

Effects of the hydrological regime on the ichthyofauna of riverine environments of the Upper Paraná River floodplain

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(With 5 figures)

Abstract

In this work, spatial and temporal variations in the diversity (species richness and Simpson's Diversity Index) and abundance (indexed by the capture per unit effort – CPUE; total and for reproductive groups) of fish from three rivers (Baía, Ivinheima and Paraná) located in a floodplain of the Upper Paraná River basin were analyzed over a period of 20 years (1987-2007). In addition, we evaluated the relationships of these ecological attributes with variations in the hydrologic regime, considering the possible effects of natural (climatic events) and artificial (discharge control by dams) disturbances. Annual variations in hydrometric attributes were calculated using PULSO software and daily water level data. We applied analysis of covariance to determine the relationships between ecological and hydrometric attributes, the latter summarized in axes of a principal component analysis. Lower values of the fish assemblage attributes (diversity and abundance) were registered in the Paraná River. Species richness, total CPUE and CPUE of long-distance migratory species were positively related to the duration of the floods and the connectivity of the area. Variations in the annual hydrological cycle and their effects on fish assemblage appear to be affected by extreme natural (ENSO) and artificial (discharge control by dams) events.

Keywords: floods, recruitment, abundance, fish diversity, fish assemblage.

Efeitos do regime hidrológico sobre a ictiofauna de ambientes fluviais da planície de inundação do Alto Rio Paraná

Resumo

Nesse trabalho foi avaliada a variação espaço-temporal na diversidade (riqueza de espécies e Índice de Diversidade de Simpson) e abundância (indexada pela captura por unidade de esforço – CPUE; total e por grupo reprodutivo) de espécies de peixes de três rios (Baía, Ivinheima e Paraná), localizados na planície de inundação do Alto Rio Paraná, ao longo de 20 anos (1987-2007). Ainda, avaliamos as relações desses atributos ecológicos (diversidade e abundância) à variação anual do regime hidrológico, considerando a influência de distúrbios naturais (eventos climáticos) e artificiais (regulação hidrológica por barragens). Para representar a variação anual do regime hidrológico de cada rio, foram utilizados os atributos hidrométricos calculados pelo programa PULSO, a partir de medidas do nível hidrométrico diário. Análise de covariância foi aplicada para avaliar a relação entre os atributos ecológicos das assembleias de peixes e a variação no regime hidrológico, esta sumarizada em eixos de uma análise de componentes principais. A riqueza de espécies, a CPUE total e a de migradores de longa distância foram relacionadas positivamente à duração das cheias e conectividade, sendo que o Rio Paraná apresentou os menores valores médios desses atributos. Dessa forma, as variações constatadas no ciclo hidrológico anual e seus reflexos sobre a estrutura das assembleias de peixes do rio Paraná parecem decorrer do efeito combinado de eventos naturais (El Niño – ENSO) e artificiais (controle da vazão pelas barragens).

Palavras-chave: cheias, recrutamento, abundância, diversidade de peixes, assembleia de peixes.

1. Introduction

The freshwater ichthyofauna of the Neotropical region is characterized by high species richness (± 6000 species; Reis et al., 2003), which contributes nearly 31% of the fish diversity of the planet. The Paraná River basin harbors a representative part of this diversity (600 species; Bonetto, 1986), and more than half of these species (52%; 310 species; Langeani et al., 2007) are found in the first one third of this basin, the upper Paraná River.

The upper Paraná River drains almost all of central-south Brazil (10.5% of the Brazilian territory), where about 30% of the population of the country is concentrated (Agostinho et al., 2008). In this region are located the main urban, industrial and agricultural centers of Brazil. Environmental problems resulting from these uses, such as pollution, eutrophication, habitat alterations, overfishing and introduction of alien (exotic) species, are the main reasons for the alteration of aquatic communities and loss of local and regional diversity (Agostinho et al., 2005). However, the regulation of river discharge with dams is the main threat to the maintenance of fish diversity in the upper Paraná River (Tundisi and Matsumura-Tundisi, 2003; Agostinho et al., 2005).

Despite the control imposed by the large number of dams, the flood regime of the upper Paraná River is still the main determinant of the structure of aquatic communities (Gomes and Agostinho, 1997; Thomaz et al., 2004; Agostinho et al., 2001; 2007a). Floods lead to increased resource availability (e.g., food and shelter), with positive effects on the development of the initial stages of fish and on the maintenance of high levels of species diversity (Agostinho et al., 2004b, 2007a). Thus, similarly to other South American river basins (Welcomme, 1979; Lowe-McConnell, 1987; Machado-Allison, 1990; Vazzoler and Menezes, 1992), seasonal variations in the hydrometric levels of the upper Paraná River have a relevant role in regulating the reproduction and recruitment of fish. This is apparent in the close synchronism between floods and the main events of the reproductive cycle (maturation of oocytes, migration, spawning and larval development). In addition, there is also a close relationship between successful recruitment and the timing, duration and amplitude of floods (Gomes and Agostinho, 1997; Agostinho et al., 2004a). However, these relationships may vary according to the life history of the species, which affects the structure of fish assemblages (Agostinho et al., 2001, 2007a). Greater dependence on hydrometric levels is more evident for long-distance migratory species, which, in general, use the seasonally floodable habitats as nurseries (Agostinho et al., 2004a; Bailly et al., 2008; Suzuki et al., 2009).

To investigate the patterns of abundance and turnover of species, we require a long series of data with sample standardization. Previous studies (such as FINEP, PADCT/CIAMB) and the PELD Project conducted in the Paraná River floodplain represent the best long-term datasets available for South American rivers. In this pa-

per, we analyzed spatial and temporal variations in species diversity and abundance (total and for reproductive groups) of fishes in the upper Paraná River floodplain over a 20-year period (1987-2007). We also determined the relationships of these variations to some attributes of the hydrometric level, considering the possible effects of natural (climatic events) and artificial (hydrologic regulation) disturbances present during the studied period.

2. Material and Methods

2.1. Study area

The Paraná River is formed by the junction of the Grande and Paranaíba Rivers in south-central Brazil, and, along with the Paraguay River, forms the Plata River in Argentina. It is the tenth longest river in the world (4,695 km), with a watershed area of 2.8×10^6 km² that includes most of south-central South America (18° S to 34° S; 45° W to 68° W) from the Andes to the Serra do Mar, near the Atlantic Ocean. The upper Paraná River encompasses the upper third of the Paraná River basin and is located within Brazilian territory, except for the stretch comprising the Itaipu Reservoir, which borders Paraguay. The upper Paraná River basin has a drainage area of 891,000 km², corresponding to 10.5% of Brazil. The wet season in the region is between October and February, when the mean rainfall reaches more than 125 mm. The dry season occurs between June and September, when the mean rainfall totals less than 80 mm. Therefore, the climate of the region may be classified as tropical/subtropical, with a mean annual temperature of 15° C (IBGE, 1990).

The upper Paraná River presents a wide floodplain on its right margin (480 km long and more than 20 km wide). However, in December 1998, the closure of Sérgio Motta Dam (also known as Porto Primavera), located in the middle of the floodplain stretch, reduced the floodplain to about 230 km in length (upstream of the Itaipu Reservoir and downstream from Porto Primavera Dam). This stretch is the only remnant of the upper Paraná River without dams inside Brazilian territory. Even after the reduction, the floodplain still presents a high heterogeneity of habitats and maintains a high diversity of aquatic and terrestrial organisms (Agostinho et al., 2004b). Due to the importance of this stretch, three conservation units were created to protect it. They are the “Área de Proteção Ambiental das Ilhas e Várzeas do rio Paraná” (100,310 ha; a Protected Area), the “Parque Nacional de Ilha Grande” (78,800 ha; National Park), and the “Parque Estadual do Ivinheima” (70,000 ha; State Park).

Despite the intense damming of the upper Paraná River (more than 46 large dams), the flood regime, especially in the lotic remnant (where the floodplain is located), has not been drastically altered due to the existence of several tributaries. Flood season in the Paraná River usually happens from November to May. The elevation of the river level characterizes this season, and some

pulses can occur with amplitudes greater than 2-3 m. The occurrence of two or three pulses is common during the flood season. Smaller pulses (less than 0.5 m) occur weekly during the dry season (Thomaz et al., 1992) due to the operation of upstream dams. On average, the Paraná's water level varies by about 2.5 m during a seasonal cycle, but greater interannual variations do occur. The amplitude of the water level may reach up to 7.5 m, but years without floods can also be registered (e.g., 1986-1987).

2.2. Sampling

Data analyzed in this paper are a discontinuous time series (from 1987 to 2007) gathered from sampling sites located in the Baía, Ivinheima and Paraná Rivers (Projects: FINEP, 1987-1988; PADCT/CIAMB, 1992-1993; PELD, 2000-2007) (Figure 1). Due to differences in the sampling periodicity, effort and fishing

gear employed in each project, we first standardized data to produce interannual unbiased comparisons of the fish assemblages. Therefore, we used only quarterly samples taken with the same effort and sampling gear in most of the years considered (from March to December, except in 2003).

Fish were captured using gillnets of different mesh sizes (ranging from 3 to 16 cm opposite knots) and trammel nets (internal mesh of 6, 7 and 8 cm opposite knots). The species abundances in every sample were indexed by the capture per unit effort (CPUE; number of individuals/1000 m² of gill nets in 24 hours).

The "Agência Nacional de Águas" (ANA – National Water Agency) supplied daily river level data for the Paraná and Ivinheima Rivers. Water levels for the Baía River were not available. Despite having its own dynamics (Souza Filho and Stevaux, 2004), we assumed that the variations in the hydrologic regime of the Baía River

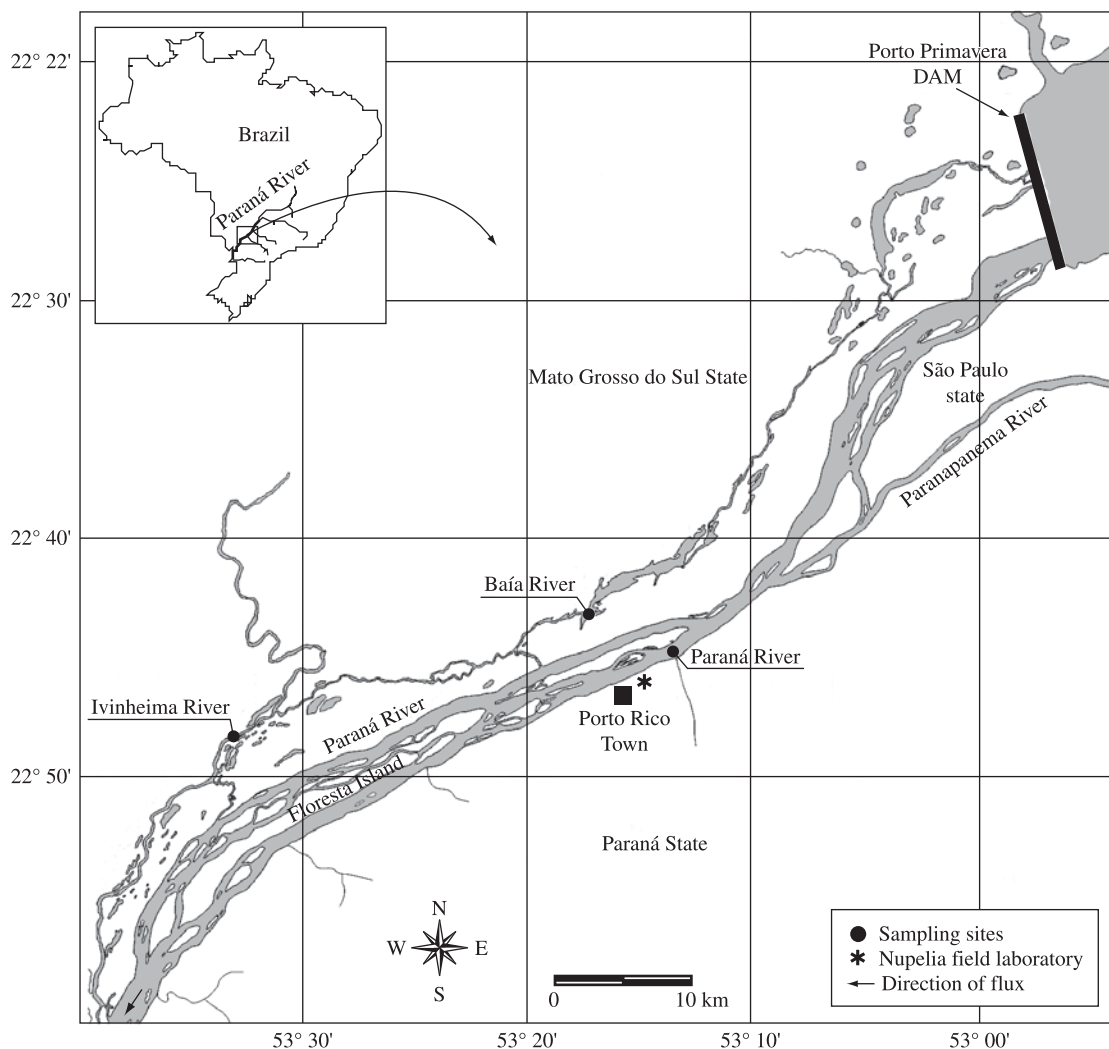


Figure 1. Map of the upper Paraná River floodplain and the locations where samplings were performed from 1987 to 2007.

were similar to those of the Paraná because it strongly influences the level of the Baía River.

2.3. Data analysis

2.3.1. Variation of the hydrologic regime

To represent the annual variations in the hydrologic regimes of each river, we calculated the hydrometric attributes of intensity of the potamophase and limnophase, days of potamophase and limnophase, elasticity, connectivity, fraction of potamophase, number of pulses and timing (for definitions, see Table 1). All hydrometric attributes were calculated using the *fFITRAS* function of the PULSO software (Neiff and Neiff, 2003), available at <http://www.neiff.com.ar>. The PULSO software is used to study phenomena that repeat themselves according to a sigmoidal function over long periods, such as seasonal fluctuations in river levels. We used the daily levels of the Ivinheima and Paraná Rivers to calculate hydrometric attributes. We established river levels of 270 and 451 cm for the Ivinheima and Paraná Rivers, respectively, as the reference intensity (threshold) levels that characterize flooding in each river. For more details on the PULSO software, see Neiff and Neiff (2003).

Information on the periods influenced by climatic anomalies (El Niño Southern Oscillation - ENSO) and their intensities was gathered from a historical dataset available at <http://www.cpc.noaa.gov/index.php> and <http://ggweather.com/enso/years.htm>.

To reduce the dimensionality of the data (number of variables), patterns of correlation of the hydrometric variables were summarized by principal component analysis (PCA). Axes with eigenvalues greater than 1 were

retained for interpretation (Kaiser-Guttman criterion; Jackson, 1993). Scores of the axes retained were used as surrogates of annual hydrometric variation. To identify the attributes that most contributed to the retained axes, we conducted Pearson correlations between the scores of the PCA axis and the original data matrix. Higher correlations ($r > 0.70$) indicated the importance of an attribute to the ordination.

2.3.2. Fish assemblages and relationship with the hydrologic regime

We used species richness (number of species captured), total abundance (CPUE) and the Diversity Index of Simpson (Magurran, 1998) to characterize the fish assemblage of every sample. Considering the hypothesis that variations in the flood regime differently affect spawning of fish with different life histories (Agostinho et al., 2001; Bailly et al., 2008), total CPUE was divided into reproductive groups (according to the classification of Agostinho et al., 2004a) as follows:

- i) Short-distance migratory or sedentary species with external fertilization and without parental care: these species undergo short migrations (less than 100 km) or only lateral migrations. They have comparatively higher fecundity and small oocytes. Spawning can be total or in several batches, and in the latter case may last several months. According to Winemiller (1989), they can be classified as “opportunistic”;
- ii) Short-distance migratory or sedentary species with external fertilization and parental care: species in this group present multiple spawnings over long periods, low fecundity, and large and

Table 1. Definitions of the hydrometric variables (attributes) considered in this study. All variables were calculated using the *fFITRAS* function within the PULSO software (Neiff and Neiff, 2003).

Variables	Definitions
Intensity of potamophase	Greater value registered in the hydrograph during the studied period (in our case, one value for each year).
Intensity of limnophase	Smaller value registered in the hydrograph during the studied period (in our case, one value for each year).
Days of potamophase	Number of days in potamophase.
Days of limnophase	Number of days in limnophase.
Elasticity	Ratio between the intensity of the potamophase(s) and the intensity of the limnophase(s) in the period.
Connectivity	Ratio between the number of days in potamophase and the number of days in limnophase.
Fraction of potamophase	Ratio between the duration (days) of the potamophase(s) and the duration (days) of the period considered.
Number of pulses	Quantity of complete pulses; cycles of potamophases and limnophases (or vice-versa) in the period.
Timing	Month when flood started. To obtain a continuous variable, we set October as the beginning of a hydrological cycle. If a flood started during 1-15 October, it was assigned the value 1; if a flood started between 16-31 October, it was assigned the value 2. A timing of 6 indicates that a flood started between 15-31 December.

adhesive oocytes. They exhibit extensive parental care, and the construction of nests is common; some species may transport the eggs adhered to the body. This group may be classified in the “equilibrium” strategy described by Winemiller (1989);

- iii) Short-distance migratory or sedentary species with internal fertilization: they present relatively low fecundity and medium-sized eggs and usually protect their offspring. Some species present sexual dimorphism and/or mating rituals related to spawning behavior. All species in this group presented external development of eggs; and
- iv) Long-distance migratory species with external fertilization: species that undergo long-distance longitudinal migrations for spawning (more than 100 km). They use more than one habitat during their lifespan: adults migrate to headwaters for spawning, and juveniles inhabit lagoons in the lower parts of rivers. Species in this group are usually large sized, with total and seasonal spawning, high fecundity, small oocytes and fast embryogenesis. Eggs are free and easily dispersed by river flow. According to Winemiller (1989), they can be classified in the strategy “periodic”.

The effects of the hydrological regime variations (PCA scores) on fish assemblages attributes (species richness, abundance (CPUE) and Simpson Diversity Index) in each river (factor) were evaluated through analysis of covariance (ANCOVA). As the effect of the hydrological variation may be distinct among rivers, we calculated the interaction between the factor (river) and the covariates (assemblage attributes). Model coefficients were used to evaluate the effect of hydrological variation on assemblage attributes (slope) and mean differences in the attributes among rivers (intercept) over the studied period. To evaluate possible spatial and temporal variations in fish assemblages attributes, which could explain any pattern found, we plotted the mean (\pm standard error) of each variable over the study period.

3. Results

3.1. The ichthyofauna of the Upper Paraná River floodplain

During the studied period, 137 species were captured, belonging to eight orders, 30 families and 86 genera. All species and their classifications are listed in <ftp://ftp.nuvelia.uem.br/publications/appendices/> according to Nelson (2006) for the categories until order and Reis et al. (2003) for families, subfamilies and the sequence of listed species, except Clariidae, which follows Eschmeyer (1998).

Fish species richness in the studied stretch of the floodplain (526,000 ha; 0.6% of the Paraná basin) represents 22% of the total richness of the upper Paraná basin. Compared with the entire biome (Mata Atlântica;

136 × 10⁶ ha), the floodplain harbors 50% of the total number of species already registered.

3.2. Variations of the hydrologic regime

Variations in the hydrometric attributes calculated using the PULSO software (FITRAS) for the Ivinheima and Paraná Rivers over the studied period were distinct (Figure 2). The intensities of potamophase and limnophase presented similar tendencies (Figure 2a and 2b, respectively). Similarly, we observed monotonic tendencies in the number of days in potamophase for the Ivinheima and Paraná Rivers (Figure 2c), with higher values in 1993 and lower values in 2000, years influenced by climatic events (El Niño and La Niña, respectively). Drier years were registered in the Paraná River after 2000 (Figure 2d), subsequent to the La Niña period and the closure of Porto Primavera Dam.

The Ivinheima River presented higher values of annual elasticity (Figure 2e) between 1987 and 1992 when compared to the Paraná River. After the year 2000, both rivers presented similar trends until 2003, characterized by the absence of pronounced peaks. Connectivity of the Paraná River was great in 1993, and after 2000 annual values of this attribute drastically decreased, increasing again in 2005 and 2007 (Figure 2f). The Ivinheima River presented peaks in 1993, 2002, 2005 and 2007. For the fraction of potamophase, the rivers presented similar trends (Figure 2g). There were no inundations in the Paraná and Ivinheima Rivers in two years each (Paraná: 2001 and 2004; Ivinheima: 2000 and 2003) (Figure 2h), and a greater number of pulses occurred in 1987 (Ivinheima), 1988, 1992 and 2006 (Paraná). Finally, the floods were most likely to occur in October and December.

Three axes of principal components analysis (PCA) were retained for interpretation. Together, these axes explained 82.5% of the data variability (hydrometric attributes; Table 2). The first axis (PCA1) represented a gradient of duration and connectivity of floods; the largest floods were associated with the timing of inundation. The second axis (PCA2) represented a gradient of intensity and duration (amplitude) of inundations. Finally, PCA3 was related to the number of pulses, indicating a gradient of disturbances (Table 2).

3.3. Spatial and temporal variations in the attributes of the fish assemblage and relationships with the hydrologic regime

Mean annual species richness was related to PCA1 ($F = 17.19$; $p < 0.001$), indicating that there was an increase in the number of species in the years with longer floods and with greater connectivity, except in the Ivinheima River, where richness was not related to PCA1 ($F = 2.61$; $p > 0.05$; Figure 3a). The Paraná River presented lower mean annual species richness (intercept = 17.21; $t = 22.07$; $p < 0.001$) as compared to the Ivinheima and Baía Rivers during the studied period. Total CPUE was also related to PCA1 ($F = 6.55$;

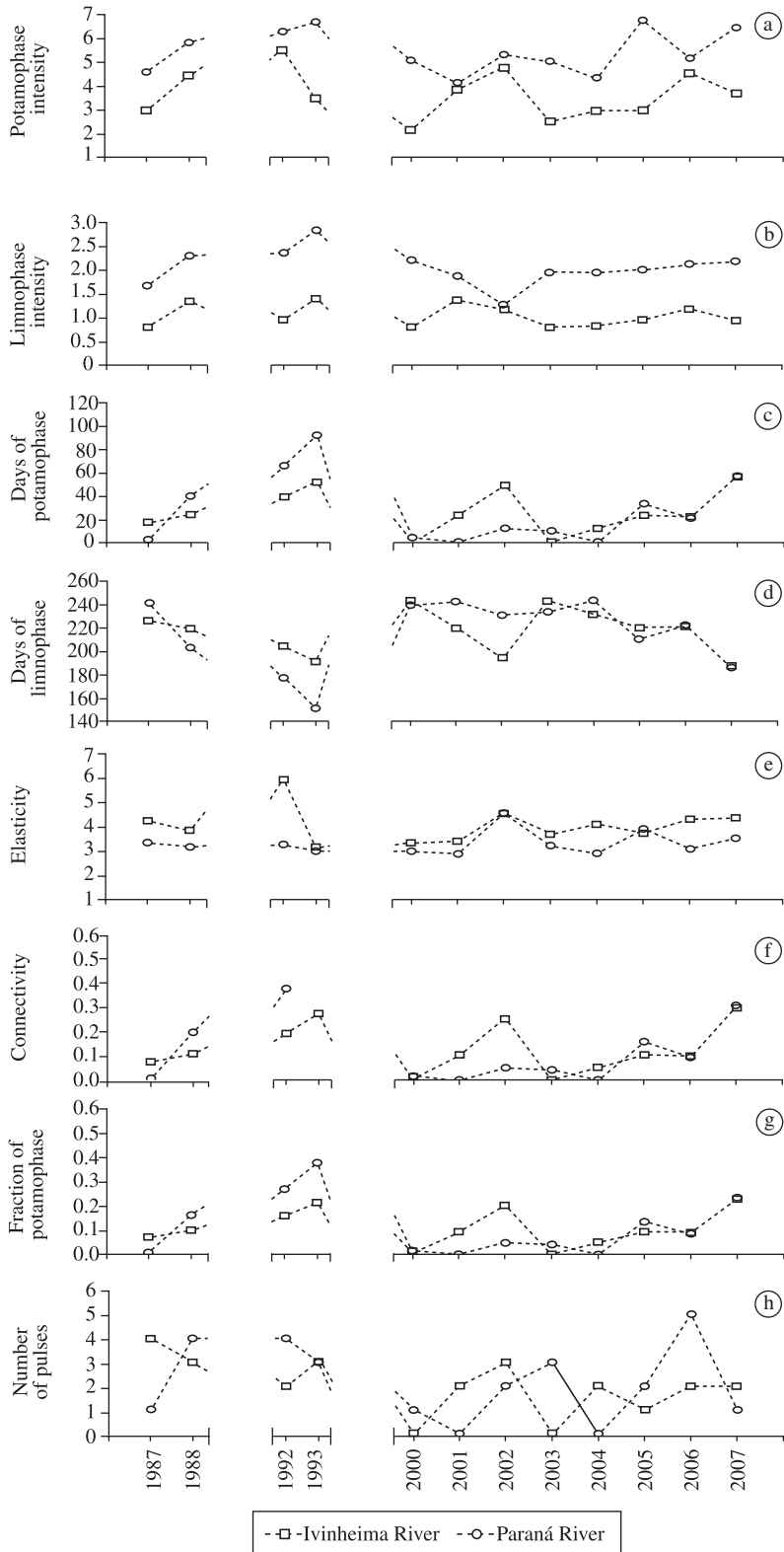


Figure 2. Annual variations in hydrometric attributes: a) intensity of potamophase; b) intensity of limmophase; c) days of potamophase; d) days of limmophase; e) elasticity; f) connectivity; g) fraction of potamophase; and h) number of pulses in the Ivinheima and Paraná Rivers.

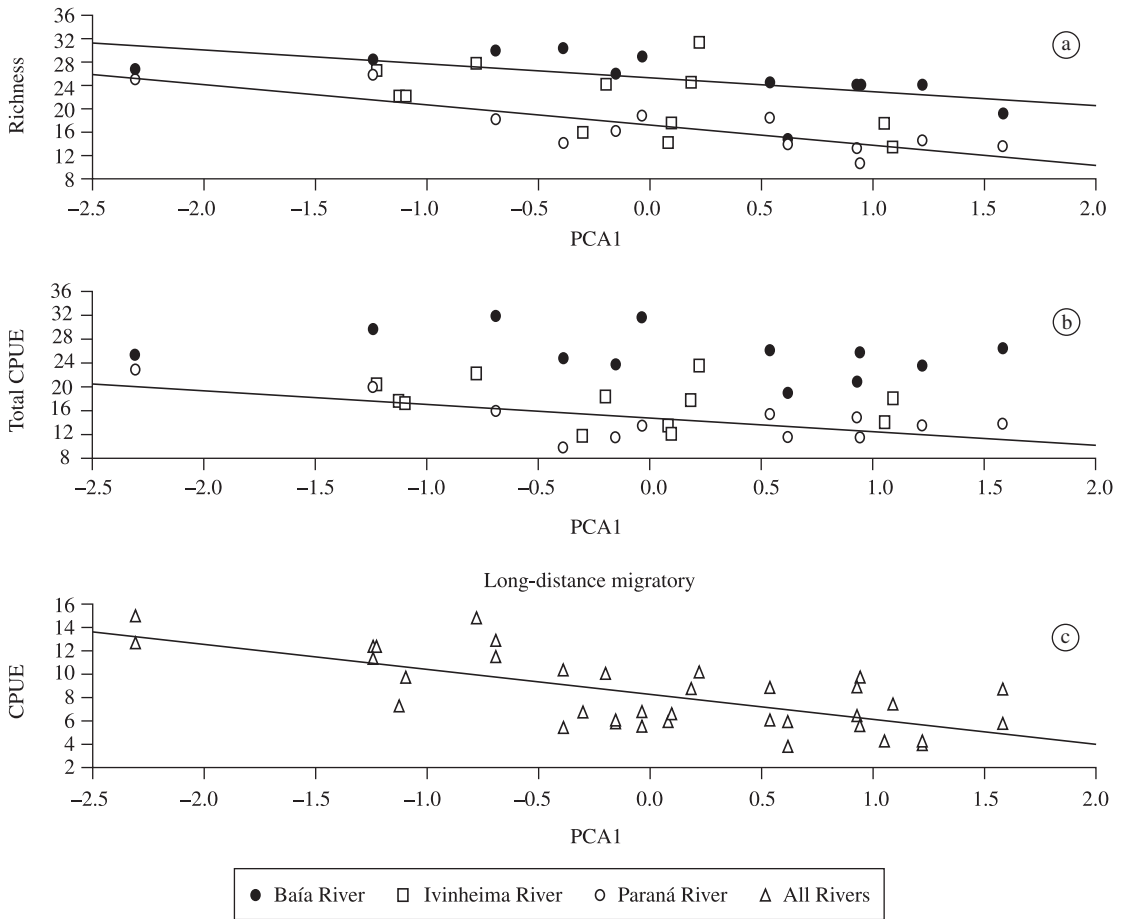


Figure 3. Relationships between species richness (Richness; a), total catch per unit effort (b; CPUE, square root transformed), and CPUE of the long-distance migratory species (c; square root transformed) and hydrological regime (PCA scores). The adjusted lines represented significant relationships.

Table 2. Correlations (coefficients of structure or eigenvectors) between the hydrometric attributes of the Ivinheima and Paraná Rivers with the three first principal components (PCA1, PCA2 and PCA3).

Variables	PCA1	PCA2	PCA3
Intensity of potamophase	-0.21	-0.94	0.20
Intensity of limnophase	-0.18	-0.89	0.20
Days of potamophase	-0.96	0.20	0.15
Days of limnophase	0.96	-0.20	-0.16
Elasticity	-0.19	-0.71	-0.03
Connectivity	-0.94	0.25	0.18
Fraction of potamophase	-0.96	0.20	0.15
Number of pulses	-0.61	0.04	-0.55
Timing	-0.54	-0.47	-0.13
Eigenvalues	4.602	2.638	1.011
Explained variation (%)	46.0	26.4	10.1

$p < 0.05$; Figure 3b), but this relationship was significant only for the Paraná ($F = 8.68$; $p < 0.05$). The Baía River presented higher mean annual CPUE (intercept = 26.4; $t = 23.37$; $p < 0.001$) as compared to the Ivinheima and Paraná. Among the reproductive groups, only the CPUE of long-distance migratory species was related to PCA1 ($F = 28.19$; $p < 0.001$; Figure 3c), but the mean values were similar among rivers (equal intercept). Interactions (factor and covariates) were not significant in all ANCOVAs.

Spatial and temporal variations in species richness were similar in all rivers, with peaks in 1992 (Baía: 30; Ivinheima: 29; and Paraná: 26 species) and 2005 (Baía: 25; Ivinheima: 32), except for the Paraná River, which presented low variation of annual richness after 2000 (Figure 4a). The Simpson diversity index did not present a clear pattern of variation (Figure 4b).

Greater values of mean total CPUE were registered in 1992 (Baía: 839 individuals/1000 m² of gillnet

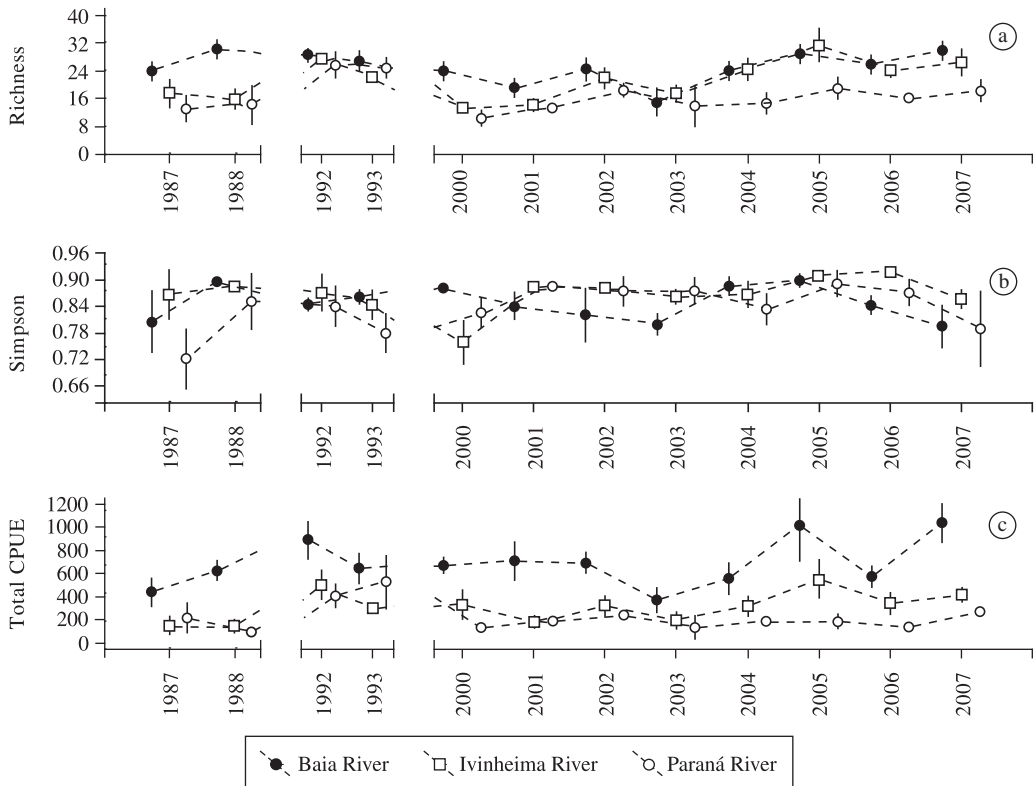


Figure 4. Annual means (\pm standard error) of a) species richness, b) Simpson Diversity Index and c) total catch per unit of effort (CPUE); for the Baía, Ivinheima and Paraná Rivers.

in 24 hours; Ivinheima: 504; Paraná: 408) and 2005 (Baía: 1017 individuals/1000 m² of gillnet in 24 hours; Ivinheima: 554; Paraná: 187) for the three rivers (Figure 4c). Considering the CPUE of each reproductive group, we verified that sedentary species with and without parental care and internal fertilization did not present any relationship with the hydrometric attributes (summarized in the axes of the PCA retained for interpretation). However, CPUEs of both groups were higher in the Baía River (Figures 5a, b, c). Greater values of the CPUE for long-distance migratory species were registered in 1992 and 1993, drastically decreasing after 2000. Some increases were verified in the Ivinheima River in 2004 and in all rivers in 2007 (Figure 5d). *Prochilodus lineatus* (Valenciennes, 1836) was the most abundant long-distance migratory species in all rivers in 1992, 1993 and 2004, whereas in 2007, in the Paraná River, *Rhinelepis aspera* Spix and Agassiz, 1829 was the most abundant species of this reproductive guild.

4. Discussion

Floods promote the enlargement of physical space available to colonizers, decrease fragmentation between habitats and environments and increase the availability of resources (e.g., food and shelter). These changes enable environments to harbor greater species richness and

abundance (Junk et al., 1989; Agostinho et al., 2004b). In addition, flood pulses homogenize the environmental conditions and fauna of habitats, ensuring maintenance of regional diversity (Thomaz et al., 2007). For the riverine environments of the upper Paraná floodplain, greater values of species richness and abundance were associated with years of longer floods and with greater connectivity, which support the considerations described above. The increased structural complexity of the environment caused by flooding of marginal areas, in years with large floods, increases colonization rates of fish and invertebrates. The latter is an important feeding resource for the former (Agostinho et al., 2001). In an opposite way, the absence of prolonged floods may lead to stressing environmental conditions (abiotic and biotic), reducing richness and species abundance (Junk et al., 1989; Agostinho et al., 2004b; Fernandes et al., 2009). Additionally, incorporation of large amounts of organic matter biomass by the aquatic environment during flood events may restrict the availability of oxygen, causing migration of several fish species to the main channel of the river. This leads to increased richness and abundance of fish in these environments (Agostinho and Julio Jr., 1999).

Despite the relationship between richness and abundance of fish with the variations in the hydrologic regime, species diversity was not affected by this factor. Similar results were described by Agostinho et al. (2001)

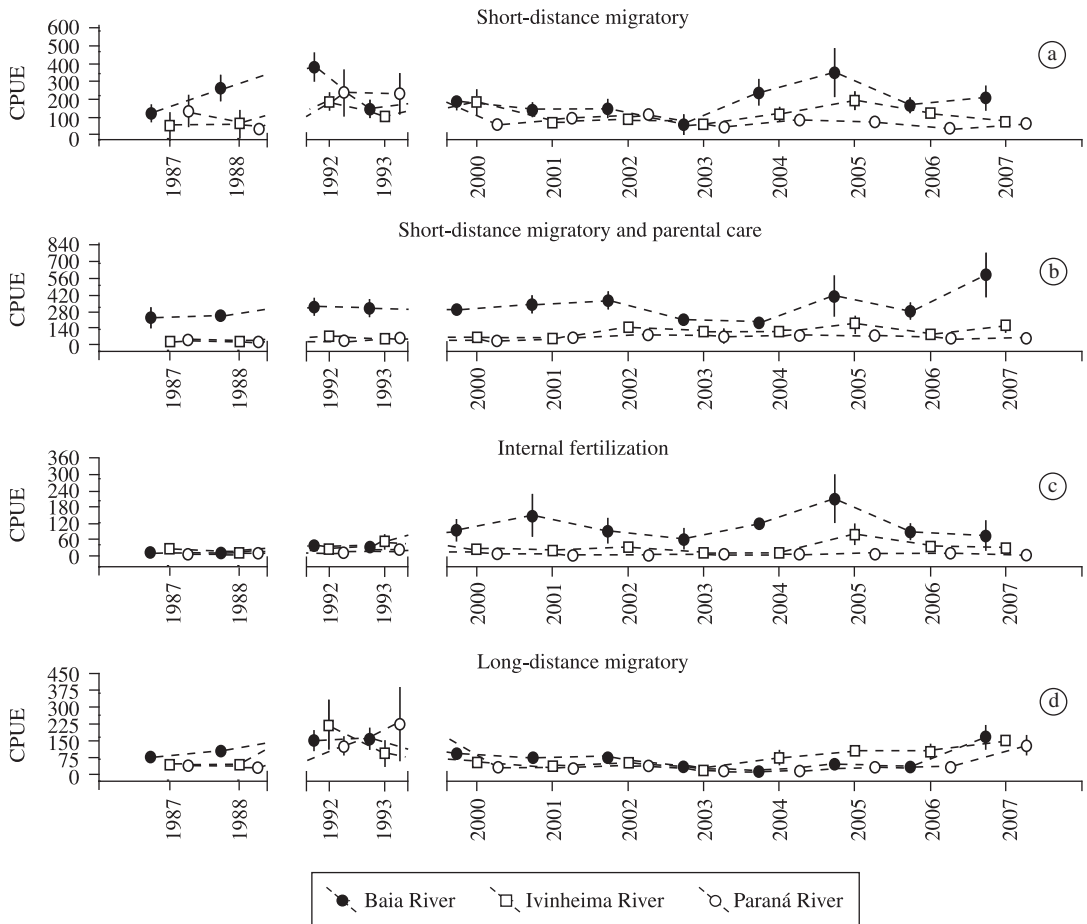


Figure 5. a) Annual means (\pm standard error) in CPUE of short-distance migratory species without parental care; b) CPUE of short-distance migratory species with parental care; c) CPUE of species with internal fertilization; and d) CPUE of long-distance migratory species for the Baía, Ivinheima and Paraná Rivers.

for distinct environments (rivers, lagoons and channels) of the upper Paraná River floodplain. For these authors, the diversity index may be low due to the dominance of some species resulting from the high number of juveniles of some long-distance migratory species (such as *P. lineatus*) in years of intense floods. When water starts receding from the floodplain, juveniles concentrate in the river channel and other remaining water bodies.

In concordance with Agostinho et al. (2001), our findings demonstrate that the flood regime seems to distinctly affect the abundance of the different reproductive groups. Sedentary species with and without parental care and internal fertilization were less dependent on the flood regime. Agostinho et al. (2004b) discuss that species of these reproductive groups, usually small-sized, seem to experience more favorable reproductive outcomes in prolonged dry conditions, but their recruitment may be prejudiced by low river levels, possibly due to higher predation. However, several species of these groups present a set of adaptive characteristics (presence of accessory respiratory organs, parental care) that favor

their persistence in such environments during drier periods (Agostinho et al., 2007b), which may be reflected in their abundance. An example of this is the high abundances of *Loricariichthys platymetopon* Isbrücker and Nijssen, 1979 and *Hoplias* spp. in all rivers during the entire study period, especially in the Paraná River, where the variation in the water level was less pronounced.

The abundance of long-distance migratory species was positively related to the duration of floods and to connectivity in all studied rivers. Gomes and Agostinho (1997) analyzed the correlation between the attributes of the hydrological cycle and the recruitment of *P. lineatus*, and they concluded that the duration of the floods was the most important variable. The results of this study indicate that this tendency may be extended to the other long-distance migratory species. It may be highlighted that the occurrence of high water levels during summer, which has been related to the spawning success of migratory species (Godoy, 1975; Agostinho et al., 1993; Vazzoler, 1996), may be less important to recruitment of juveniles into adult stocks if the floods have short du-

rations (Agostinho et al., 2004a). However, long-lasting floods are more effective if they happen during summer and autumn, when most of the species spawn; the prolonged supply of shelter and food in this situation would result in larger sized individuals that, when the water recedes, would be less exposed to aquatic and terrestrial predators (Agostinho et al., 2005, Suzuki et al., 2009). The reduction of the stress period linked to dry conditions when floods are long also favors juveniles. Additionally, long-lasting floods result in increased dispersion of migratory species, and the increase in connectivity allows colonization of more patches, favoring persistence through metapopulation dynamics (Gubiani et al., 2007).

The detected variations in the annual hydrological cycle and their reflection in the fish assemblage of the Paraná River seem to be a combined effect of natural (El Niño Southern Oscillation - ENSO) and artificial (discharge control prompted by dams located upstream) events. Extreme climatic events affect fish assemblages due to their influence on the variation of the hydrological regime, as has been widely demonstrated for estuaries (Garcia et al., 2004) but still not intensely evaluated for inland waters.

During the studied period, only the extreme events of El Niño (1991-1992 and 2006-2007) resulted in relevant floods, which positively affected species richness and abundance of fish (1992 and 2007). Moderate effects on fish may be verified when reasonable events of ENSO happened after extreme years. This can be explained by the low capacity of dams to retain water and, consequently, less discharge control. The only extreme event verified in the period that did not positively affect the ichthyofauna was in 1997-1998. This event seemed to be neutralized by the filling of Porto Primavera Reservoir (December 1998 to January 2000; 225,000 ha). Studies on the distribution of eggs and larvae of long-distance migratory fish conducted below Porto Primavera Dam revealed high densities in this period, especially in tributaries (Sanches et al., 2006). However, the absence of connectivity between the river channels and the adjacent floodplain (nurseries) did not allow their development, negatively affecting recruitment of these species (Agostinho et al., 2004a).

On the other hand, the attributes of the annual hydrological cycle showed that years with regular floods were similar to those of La Niña (1988-1989; 1998-1999; 1999-2000; 2000-2001), with similar effects on fish assemblages, indicating a tendency of homogenization in the results between different annual periods under the effect of interannual discharge regulation by dams. Thus, regulation of hydrometric levels by dams located upstream leads, in most of the studied years, to a hydrological condition similar to drought, which is only altered in periods of extreme ENSOs. This condition mainly affects the species with greater dependence on the flooded habitats of the floodplain and the reduction in the abundance of long-distance migratory species. The data from the

year 2000 corroborate this hypothesis. Studies conducted by Abujanra et al. (2009) and Luz-Agostinho et al. (2009) indicate that the natural alternation between dry and flood years is fundamental to these species. During dry years, species improve their nutritional conditions (reserves), which may be used in subsequent years for successful migration and spawning.

The presence of large undammed tributaries, such as the Ivinheima, in the floodplain ensures spawning success and the maintenance of migratory species in the area (Agostinho et al., 2007a; Antonio et al., 2007). The increase in larvae density of long-distance migratory species in the Ivinheima River demonstrates the importance of this river to spawning in the upper Paraná River floodplain (Baumgartner et al., 1997; Nakatani et al., 1997; Sanches et al., 2006). In this sense, the creation of conservation units such as the "Parque Estadual do Ivinheima" (Ivinheima State Park) favors the integrity of the ecosystem and the maintenance of regional diversity. However, the regulation of the Paraná River discharge has relevant influences on the seasonal level fluctuations of the lower stretches of the Ivinheima River, where the main areas of initial development are located (Souza Filho, 2009).

Despite human occupation of part of the upper Paraná River floodplain and the regulation of the hydrological regime by dams located upstream, this area still plays an important role in maintaining regional diversity. The conservation of fish diversity, especially for long-distance migratory species, in the last stretch of running water of the upper Paraná River within Brazilian territory depends on the integrity of the land-water ecotone represented by the floodplain. Nevertheless, to maintain the integrity of the floodplain, it is necessary to establish a better scheme to operate the dams upstream. The artificial control of the floods by the dams appears to have great potential to improve recruitment success. However, information on the biology of the species involved and a profound knowledge of their specific responses to the inundation regime are fundamental to determining how the artificial control of discharge should be performed. Therefore, detailed studies are necessary to evaluate the biological needs of threatened species and to identify the mean water level, duration and timing of floods that stimulate spawning and ensure the viability of eggs and larvae. To achieve these goals, long-term ecological studies that consider the evaluation of several hydrological scenarios and the responses of species to these variations are needed.

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