.81± 0.71 | 5.02± 5.19 |
| Flooding | 7.05± 6.28 | 7.71± 6.53 | 7.56± 4.55 | 0.03± 0.02 | 0.77± 0.40 | 2.93± 6.01 | 2.99± 2.15 | 5.92± 7.98 | 0.44± 0.11 | 7.37± 0.77 | 7.89± 0.79 | 2.12± 3.60 | 116.42± 28.67 | 0.01± 0.01 | 31.24± 0.36 | 0.92± 0.86 | 6.43± 5.44 |
| High water | 5.00± 2.02 | 25.69± 35.27 | 10.98± 8.87 | 0.07± 0.03 | 1.75± 0.24 | 10.96± 6.84 | 5.18± 5.47 | 16.13± 6.13 | 0.31± 0.20 | 7.05± 0.84 | 13.52± 21.11 | 3.03± 3.41 | 68.47± 33.35 | 0.04± 0.02 | 28.60± 1.28 | 0.49± 0.21 | 22.17± 13.36 |

**Appendix 2.** Taxonomic list of the fish species collected during the present study and their respective CPUE (ind./km2/h) for each hydrological period between July/2012 and April/2013 (Laboratório de Ictiologia de Altamira - LIA and Museu Paraense Emílio Goeldi - MPEG).

| Taxon / Authority | Voucher | High Water (ind./km$^2$/h) | Flooding (ind./km$^2$/h) | Low Water (ind./km$^2$/h) | Receding Water (ind./km$^2$/h) | Total (ind./km$^2$/h) |
|---|---|---|---|---|---|---|
| **BELONIFORMES** | | | | | | |
| **Belonidae** | | | | | | |
| *Pseudotylosurus microps* (Günther, 1866) | LIA 404 | 3.741 | 2.721 | 0.000 | 0.227 | 6.689 |
| **CHARACIFORMES** | | | | | | |
| **Acestrorhynchidae** | | | | | | |
| *Acestrorhynchus falcatus* (Bloch, 1794) | MPEG 29909 | 6.198 | 0.454 | 1.361 | 4.308 | 12.320 |
| *Acestrorhynchus microlepis* (Jardine, 1841) | MPEG 28903 | 22.751 | 15.420 | 8.503 | 7.370 | 54.044 |
| **Anostomidae** | | | | | | |
| *Anostomoides passionis* Santos & Zuanon, 2006 | LIA 417 | 0.227 | 0.227 | 0.000 | 0.000 | 0.454 |
| *Hypomasticus julii* (Santos, Jégu & Lima, 1996) | MPEG 29314 | 2.494 | 0.227 | 0.000 | 2.041 | 4.762 |
| *Laemolyta fernandezi* Myers, 1950 | MPEG 29078 | 0.454 | 0.227 | 0.000 | 0.000 | 0.680 |
| *Laemolyta proxima* (Garman, 1890) | LIA 161 | 6.311 | 5.442 | 0.680 | 0.000 | 12.434 |
| *Leporinus* aff. *fasciatus* | LIA 134 | 15.004 | 2.041 | 3.061 | 8.277 | 28.328 |
| *Leporinus brunneus* Myers, 1950 | LIA 418 | 0.454 | 0.000 | 0.000 | 0.227 | 0.680 |
| *Leporinus desmotes* Fowler, 1914 | LIA 313 | 1.663 | 0.000 | 1.701 | 0.113 | 3.477 |
| *Leporinus friderici* (Bloch, 1794) | MPEG 28073 | 10.204 | 2.721 | 2.834 | 3.515 | 19.274 |
| *Leporinus maculatus* Müller & Troschel, 1844 | LIA 370 | 12.207 | 3.628 | 2.154 | 4.082 | 22.071 |
| *Leporinus* sp. 1 | MPEG 28837 | 0.000 | 0.000 | 0.000 | 0.227 | 0.227 |
| *Leporinus* sp. 2 | MPEG 28938 | 0.756 | 0.000 | 0.227 | 0.000 | 0.983 |
| *Leporinus tigrinus* Borodin, 1929 | MPEG 28996 | 0.907 | 0.000 | 0.000 | 0.907 | 1.814 |
| *Petulanos intermedius* (Winterbottom, 1980) | MPEG 29626 | 0.529 | 0.227 | 0.000 | 0.000 | 0.756 |
| *Pseudanos trimaculatus* (Kner, 1858) | MPEG 29440 | 0.869 | 0.227 | 0.000 | 0.340 | 1.436 |
| *Sartor respectus* Myers & Carvalho, 1959 | MPEG 28924 | 0.227 | 0.000 | 0.227 | 0.000 | 0.454 |
| *Schizodon vittatus* (Valenciennes, 1850) | MPEG 29057 | 1.134 | 0.680 | 0.113 | 0.340 | 2.268 |
| *Synaptolaemus latofasciatus* (Steindachner, 1910) | | 0.151 | 0.000 | 0.000 | 0.000 | 0.151 |
| **Characidae** | | | | | | |
| *Acestrocephalus stigmatus* Menezes, 2006 | MPEG 28849 | 0.302 | 0.000 | 0.113 | 0.000 | 0.416 |
| *Agoniates halecinus* Müller & Troschel, 1845 | LIA 409 | 4.460 | 2.721 | 1.701 | 3.741 | 12.623 |
| *Astyanax* gr. *bimaculatus* | LIA 419 | 0.756 | 0.000 | 0.000 | 0.680 | 1.436 |
| *Brycon* sp. 1 | LIA 203 | 5.518 | 1.361 | 1.927 | 1.134 | 9.939 |
| *Brycon* sp. 2 | LIA 420 | 2.230 | 0.000 | 1.020 | 0.000 | 3.250 |
| *Brycon falcatus* Müller & Troschel, 1844 | MPEG 28992 | 2.381 | 0.227 | 1.361 | 0.227 | 4.195 |

**Appendix 2.** Continued...

| Taxon / Authority | Voucher | High Water (ind./ $km^2$/h) | Flooding (ind./ $km^2$/h) | Low Water (ind./ $km^2$/h) | Receding Water (ind./ $km^2$/h) | Total (ind./ $km^2$/h) |
|---|---|---|---|---|---|---|
| *Bryconops alburnoides* Kner, 1858 | MPEG 28979 | 2.608 | 0.227 | 0.794 | 1.587 | 5.215 |
| *Bryconops caudomaculatus* (Günther, 1864) | MPEG 29003 | 0.227 | 0.227 | 0.000 | 0.000 | 0.453 |
| *Bryconops giacopinii* (Fernández-Yépez, 1950) | MPEG 29402 | 0.000 | 0.567 | 0.000 | 0.000 | 0.566 |
| *Chalceus epakros* Zanata & Toledo-Piza, 2004 | LIA 157 | 1.134 | 0.000 | 0.680 | 0.000 | 1.814 |
| *Charax gibbosus* (Linnaeus, 1758) | LIA 342 | 0.907 | 0.000 | 0.907 | 0.000 | 1.814 |
| *Ctenobrycon spilurus* (Valenciennes, 1850) | MPEG 29817 | 2.305 | 0.000 | 0.340 | 1.587 | 4.232 |
| *Cynopotamus xinguano* Menezes, 2007 | MPEG 29587 | 3.364 | 0.227 | 1.020 | 2.154 | 6.764 |
| *Jupiaba polylepis* (Günther, 1864) | MPEG 29017 | 1.020 | 0.907 | 0.113 | 0.000 | 2.040 |
| *Moenkhausia heikoi* Géry & Zarske, 2004 | MPEG 28982 | 6.274 | 4.762 | 0.227 | 0.000 | 11.262 |
| *Moenkhausia intermedia* Eigenmann, 1908 | MPEG 28844 | 36.168 | 16.440 | 9.524 | 11.451 | 73.582 |
| *Moenkhausia lepidura* (Kner, 1858) | MPEG 28867 | 0.567 | 0.227 | 0.000 | 0.340 | 1.133 |
| *Moenkhausia xinguensis* (Steindachner, 1882) | MPEG 28083 | 8.428 | 3.175 | 0.454 | 1.134 | 13.189 |
| *Poptella brevispina* Reis, 1989 | LIA 410 | 5.329 | 0.000 | 0.227 | 5.669 | 11.224 |
| *Poptella compressa* (Günther, 1864) | MPEG 29019 | 9.259 | 2.381 | 4.875 | 0.000 | 16.515 |
| *Roeboexodon guyanensis* (Puyo, 1948) | MPEG 29407 | 0.567 | 0.227 | 0.000 | 0.340 | 1.133 |
| *Roeboides* sp. | MPEG 28899 | 2.608 | 0.227 | 2.041 | 0.340 | 5.215 |
| *Tetragonopterus argenteus* (Puyo, 1948) | MPEG 29871 | 1.474 | 0.680 | 0.000 | 0.794 | 2.947 |
| *Tetragonopterus chalceus* Spix & Agassiz, 1829 | MPEG 28943 | 3.288 | 1.134 | 1.247 | 0.794 | 6.462 |
| *Triportheus albus* Cope, 1872 | MPEG 29112 | 19.048 | 5.556 | 0.000 | 1.361 | 25.963 |
| *Triportheus auritus* (Valenciennes, 1850) | MPEG 29631 | 4.649 | 0.680 | 0.000 | 4.535 | 9.863 |
| *Triportheus rotundatus* (Jardine, 1841) | MPEG 29352 | 10.280 | 1.587 | 0.000 | 9.864 | 21.730 |
| **Chilodontidae** | | | | | | |
| *Caenotropus labyrinthicus* (Kner, 1858) | MPEG 28838 | 27.211 | 4.308 | 6.009 | 15.646 | 53.174 |
| *Chilodus punctatus* Müller & Troschel, 1844 | MPEG 29059 | 15.684 | 10.091 | 2.041 | 1.814 | 29.629 |
| **Ctenoluciidae** | | | | | | |
| *Boulengerella cuvieri* (Spix & Agassiz, 1829) | MPEG 28070 | 13.568 | 6.689 | 4.082 | 0.227 | 24.565 |
| *Boulengerella maculata* (Valenciennes, 1850) | LIA 272 | 1.587 | 1.134 | 0.454 | 0.000 | 3.174 |
| **Curimatidae** | | | | | | |
| *Curimata inornata* Vari, 1989 | MPEG 28876 | 37.906 | 18.367 | 4.308 | 15.193 | 75.774 |

**Appendix 2.** Continued...

| Taxon / Authority | Voucher | High Water (ind./ $km^2/h$) | Flooding (ind./ $km^2/h$) | Low Water (ind./ $km^2/h$) | Receding Water (ind./ $km^2/h$) | Total (ind./ $km^2/h$) |
|---|---|---|---|---|---|---|
| *Curimata vittata* (Kner, 1858) | LIA 421 | 0.907 | 0.907 | 0.000 | 0.000 | 1.814 |
| *Curimatella dorsalis* (Eigenmann & Eigenmann, 1889) | MPEG 29838 | 1.512 | 0.000 | 0.907 | 0.000 | 2.418 |
| *Curimatella immaculata* (Fernández-Yépez, 1948) | MPEG 29526 | 10.506 | 7.596 | 0.000 | 0.000 | 18.102 |
| *Cyphocharax festivus* Vari, 1992 | LIA 366 | 39.985 | 43.084 | 0.000 | 0.000 | 83.068 |
| *Cyphocharax gouldingi* Vari, 1992 | MPEG 28893 | 16.289 | 2.268 | 4.308 | 37.528 | 60.393 |
| *Cyphocharax leucostictus* (Eigenmann & Eigenmann, 1889) | MPEG 29535 | 7.181 | 8.957 | 1.020 | 0.000 | 17.157 |
| *Cyphocharax stilbolepis* Vari, 1992 | LIA 367 | 2.230 | 0.454 | 0.000 | 0.000 | 2.683 |
| *Psectrogaster falcata* (Eigenmann & Eigenmann, 1889) | LIA 308 | 0.340 | 0.227 | 0.000 | 0.000 | 0.566 |
| **Cynodontidae** | | | | | | |
| *Cynodon gibbus* (Agassiz, 1829) | MPEG 28908 | 2.683 | 0.454 | 0.340 | 1.134 | 4.610 |
| *Hydrolycus armatus* (Jardine, 1841) | LIA 401 | 10.242 | 2.948 | 3.855 | 0.227 | 17.271 |
| *Hydrolycus tatauaia* Toledo-Piza, Menezes & Santos, 1999 | MPEG 29086 | 3.477 | 0.907 | 1.134 | 0.680 | 6.198 |
| *Rhaphiodon vulpinus* Spix & Agassiz, 1829 | MPEG 29085 | 3.704 | 0.227 | 1.134 | 1.474 | 6.538 |
| **Erythrinidae** | | | | | | |
| *Hoplias aimara* (Valenciennes, 1847) | MPEG 29904 | 0.680 | 0.567 | 0.000 | 0.227 | 1.473 |
| *Hoplias malabaricus* (Bloch, 1794) | MPEG 28067 | 1.701 | 0.680 | 0.794 | 0.113 | 3.287 |
| **Hemiodontidae** | | | | | | |
| *Argonectes robertsi* Langeani, 1999 | MPEG 28961 | 21.958 | 10.431 | 2.608 | 1.814 | 36.810 |
| *Bivibranchia fowleri* (Steindachner, 1908) | MPEG 28883 | 5.102 | 1.814 | 4.195 | 0.000 | 11.111 |
| *Bivibranchia velox* (Eigenmann & Myers, 1927) | MPEG 29105 | 6.463 | 2.154 | 2.381 | 3.401 | 14.399 |
| *Hemiodus* cf. *semitaeniatus* | LIA 422 | 6.122 | 6.122 | 0.000 | 0.000 | 12.244 |
| *Hemiodus* sp. 1 | MPEG 29072 | 22.373 | 0.680 | 7.937 | 9.864 | 40.854 |
| *Hemiodus unimaculatus* (Bloch, 1794) | MPEG 28887 | 99.471 | 39.569 | 19.955 | 26.871 | 185.865 |
| *Hemiodus vorderwinckleri* (Géry, 1964) | LIA 371 | 16.667 | 7.256 | 2.268 | 6.009 | 32.199 |
| **Prochilodontidae** | | | | | | |
| *Prochilodus nigricans* Spix & Agassiz, 1829 | LIA 298 | 3.401 | 1.361 | 1.020 | 0.454 | 6.235 |
| *Semaprochilodus brama* (Valenciennes, 1850) | MPEG 28968 | 6.236 | 2.721 | 2.948 | 1.814 | 13.718 |
| **Serrasalmidae** | | | | | | |
| *Acnodon normani* Gosline, 1951 | LIA 181 | 4.611 | 1.927 | 2.608 | 0.113 | 9.259 |
| *Metynnis* cf. *luna* | LIA 423 | 4.157 | 2.494 | 0.454 | 1.134 | 8.238 |
| *Myleus setiger* Müller & Troschel, 1844 | LIA 413 | 3.099 | 0.907 | 1.701 | 0.454 | 6.160 |
| *Myloplus arnoldi* (Ahl, 1936) | MPEG 28966 | 6.387 | 0.454 | 0.567 | 5.669 | 13.076 |
| *Myloplus rhomboidalis* (Cuvier, 1818) | LIA397 | 2.948 | 1.134 | 0.907 | 0.907 | 5.895 |

**Appendix 2.** Continued...

| Taxon / Authority | Voucher | High Water (ind./ km$^2$/h) | Flooding (ind./ km$^2$/h) | Low Water (ind./ km$^2$/h) | Receding Water (ind./ km$^2$/h) | Total (ind./ km$^2$/h) |
|---|---|---|---|---|---|---|
| *Myloplus rubripinnis* (Müller & Troschel, 1844) | LIA 374 | 11.300 | 3.741 | 2.494 | 0.000 | 17.535 |
| *Myloplus schomburgkii* (Jardine, 1841) | LIA163 | 2.494 | 0.227 | 1.361 | 0.794 | 4.875 |
| *Pristobrycon eigenmanni* (Norman, 1929) | LIA 297 | 0.227 | 0.000 | 0.227 | 0.000 | 0.453 |
| *Pristobrycon striolatus* (Steindachner, 1908) | LIA 411 | 3.401 | 1.587 | 1.247 | 0.567 | 6.802 |
| *Pygocentrus nattereri* Kner, 1858 | LIA 300 | 1.474 | 0.000 | 0.680 | 0.794 | 2.947 |
| *Serrasalmus altispinis* Merckx, Jégu & Santos, 2000 | LIA 424 | 2.834 | 0.000 | 2.834 | 0.000 | 5.668 |
| *Serrasalmus gouldingi* Fink & Machado-Allison, 1992 | MPEG 28860 | 1.587 | 0.227 | 0.000 | 1.361 | 3.174 |
| *Serrasalmus manueli* (Fernández-Yépez & Ramírez, 1967) | LIA 393 | 22.978 | 2.494 | 13.152 | 6.689 | 45.313 |
| *Serrasalmus rhombeus* (Linnaeus, 1766) | LIA 351 | 17.385 | 1.020 | 4.195 | 10.317 | 32.917 |
| *Tometes* sp. | LIA 59 | 2.948 | 0.907 | 0.567 | 0.794 | 5.215 |
| **CLUPEIFORMES** | | | | | | |
| **Engraulidae** | | | | | | |
| *Anchoviella* sp. | MPEG 28064 | 0.680 | 0.680 | 0.000 | 0.000 | 1.360 |
| *Lycengraulis batesii* (Günther, 1868) | LIA 360 | 0.907 | 0.454 | 0.000 | 0.454 | 1.814 |
| **Pristigasteridae** | | | | | | |
| *Ilisha amazonica* (Miranda & Ribeiro, 1920) | MPEG 28870 | 12.812 | 5.215 | 0.907 | 0.907 | 19.841 |
| *Pellona castelnaeana* Valenciennes, 1847 | LIA 425 | 0.794 | 0.000 | 0.227 | 0.227 | 1.247 |
| **GYMNOTIFORMES** | | | | | | |
| **Electrophoridae** | | | | | | |
| *Electrophorus electricus* (Linnaeus, 1766) | LIA 426 | 0.113 | 0.000 | 0.000 | 0.113 | 0.226 |
| **Gymnotidae** | | | | | | |
| *Gymnotus carapo* Linnaeus, 1758 | LIA 427 | 0.529 | 0.000 | 0.000 | 0.000 | 0.529 |
| **Hypopomidae** | | | | | | |
| *Steatogenys elegans* (Steindachner, 1880) | MPEG 29292 | 0.227 | 0.000 | 0.000 | 0.227 | 0.453 |
| **Rhamphichthyidae** | | | | | | |
| *Rhamphichthys drepanium* Triques, 1999 | LIA 428 | 0.416 | 0.227 | 0.113 | 0.000 | 0.755 |
| **Sternopygidae** | | | | | | |
| *Archolaemus janeae* Vari, de Santana & Wosiacki, 2012 | MPEG 28896 | 4.308 | 0.000 | 1.701 | 2.494 | 8.503 |
| *Eigenmannia* aff. *trilineata* | MPEG 29595 | 0.076 | 0.000 | 0.000 | 0.000 | 0.075 |
| **MYLIOBATIFORMES** | | | | | | |
| **Potamotrygonidae** | | | | | | |
| *Paratrygon aiereba* (Müller & Henle, 1841) | LIA 314 | 0.227 | 0.227 | 0.000 | 0.000 | 0.453 |
| **OSTEOGLOSSIFORMES** | | | | | | |
| **Osteoglossidae** | | | | | | |
| *Osteoglossum bicirrhosum* (Cuvier, 1829) | LIA 276 | 1.361 | 0.000 | 1.361 | 0.000 | 2.721 |
| **PERCIFORMES** | | | | | | |
| **Cichlidae** | | | | | | |
| *Aequidens michaeli* Kullander, 1995 | MPEG 28846 | 0.227 | 0.227 | 0.000 | 0.000 | 0.453 |

**Appendix 2.** Continued...

| Taxon / Authority | Voucher | High Water (ind./ km²/h) | Flooding (ind./ km²/h) | Low Water (ind./ km²/h) | Receding Water (ind./ km²/h) | Total (ind./ km²/h) |
|---|---|---|---|---|---|---|
| *Caquetaia spectabilis* (Steindachner, 1875) | MPEG 28840 | 0.454 | 0.227 | 0.000 | 0.113 | 0.793 |
| *Cichla melaniae* Kullander & Ferreira, 2006 | LIA 64 | 2.268 | 0.000 | 0.113 | 1.587 | 3.968 |
| *Cichla monoculus* Agassiz, 1831 | LIA 63 | 0.227 | 0.000 | 0.227 | 0.000 | 0.453 |
| *Crenicichla* gr. *saxatilis* | LIA 429 | 0.113 | 0.000 | 0.000 | 0.113 | 0.226 |
| *Crenicichla lugubris* Heckel, 1840 | MPEG 28959 | 0.227 | 0.000 | 0.113 | 0.340 | 0.680 |
| *Crenicichla* sp. | LIA 81 | 1.134 | 0.454 | 0.000 | 0.680 | 2.267 |
| *Geophagus altifrons* Heckel, 1840 | MPEG 28081 | 12.094 | 4.422 | 7.143 | 0.794 | 24.452 |
| *Geophagus argyrostictus* Kullander, 1991 | MPEG 28962 | 7.521 | 0.794 | 4.649 | 1.247 | 14.210 |
| *Retroculus xinguensis* Gosse, 1971 | MPEG 29203 | 1.020 | 0.227 | 0.567 | 0.567 | 2.380 |
| *Satanoperca* sp. | MPEG 29334 | 0.340 | 0.000 | 0.113 | 0.113 | 0.566 |
| *Teleocichla* sp. | LIA 5 | 0.227 | 0.000 | 0.227 | 0.000 | 0.453 |
| **Sciaenidae** | | | | | | |
| *Pachyurus junki* Soares & Casatti, 2000 | MPEG 28085 | 20.446 | 4.422 | 9.751 | 4.649 | 39.266 |
| *Plagioscion squamosissimus* (Heckel, 1840) | LIA 362 | 8.957 | 1.814 | 3.175 | 0.794 | 14.739 |
| **PLEURONECTIFORMES** | | | | | | |
| **Achiridae** | | | | | | |
| *Hypoclinemus mentalis* (Günther, 1862) | MPEG 29117 | 0.000 | 0.000 | 0.113 | 0.000 | 0.113 |
| **SILURIFORMES** | | | | | | |
| **Auchenipteridae** | | | | | | |
| *Ageneiosus inermis* (Linnaeus, 1766) | | 4.308 | 2.608 | 0.454 | 0.227 | 7.596 |
| *Ageneiosus ucayalensis* Castelnau, 1855 | MPEG 29114 | 43.915 | 23.696 | 2.381 | 0.567 | 70.559 |
| *Auchenipterichthys longimanus* (Günther, 1864) | MPEG 28834 | 19.992 | 5.329 | 0.567 | 1.020 | 26.908 |
| *Auchenipterus nuchalis* (Spix & Agassiz, 1829) | LIA 383 | 63.492 | 22.789 | 1.247 | 0.794 | 88.321 |
| *Centromochlus heckelii* (De Filippi, 1853) | MPEG 28063 | 12.245 | 9.977 | 0.000 | 2.268 | 24.489 |
| *Centromochlus schultzi* Rössel, 1962 | MPEG 29752 | 0.454 | 0.567 | 0.000 | 0.113 | 1.133 |
| *Tatia intermedia* (Steindachner, 1877) | MPEG 28925 | 0.529 | 0.454 | 0.000 | 0.000 | 0.982 |
| *Tocantinsia piresi* (Miranda Ribeiro, 1920) | LIA 363 | 34.014 | 22.676 | 0.000 | 0.000 | 56.689 |
| *Trachelyopterus ceratophysus* (Kner, 1858) | LIA 339 | 0.454 | 0.000 | 0.000 | 0.000 | 0.453 |
| **Callichthyidae** | | | | | | |
| *Megalechis picta* (Müller & Troschel, 1849) | MPEG 29903 | 0.113 | 0.000 | 0.000 | 0.113 | 0.226 |
| **Cetopsidae** | | | | | | |
| *Cetopsis coecutiens* (Lichtenstein, 1819) | MPEG 28061 | 3.628 | 0.000 | 0.227 | 3.401 | 7.256 |

**Appendix 2.** Continued...

| Taxon / Authority | Voucher | High Water (ind./ $km^2$/h) | Flooding (ind./ $km^2$/h) | Low Water (ind./ $km^2$/h) | Receding Water (ind./ $km^2$/h) | Total (ind./ $km^2$/h) |
|---|---|---|---|---|---|---|
| **Doradidae** | | | | | | |
| *Doras higuchii* Sabaj Pérez & Birindelli, 2008 | MPEG 29368 | 8.919 | 1.474 | 5.215 | 2.494 | 18.102 |
| *Hassar gabiru* Birindelli, Fayal & Wosiacki, 2011 | MPEG 28965 | 17.952 | 5.669 | 7.596 | 2.268 | 33.484 |
| *Hassar orestis* (Steindachner, 1875) | MPEG 28871 | 21.542 | 6.803 | 0.000 | 14.286 | 42.630 |
| *Leptodoras hasemani* (Steindachner, 1915) | MPEG 29120 | 2.494 | 1.701 | 2.041 | 0.000 | 6.235 |
| *Leptodoras praelongus (*Myers & Weitzman, 1956) | MPEG 29740 | 0.113 | 0.000 | 0.000 | 0.113 | 0.226 |
| *Megalodoras uranoscopus* (Eigenmann & Eigenmann, 1888) | MPEG 28076 | 1.058 | 0.340 | 0.000 | 0.567 | 1.965 |
| *Nemadoras elongatus* (Boulenger, 1898) | LIA 430 | 0.227 | 0.227 | 0.000 | 0.000 | 0.453 |
| *Ossancora asterophysa* Birindelli & Sabaj Pérez, 2011 | LIA 275 | 1.134 | 0.680 | 0.000 | 0.454 | 2.267 |
| *Oxydoras níger* (Valenciennes, 1821) | LIA 369 | 1.587 | 1.701 | 0.000 | 0.113 | 3.401 |
| *Platydoras armatulus* (Valenciennes, 1840) | MPEG 28062 | 2.343 | 0.907 | 0.454 | 0.567 | 4.270 |
| *Platydoras* sp. | LIA 139 | 4.119 | 2.494 | 0.000 | 0.454 | 7.067 |
| *Rhinodoras boehlkei* Glodek, Whitmire & Orcés, 1976 | MPEG 28857 | 0.454 | 0.454 | 0.000 | 0.000 | 0.907 |
| **Heptapteridae** | | | | | | |
| *Imparfinis* aff. *hasemani* | LIA 431 | 0.113 | 0.000 | 0.000 | 0.113 | 0.226 |
| *Pimelodella cristata* (Müller & Troschel, 1849) | MPEG 28892 | 4.535 | 0.000 | 2.154 | 2.154 | 8.843 |
| *Pimelodella* sp. 1 | MPEG 29481 | 0.567 | 0.000 | 0.000 | 0.000 | 0.567 |
| *Pimelodella* sp. 2 | MPEG 28969 | 0.113 | 0.000 | 0.000 | 0.113 | 0.226 |
| **Loricariidae** | | | | | | |
| *Ancistrus ranunculus* Muller, Rapp Py-Daniel & Zuanon, 1994 | LIA 131 | 0.227 | 0.227 | 0.000 | 0.000 | 0.453 |
| *Ancistrus* sp. 1 | LIA 169 | 0.454 | 0.454 | 0.000 | 0.000 | 0.907 |
| *Ancistrus* sp. 2 | LIA 77 | 0.680 | 0.340 | 0.227 | 0.000 | 1.247 |
| *Baryancistrus* aff. *niveatus* | LIA 170 | 6.236 | 0.227 | 2.948 | 3.288 | 12.698 |
| *Baryancistrus chrysolomus* Rapp Py-Daniel, Zuanon & Ribeiro de Oliveira, 2011 | LIA 387 | 1.587 | 0.227 | 1.134 | 0.227 | 3.174 |
| *Baryancistrus xanthellus* Rapp Py-Daniel, Zuanon & Ribeiro de Oliveira, 2011 | LIA 171 | 1.474 | 0.340 | 1.020 | 0.113 | 2.947 |
| *Hemiodontichthys acipenserinus* (Kner, 1853) | LIA 432 | 1.134 | 0.000 | 0.000 | 0.907 | 2.040 |
| *Hopliancistrus* sp. | LIA 433 | 0.227 | 0.227 | 0.000 | 0.000 | 0.454 |
| *Hypancistrus* sp. | LIA 21 | 0.227 | 0.000 | 0.227 | 0.000 | 0.453 |
| *Hypoptopoma inexpectatum* (Holmberg, 1893) | LIA 321 | 27.022 | 21.995 | 1.020 | 0.113 | 50.151 |
| *Hypostomus* aff. *plecostomus* | LIA 434 | 0.227 | 0.000 | 0.000 | 0.000 | 0.226 |
| *Hypostomus hemicochliodon* Armbruster, 2003 | LIA 359 | 2.041 | 0.454 | 0.680 | 0.340 | 3.514 |
| *Limatulichthys griseus* (Eigenmann, 1909) | LIA 380 | 5.556 | 0.454 | 2.268 | 0.000 | 8.276 |

**Appendix 2.** Continued...

| Taxon / Authority | Voucher | High Water (ind./km$^2$/h) | Flooding (ind./km$^2$/h) | Low Water (ind./km$^2$/h) | Receding Water (ind./km$^2$/h) | Total (ind./km$^2$/h) |
|---|---|---|---|---|---|---|
| *Loricaria birindellii* Thomas & Sabaj Pérez, 2010 | LIA 85 | 8.163 | 2.268 | 2.041 | 4.989 | 17.460 |
| *Loricaria cataphracta* Linnaeus, 1758 | LIA 365 | 7.143 | 0.000 | 2.721 | 5.215 | 15.079 |
| *Panaque armbrusteri* Lujan, Hidalgo & Stewart, 2010 | LIA 137 | 0.794 | 0.227 | 0.340 | 0.227 | 1.587 |
| *Parancistrus nudiventris* Rapp Py-Daniel & Zuanon, 2005 | LIA 177 | 0.794 | 0.000 | 0.794 | 0.000 | 1.587 |
| *Peckoltia* cf. *cavatica* | LIA 435 | 0.454 | 0.227 | 0.227 | 0.000 | 0.907 |
| *Peckoltia feldbergae* de Oliveira, Rapp Py-Daniel, Zuanon & Rocha, 2012 | LIA 107 | 0.680 | 0.000 | 0.000 | 1.020 | 1.700 |
| *Peckoltia sabaji* Armbruster, 2003 | LIA 358 | 0.454 | 0.454 | 0.000 | 0.000 | 0.907 |
| *Peckoltia vittata* (Steindachner, 1881) | LIA 291 | 4.611 | 1.134 | 1.927 | 1.927 | 9.599 |
| *Pseudacanthicus* sp. | LIA 178 | 0.794 | 0.000 | 0.000 | 0.794 | 1.587 |
| *Pseudancistrus* sp. | LIA 309 | 0.794 | 0.000 | 0.794 | 0.000 | 1.587 |
| *Pseudoloricaria laeviuscula* (Valenciennes, 1840) | LIA 415 | 6.916 | 3.401 | 0.680 | 2.041 | 13.038 |
| *Pterygoplichthys xinguensis* (Weber, 1991) | LIA 299 | 2.116 | 1.701 | 0.113 | 0.227 | 4.157 |
| *Rineloricaria* sp. | LIA 248 | 0.113 | 0.000 | 0.000 | 0.000 | 0.113 |
| *Scobinancistrus aureatus* Burgess, 1994 | LIA 111 | 0.340 | 0.000 | 0.227 | 0.113 | 0.680 |
| *Scobinancistrus pariolispos* Isbrücker & Nijssen, 1989 | LIA 141 | 0.567 | 0.113 | 0.000 | 0.567 | 1.247 |
| *Squaliforma* aff. *emarginata* | LIA 294 | 17.763 | 4.989 | 7.370 | 3.401 | 33.522 |
| *Spectracanthicus punctatissimus* (Steindachner, 1881) | LIA 118 | 1.361 | 0.227 | 0.454 | 0.680 | 2.721 |
| *Spectracanthicus* sp. | LIA 136 | 2.381 | 0.227 | 1.474 | 1.134 | 5.215 |
| **Pimelodidae** | | | | | | |
| *Brachyplatystoma filamentosum* (Lichtenstein, 1819) | | 0.227 | 0.000 | 0.000 | 0.227 | 0.453 |
| *Hemisorubim platyrhynchos* (Valenciennes, 1840) | MPEG 29084 | 0.000 | 0.000 | 0.113 | 0.000 | 0.113 |
| *Megalonema* sp. | MPEG 29868 | 0.907 | 0.454 | 0.454 | 0.000 | 1.814 |
| *Phractocephalus hemioliopterus* (Bloch & Schneider, 1801) | LIA 389 | 2.646 | 0.680 | 0.000 | 1.701 | 5.026 |
| *Pimelodus blochii* Valenciennes, 1840 | LIA 348 | 22.071 | 10.884 | 2.381 | 9.864 | 45.200 |
| *Pimelodus ornatus* Kner, 1858 | LIA 436 | 0.227 | 0.000 | 0.000 | 0.227 | 0.453 |
| *Pinirampus pirinampu* (Spix & Agassiz, 1829) | MPEG 29383 | 2.759 | 0.680 | 0.567 | 1.814 | 5.820 |
| *Platynematichthys notatus* (Jardine, 1841) | MPEG 29083 | 1.134 | 0.000 | 0.227 | 0.907 | 2.267 |
| *Pseudoplatystoma punctifer* (Castelnau, 1855) | LIA 395 | 0.113 | 0.000 | 0.000 | 0.000 | 0.113 |
| *Sorubim lima* (Bloch & Schneider, 1801) | LIA 437 | 0.529 | 0.454 | 0.000 | 0.000 | 0.982 |
| *Sorubim trigonocephalus* Miranda Ribeiro, 1920 | LIA 438 | 0.113 | 0.000 | 0.000 | 0.113 | 0.226 |
| **Pseudopimelodidae** | | | | | | |
| *Pseudopimelodus bufonius* (Valenciennes, 1840) | LIA 318 | 0.454 | 0.454 | 0.000 | 0.000 | 0.907 |
| **Trichomycteridae** | | | | | | |
| *Henonemus* sp. | LIA 439 | 0.340 | 0.227 | 0.000 | 0.000 | 0.566 |
| **TOTAL** | | 1157.407 | 460.544 | 241.383 | 323.582 | |