Fish assemblages of tropical floodplain lagoons: exploring the role of connectivity in a dry year

Ana Cristina Petry*, Angelo Antonio Agostinho** and Luiz Carlos Gomes**

Irregular rainfall and pronounced reductions of the hydrometric level in the year 2000 resulted in drastically altered hydrological connectivity of lentic environments in the upper Paraná River floodplain. The objective of the present work was to examine spatial and temporal patterns of fish assemblage attributes and structure in relation to limnological variables associated with hydrological connectivity. Fish were collected quarterly by seining in the marginal areas of 15 lagoons belonging to two biotopic categories (connected and disconnected). Variation in assemblage composition reflected the degree of hydrological connectivity. Values of assemblage attributes (species richness, density and biomass) were significantly lower in connected lagoons than in disconnected lagoons. Significantly higher values of species richness and biomass were recorded in November than in August. Rare species had the greatest effect on observed patterns in fish assemblage ordination (DCA). Observed patterns of variation in assemblage attributes were directly correlated with factors related to hydrological connectivity, such as depth, resources (zooplankton and chlorophyll *a*) and nutrients (total phosphorus).

A irregularidade das chuvas e as reduções pronunciadas no nível hidrométrico alteraram drasticamente a conectividade hidrológica dos ambientes lênticos da planície de inundação do alto rio Paraná em 2000. O presente trabalho teve como objetivo examinar os padrões espaciais e temporais dos atributos e da estrutura das assembléias de peixes em relação a variáveis limnológicas associadas à conectividade hidrológica. Os peixes foram coletados em arrastos trimestrais, na área marginal de 15 lagoas, pertencentes a duas categorias de biótopos (lagoas conectadas e desconectadas). Variações na composição das assembléias refletiram o grau de conectividade hidrológica. Os valores dos atributos das assembléias (riqueza de espécies, densidade e biomassa capturada) foram significativamente menores em lagoas conectadas em relação a lagoas desconectadas. Valores significativamente elevados de riqueza de espécies e biomassa capturada foram registrados em novembro em relação a agosto. Espécies raras tiveram os maiores efeitos nos padrões observados na ordenação das assembléias de peixes (DCA). Padrões observados na variação dos atributos das assembléias foram diretamente correlacionados a fatores relacionados à conectividade hidrológica, como a profundidade, os recursos (zooplâncton e clorofila *a*) e os nutrientes (fósforo total).

Key words: Neotropical fishes, fish assemblage structure, hydrological connectivity, floodplain.

Introduction

The dynamic nature of the hydrological regime in riverfloodplain systems directly affects connectivity, especially between superficial compartments of the river channel and adjacent areas. High hydrometric levels result in lateral floodplain expansion and greater connectivity by forming temporary waterbodies and increasing water volume in permanent lagoons. Disconnection occurs with reduction of the hydrometric level, in an asynchronous manner between biotopes as a function of topographical and morphometric factors (e.g. lagoon shape), producing a spatially heterogeneous landscape. The intensity and duration of the disconnection process can strongly affect chemical, physical and biological characteristics of the aquatic environment (Amoros & Roux, 1988; Tockner *et al.*, 1999).

^{*}Programa de Pós-Graduação em Ecologia de Ambientes Aquáticos Continentais. e-mail: anapetry@bol.com.br

^{**}Departamento de Biologia, Nupélia, Universidade Estadual de Maringá, Av. Colombo, 5790, 87020-900 Maringá, PR, Brazil. e-mail: agostinhoaa@nupelia.uem.br; lcgomes@nupelia.uem.br

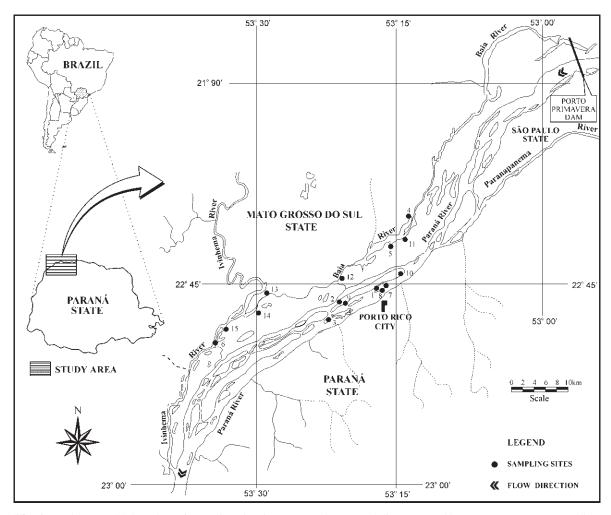


Fig. 1. Study area with location of sampling sites in connected (1-6) and disconnected lagoons (7-15): 1 (Leopoldo), 2 (Manezinho), 3 (Pombas), 4 (Maria Luíza), 5 (Porcos), 6 (Ipoitã), 7 (Clara), 8 (Genipapo), 9 (Osmar), 10 (Pousada), 11 (Aurélio), 12 (Traíra), 13 (Cervo), 14 (Jacaré), 15 (Capivara).

Past studies in the Paraná River floodplain revealed direct relationships between the hydrological dynamic and limnological variables, with spatial heterogeneity in the dry season and homogeneity during flood periods (Agostinho et al., 1995; Thomaz et al., 1997). Fish assemblage structure can vary drastically even between adjacent biotopes, depending on intrinsic factors of each species in relation to environmental factors, such as accessibility, habitat quality and resources availability (Winemiller et al., 2000; Súarez et al., 2001; Okada et al., 2003). Lentic environments of the upper Paraná River floodplain are preferential habitats for many small-sized and sedentary species, and are important nursery areas for migratory species (Agostinho et al., in press). The maintenance and integrity of these biotopes, however, has been seriously threatened by control of the hydrological regime by dam operations upstream (Agostinho & Zalewski, 1996; Agostinho et al., in press).

Prior to 1998 the hydrological regime of the Paraná River was strongly seasonal with pronounced wet and dry periods (Agostinho *et al.*, in press). In 2000, the floodplain did not experience sustained inundation (< 10 days in February and in late March) due to scarcity of rainfall and outflow regulation of the Paraná River and its main tributaries. Consequently, the hydrological connectivity of most lentic environments of the floodplain was not re-established in what typically would be the high water period. This atypical condition allowed us to assess the effect of the hydrological connectivity degree upon the fish fauna. Therefore, in this study we (*i*) evaluate attributes (species richness, density and biomass) and structure (composition and abundance) of fish assemblages in connected and disconnected floodplain lagoons both spatially and temporally, and (*ii*) assess relationships between observed attributes and structure of the fish assemblages and abiotic and biotic variables directly related to hydrological connectivity in a dry year.

Material and Methods

Study area. The Paraná River begins in the central Brazilian plateau and drains into the La Plata River after a journey of

approximately 4,695 km south. In Brazilian territory, only the stretch between Porto Primavera Dam and Itaipu Reservoir (230 km) still has an extensive floodplain on its west margin (≤ 20 km wide; Fig. 1). Species composition and abundance of several communities (zooplankton, phytoplankton, benthic invertebrates, fishes and macrophytes) varies among the main aquatic and terrestrial biotopes (river channels, secondary channels, permanent and temporary lagoons, wetlands, alluvial plain and islands) of the upper Paraná River floodplain (Agostinho *et al.*, 1995; Agostinho *et al.*, in press). In addition to resident fish species that spend their entire life cycle in the floodplain, many migratory species use the floodplain only during a certain stage of the life cycle (Agostinho *et al.*, 1993).

The upper Paraná River floodplain therefore supports biodiversity in other regions as well (Agostinho & Zalewski, 1996).

Prior to 1998, when filling of Porto Primavera Reservoir began, the hydrological regime of the Paraná River was characterized by strong seasonal variation with pronounced flood (November to May) and dry (June to October) periods. In 2000, after completion of Porto Primavera, the hydrometric level of the Paraná River was much lower than in the previous decade due to highly variable rainfall coupled with outflow control by the dam (Fig. 2). Reduction of the flood intensity resulted in decreased hydrological connectivity among most lagoons located in fluvial islands and in the floodplain.

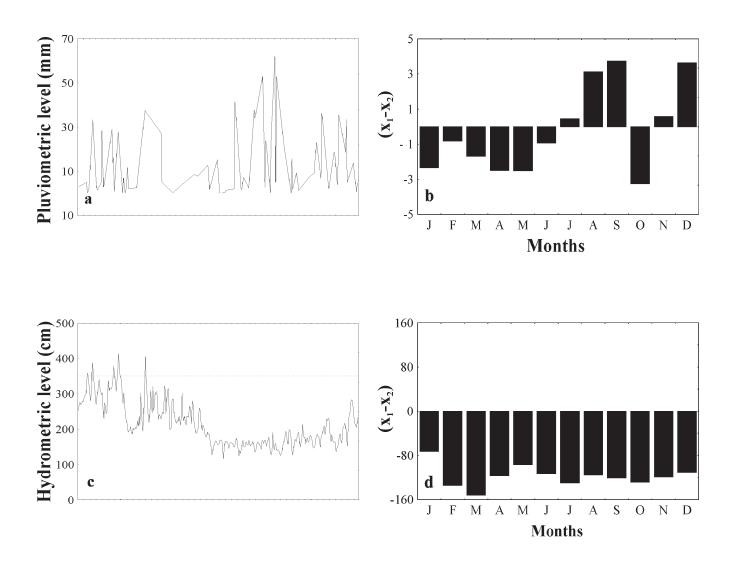


Fig. 2. Daily variation of pluviometric (a) and hydrometric levels (c) of the Paraná River in 2000, measured at Porto São José municipality, and difference between mean monthly pluviometric (b) and hydrometric levels (d) in 2000 (x_1) and the last 10 years (x_2). Data supplied by DNAEE (Departamento Nacional de Águas e Energia Elétrica). Dashed line indicates water level required for initial inundation of the floodplain (Veríssimo, 1994).

Six connected and nine disconnected lagoons of the upper Paraná River floodplain (22°35'-22°55'S; 53°10'-53°40'W) were sampled in February, May, August and November 2000. Connected lagoons were permanently linked to the main river by channels varying from 5 to 80 m long and 5 to 35 m wide. Disconnected lagoons were generally more distant from the main river channel (10-500 m) and were isolated from March 1999 throughout the study period (although very short duration connection may have occurred for lagoons close to the river channel during the brief events mentioned previously, see Fig. 2). Lagoons were generally elongate in shape with surface area ranging between 0.5 and 15 ha. Substrates consisted of either sand or mud, and the vegetation was composed of free-floating macrophytes (e.g. Eichhornia crassipes (Mart.) Solms) in open water areas and emergent plants (e.g. Polygonum sp.) in littoral zones.

Sampling. Fishes were collected by diurnal seining (20 m x 2.4 m, 0.5 cm mesh) in marginal areas of each lagoon. All individuals were identified, enumerated, weighed (g) and classified according to Britski *et al.* (1999). Voucher specimens were deposited in the Ichthyological Collection of Núcleo de pesquisas em Limnologia, Ictiologia e Aqüicultura (Nupélia), Universidade Estadual de Maringá. We standardized the data by calculating fish density (number of individuals per 100 m²) and biomass (total g per 100 m²). Limnological data (water temperature, depth, turbidity, pH, conductivity, dissolved oxygen, total nitrogen, total phosphorus, chlorophyll *a*, and zooplankton density) from each lagoon during the sampling period were provided by the Limnology and Zooplankton Laboratories of Nupélia.

Data Analysis. Spatial (disconnected or connected) and temporal (February, May, August, November) variation in assemblage attributes (species richness, density and biomass) were tested by two-way ANOVA. Patterns of fish assemblage structure were evaluated using detrended correspondence analysis (DCA) performed with density data. Limnological variables were summarized by principal components analysis (PCA) using the program PC-ORD 3.0 (McCune & Mefford, 1997). All limnological data excluding pH were $\log_{10}(x + 1)$ transformed prior to analysis. Spatial and temporal variation in axes scores from DCA and PCA (only axes with eigenvalues > 1; criterion of Kaiser-Guttman, Jackson, 1993) were tested by two-way ANOVA.

Pearson correlations were performed between PCA axes scores and species richness, density, biomass, and axes scores from DCA to investigate the potential influence of limnological variables on fish assemblage attributes and structure. Fish assemblage attributes and DCA axes scores were transformed [log (log₁₀) or square root (sqrt)] when assumptions of normality (Shapiro-Wilk's Test) and homocedasticity (Levene's Test) were not met. Tukey's Test was applied when significant differences were detected between averages. These analyses were performed using the program StatisticaTM (StatSoft, 1996). Significance level in all tests implies P < 0.05.

Results

In total 57 fish species were recorded, of which 32 (56%) were shared between connected and disconnected lagoons during at least one sampling event. Although approximately half of the species were shared among biotopes, only 8 species (14%) were exclusive to connected lagoons, whereas 17 species (30%) were exclusive to disconnected lagoons. Representatives from the order Characiformes, mainly of them small-sized species with short life cycles, dominated the samplings. The species Serrapinnus notomelas, Astyanax altiparanae, Steindachnerina insculpta and Moenkhausia sanctaefilomenae, were abundant (> 66% from the total density) and broadly distributed between both biotopes (Appendix 1). Approximately half of the total biomass (46%) is made up of these small species. Twenty-three species (40%)were recorded during all months, while 10 species (18%) were collected in only one month (six in February, two in May and August). In general, density and biomass were highest in November due to an increase in the abundance of mediumsized species such as Loricariichthys platymetopon, Hoplias aff. malabaricus and S. insculpta.

Spatial and temporal variations. Because ANOVAs applied to the fish assemblage attributes did not present significant interactions, we were able to evaluate the influence of each factor independently (Table 1). Connected lagoons presented significantly lower values of species richness, density and biomass than disconnected lagoons (Fig. 3; Table 1). Significantly higher values of species richness were recorded in February and November than in August (Fig. 3a; Table 1). Biomass was significantly higher in November than in August (Fig. 3c; Table 1).

DCA elucidated spatial and temporal patterns in the fish assemblages. ANOVA identified significant differences between biotopes on DC1, and between months for the second axis (February and May; February and August) (Fig. 4, Table 1). Although samples were dominated by a few common taxa (Appendix 1), rare species (densities represented less than 5% of the total) had the greatest effect on observed patterns in the ordination. Species restricted to (such as Hyphessobrycon sp.) or most abundant in (such as Hemigrammus marginatus) connected lagoons were positively correlated with DC1, whereas species restricted to disconnected lagoons, such as Hoplerythrinus unitaeniatus, Synbranchus marmoratus and Gymnotus spp, were negatively correlated with DC1. Species with higher densities in February, such as Bryconamericus stramineus, were positively correlated with DC2, whereas species captured in lower densities in August, especially H. marginatus, were negatively correlated with DC2 (Fig. 4). Samples collected in May from disconnected lagoons located near Paraná River main channel (< 30m), such as Clara lagoon, Genipapo lagoon and Osmar lagoon, were positively correlated with DC1, possibly due to changes in the fish assemblage resulting from connectivity during the brief inundation in late February (Fig. 4).

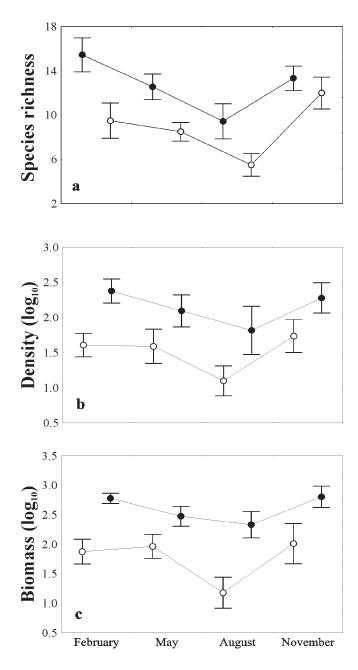


Fig. 3. Average values (\pm standard error) of species richness (a), density (b), and biomass (c) in connected (\circ) and disconnected (\bullet) lagoons.

Relationship between the fish assemblage and limnological variables. In general upper Paraná River floodplain lagoons were shallow, with moderately oxygenated water and trophic state varying from hiper- to eutrophic (based on total phosphorus concentrations; criterion of Wetzel, 1981). Maximum values for all limnological variables measured (excluding depth) were recorded in disconnected lagoons (Table 2). Additionally, disconnected lagoons were more variable than connected lagoons for dissolved oxygen, total nitrogen, total phosphorus, chlorophyll *a*, and zooplankton density (Table 2).

The first three axes from PCA (PC1 eigenvalue = 2.27; PC2 eigenvalue = 1.74; PC3 eigenvalue = 1.39) were retained for interpretation and together explained 54.03% of the variability in limnological factors, with PC1 alone explaining 22.74% of the variability. Depth was positively correlated with PC1 (eigenvector = 0.34), whereas zooplankton, total phosphorus and chlorophyll a (eigenvectors of 0.53, 0.44, and 0.36 respectively) were negatively correlated. Turbidity was positively correlated (eigenvector = 0.43), whereas pH (eigenvector = 0.54) was negatively correlated with PC2. Dissolved oxygen (eigenvector = 0.52) was positively correlated with PC3, whereas water temperature (eigenvector = 0.52) was negatively correlated. ANOVAs applied to PCA scores did not present significant interactions therefore we were able to evaluate the influence of each factor inde pendently (Table 3). Significant differences were observed between biotopes and months (August and November) on PC1, and between months (February and August; November and August) on PC3 (Table 3).

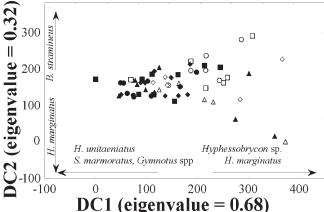


Fig. 4. DCA ordination of sample sites by month in connected [February (\circ), May (\triangle), August (\square), November (\diamond)] and disconnected lagoons [February (\bullet), May (\blacktriangle), August (\blacksquare), November (\bullet)]. Arrows indicate the direction of influence of species in the ordination.

A significant correlation was found only between PC1 and fish assemblage attributes; suggesting a strong relationship between limnological variables (depth, zooplankton, total phosphorus and chlorophyll*a*) and species richness, density and biomass of the ichthyofauna in upper Paraná River floodplain lagoons (Fig. 5).

Discussion

Fish assemblages of lentic environments of the upper Paraná River floodplain during a dry year were dominated by opportunist species (*sensu* Winemiller, 1989), characterized by small size and short sedentary life cycles. Lower species richness, density and biomass were recorded in connected lagoons compared to disconnected lagoons, especially in August. Spatial and temporal variation in fish assemblage

Table 1. Results of two-way ANOVAs applied to attributes (species richness, density, and biomass) and structure (scores from DCA axes 1 and 2) of the fish assemblage. Letters (*a* and *b*) identify averages that differed significantly between months according to Tukey's Test (P').

Factors	df	MS	F	Р	P'				
					Feb	May	Aug	Nov	
Richness									
<u>B</u> iotopes	1	210.07	15.06	< 0.01					
Month	3	83.66	6.00	< 0.01	а	ab	b	а	
<u>B</u> x <u>M</u>	3	12.92	0.93	ns					
Error	52	13.95							
Density									
(\log_{10})									
<u>B</u> iotopes	1	5.80	12.91	< 0.01					
Month	3	0.94	2.10	ns					
<u>B</u> x <u>M</u>	3	0.06	0.14	ns					
Error	52	0.45							
Biomass									
(log 10)									
B iotopes	1	10.18	31.85	< 0.01					
<u>M</u> onth	3	1.23	3.85	0.01	ab	ab	b	а	
<u>B</u> x <u>M</u>	3	0.26	0.80	ns					
Error	52	0.32							
DC1									
(sqrt)									
Biotopes	1	145.10	12.77	< 0.01					
Month	3	0.18	0.12	ns					
<u>B</u> x <u>M</u>	3	7.98	0.70	ns					
Error	52	11.36							
DC2									
Biotopes	1	5609.00	2.89	ns					
<u>M</u> ontĥ	3	9482.33	4.88	< 0.01	а	b	b	ab	
$\overline{\mathbf{B}} \times \mathbf{M}$	3	3396.84	1.75	ns					
Error	52	1942.83							

structure was most strongly influenced by rare species. PCA distinguished connected and disconnected lagoons based on productivity (resources and nutrients). Fish assemblage attributes (species richness, density, and biomass) were correlated with PCA axes, while observed patterns of assemblage structure were not.

The absence of direct relation between patterns of fish assemblage structure and limnological variables (PCA axes) contrasts with results obtained in floodplains from other South American rivers. Differences in water transparency in lagoons of the Orinoco River (Rodríguez & Lewis Jr., 1997) and Araguaia River (Tejerina-Garro *et al.*, 1998) were correlated with patterns of fish species composition, due to differential predation effects of visually oriented piscivores in clearwater lagoons and piscivores adapted for low light in turbid lagoons. Upper Paraná River floodplain lagoons were characterized by low abundance of piscivorous species, with the exception of *H. aff. malabaricus*, which was broadly distributed between both biotopes.

We expected to observe extreme values of abiotic factors acting in detriment of the fish assemblages in disconnected lagoons. However, opportunistic species seem to have been

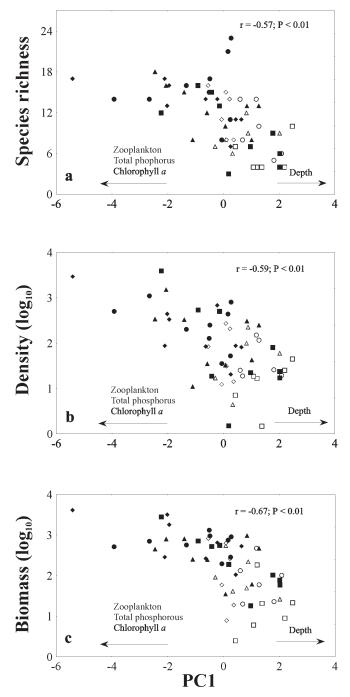


Fig. 5. Correlation between PCA axis 1 and species richness (a), density (b), and biomass (c) in connected [February (\circ), May (\triangle), August (\Box), November (\diamond)] and disconnected lagoons [February (\bullet), May (\triangle), August (\blacksquare), November (\diamond)]. Arrows indicate the direction of the limnological variables influence.

favored by the autogenic conditions that prevailed in most disconnected lagoons. Considering the strong relation found between limnological variables and fish species richness, density and biomass, two non-exclusive explanations are suggested. First, an increase in autogenic processes in disconnected lagoons support greater species richness, density and biomass. Those lagoons are shallower and the predominance of diel mixing increases productivity (Thomaz et al., 1997), as suggested by high total phosphorus and chlorophyll a concentrations. Second, a dilution effect due to permanent hydrological connectivity between connected lagoons and the Paraná River results in lower productivity and species richness, density and biomass. In the Paraná River basin nutrient concentrations are low (especially phosphate), because the Paraná River dilutes nutrient concentrations of environments connected to it (Thomaz et al., 1992; Agostinho et al., 1995), not following the general tendencies observed in temperate (Tockner et al., 1999) and other tropical floodplain systems (Junk et al., 1989). This is due to chains of reservoirs in the main channel and in its tributaries, which modify the hydrologic regime and retain nutrients and solids (Barbosa et al., 1999), negatively influencing the productivity of downstream areas. In recent work, Gomes et al. (2002) support the hypothesis that primary production (based on chlorophyll a concentration) in the Paraná River basin functions as limiting factor of fisheries vield.

In our investigation, limnological variables related to primary and secondary productivity were significantly correlated with fish assemblage attributes. Although we acknowledge correlation does not denote causation, productivity has been considered a reasonable hypothesis to explain patterns of diversity (Connell & Orias, 1964, but see Rosenzweig & Abramsky, 1993; Smith, 1996). This remains a broad and curious subject to be explored in more detail in the lentic environments of the upper Paraná River floodplain. Fish assemblage regulation by bottom up processes (Hanson & Leggett, 1982; Horne & Goldman, 1994; Scheffer, 1998) should be evaluated by future research utilizing controlled experiments designed to specifically test these hypotheses.

Acknowledgments

This work was supported by a grant and fellowship for the senior author (Proc. 132962100-4) from Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) and Pesquisas Ecológicas de Longa Duração (PELD). We thank Renata Rocha, Sidinei M. Thomaz, Cláudia C. Bonecker and Fábio A. Lansac-Tôha for concession of unpublished

Table 2. Limnological characteristics of connected and disconnected lagoons.

Limnological variables	C	Connected lagoo	ns	Disconnected lagoons			
	Min	Mean	Max	Min	Mean	Max	
Temperature (°C)	17.2	24.6	31.1	18.1	24.5	32.0	
Depth (cm)	25.0	111.3	250.0	10.0	90.7	200.0	
Turbidity (NTU)	2.6	11.9	34.2	0.6	29.6	217.0	
pH	5.8	6.5	7.2	5.7	6.5	8.2	
Conductivity (μ S/cm)	23.6	46.7	67.0	21.0	51.3	107.5	
Dissolved oxygen (mg/L)	2.3	5.4	8.0	0.4	4.5	8.1	
Total nitrogen (µg/L)	204.8	320.4	504.9	1.1	471.4	840.1	
Total phosphorus (µg/L)	13.5	33.5	71.7	14.8	92.6	296.5	
Chlorophyll a (µg/L)	2.3	11.1	37.3	0.0	22.4	129.7	
Zooplankton (ind/m^3)	5,785.7	72,327.4	373,078.0	9,612.4	304,189.3	2,531,666.7	

Table 3. Results of two-way ANOVAs applied to PCA scores. Letters (*a* and *b*) identify averages that differed significantly between months according to Tukey's Test (P').

Factors	df	MS	F	Р	P'			
					Feb	May	Aug	Nov
PC1								
<u>B</u> iotopes	1	28.99	17.31	< 0.01				
Month	3	5.45	3.25	0.02	ab	ab	b	а
<u>B</u> x <u>M</u>	3	0.98	0.58	ns				
Error	52	1.68						
PC2								
<u>B</u> iotopes	1	1.82	0.95	ns				
Month	3	0.51	0.26	ns				
<u>B</u> x <u>M</u>	3	0.25	0.13	ns				
Error	52	1.92						
PC3								
<u>B</u> iotopes	1	0.12	0.10	ns				
<u>M</u> onth	3	6.88	5.81	< 0.01	а	ab	b	а
<u>B</u> x <u>M</u>	3	0.10	0.09	ns				
Error	52	1.18						

limnological data, Carla S. Pavanelli for providing initial identification of fishes, Nupélia-UEM staff and students for field support, and David Hoeinghaus for assisting with the English translation. The comments of Sidinei M. Thomaz and David Hoeinghaus helped to improve an earlier version of the manuscript.

Literature Cited

- Agostinho, A. A., A. E. A. de M. Vazzoler, L. C. Gomes & E. K. Okada. 1993. Estratificación espacial y comportamiento de *Prochilodus scrofa* en distintas fases del ciclo de vida, en la planície de inundación del alto río Paraná y embalse de Itaipu, Paraná, Brasil. Revue D' Hydrobiologie Tropicale, 26(1): 79-90.
- Agostinho, A. A., A. E. A. de M. Vazzoler & S. M. Thomaz. 1995. The high River Paraná basin: limnological and ichthyological aspects. Pp. 59-103. In: Tundisi, J. G., Bicudo, C. E. M. & T. Matsumura-Tundisi (Eds.). Limnology in Brazil. Rio de Janeiro, Brazilian Academy of Sciences, Brazilian Limnological Society, 376p.
- Agostinho, A. A., S. M. Thomaz & L. C. Gomes. (in press). Threats for biodiversity in the floodplain of the Upper Paraná River: effects of hydrological regulation by dams. Ecohydrology & Hydrobiology.
- Agostinho, A. A. & M. Zalewski. 1996. A planície alagável do alto rio Paraná: importância e preservação. Maringá, EDUEM, 100p.
- Amoros, C. & A. L. Roux. 1988. Interaction between water bodies within the floodplains of large rivers: function and development of connectivity. In: Schreiber, K. F. (Ed.). Connectivity in Landscape Ecology. Münster. Münstersche Geographische Arbeiten, 29: 125-130.
- Barbosa, F. A. R., J. Padisák, E. L. G. Espíndola, G. Borics & O. Rocha. 1999. The cascading reservoir continuum concept (CRCC) and its application to the river Tietê-basin, São Paulo State, Brazil. Pp. 425-437. In: Tundisi, J. G. & M. Straskraba (Eds.). Theoretical Reservoir Ecology and its Applications. Leiden, International Institute of Ecology, Brazilian Academy of Sciences, Backhuys, 585p.
- Britski, H. A., K. Z. de S. de Silimon & B. S. Lopes. 1999. Peixes do Pantanal: manual de identificação. Brasília, Corumbá, Embrapa, 184p.
- Connell, J. H. & E. Orias. 1964. The ecological regulation of species diversity. American Naturalist, 98(903): 399-414.
- Gomes, L. C., L. E. Miranda & A. A. Agostinho. 2002. Fishery yield relative to chlorophyll a in reservoirs of the Upper Paraná River, Brazil. Fisheries Research, 55(1-3): 335-340.
- Hanson, J. M. & W. C. Leggett. 1982. Empirical prediction of fish biomass and yield. Canadian Journal of Fisheries and Aquatic Sciences, 39: 257-263.
- Horne, A. J. & C. R. Goldman. 1994. Limnology. New York, McGraw-Hill, 576p.
- Jackson, D. A. 1993. Stopping rules in principal components analysis: a comparison of heuristical and statistical approaches. Ecology, 74(8): 2204-2214.

- Junk, W. J., P. B. Bayley & R. E. Sparks. 1989. The flood pulse concept in river-floodplain systems. Canadian Special Publication in Fisheries and Aquatic Sciences, 106: 110-127.
- MacCune, B. & M. J. Mefford. 1997. PC-ORD: Multivariate analysis of ecological data. Version 3.0. Oregon, MjM Software Design.
- Okada, E. K., A. A. Agostinho, M. Petrere Jr. & T. Penczak. 2003. Factors affecting fish diversity and abundance in drying ponds and lagoons in the upper Paraná River basin, Brazil. Ecohydrology & Hydrobiology, 3(1): 97-110.
- Rodríguez, M. A. & W. M. Lewis Jr. 1997. Structure of fish assemblages along environmental gradients in floodplain lakes of the Orinoco River. Ecological Monographs, 67(1): 109-128.
- Rosenzweig, M. L. & Z. Abramsky. 1993. How are diversity and productivity related? Pp. 52-65. In: Ricklefs, R. E. & D. Schluter (Eds). Species diversity in ecological communities: historical and geographical perspectives. Chicago, The University of Chicago Press, 416p.
- Scheffer, M. 1998. Ecology of shallow lakes. London, Chapman & Hall, 357p.
- Smith, R. L. 1996. Ecology and field biology. 5th Ed. New York, Harper Collins, 850p.
- StatSoft. 1996. Statistica. Version 3.0. Tulsa, SatSoft Inc.
- Súarez, Y. R., M. Petrere Jr. & A. C. Catella. 2001. Factors determining the structure of fish communities in Pantanal lagoons (MS, Brazil). Fisheries Management and Ecology, 8: 173-186.
- Tejerina-Garro, F. L., R. Fortin & M. A. Rodríguez. 1998. Fish community structure in relation to environmental variation in floodplain lakes of the Araguaia River, Amazon Basin. Environmental Biology of Fishes, 51: 399-410.
- Thomaz, S. M., M. C. Roberto & L. M. Bini. 1997. Caracterização limnológica dos ambientes aquáticos e influência dos níveis fluviométricos. Pp. 73-102. In: Vazzoler, A. E. de M., Agostinho, A. A. & N. S. Hahn (Eds.). A planície de inundação do alto rio Paraná: aspectos físicos, biológicos e socioeconômicos. Maringá, EDUEM, 460p.
- Thomaz, S. M., M. C. Roberto, F. A. Lansac Toha, A. F. Lima & F. A. Esteves. 1992. Características limnológicas de uma estação de amostragem do alto rio Paraná e outra do baixo rio Ivinheima - (PR, MS-Brasil). Acta Limnologica Brasiliensia, 4: 32-51.
- Tockner, K., D. Pennetzdorfer, N. Reiner, F. Schiemer & J. V. Ward. 1999. Hydrological connectivity, and the exchange of organic matter and nutrients in a dynamic riverfloodplain system (Danube, Austria). Freshwater Biology, 41: 521-535.
- Veríssimo, S. 1994. Variações na composição da ictiofauna em três lagoas sazonalmente isoladas, na planície de inundação do alto rio Paraná, ilha Porto Rico, PR-Brasil. MSc. Dissertation, Universidade Federal de São Carlos, São Carlos. 77p.

Wetzel, R. G. 1981. Limnología. Barcelona, Omega, 679p.

Winemiller, K. O. 1989. Patterns of variation in life history among South American fishes in seasonal environments. Oecologia, 81: 225-241.

Received September 16, 2003 Accepted October 22, 2003

Appendix 1. Species collected during the study period, with mean density and biomass (in parentheses) in connected (C) and disconnected lagoons (D) for each month. *denotes values less than 0.1.

Species	February		May		August		November	
1	C	D	С	D	С	D	С	D
Myliobatiformes					_		-	
Potamotrygon motoro	-	-	0.1 (89.7)	-	-	-	0.1 (22.2)	-
Characiformes								
Astyanax altiparanae	0.1 (0.1)	5.3 (31.9)	3.9 (4.0)	110.4(73.8)	0.1(*)	142.8(112.6)	7.5 (18.5)	43.5 (94.7)
Astyanax fasciatus	0.1	* (0.2)	-	-	-	-	-	-
Astyanax schubarti	-	0.4 (3.0)	-	-	-	0.1 (0.5)	-	-
Bryconamericus stramineus	14.1 (9.2)	0.1(0.1)	2.3 (2.0)	14.4 (9.3)	4.6 (4.7)	8.6 (7.7)	3.2 (1.4)	4.1 (7.6)
Hemigrammus marginatus	3.3 (2.7)	0.8 (0.8)	38.4 (33.7)	51.7 (6.1)	0.3 (*)	0.3 (0.2)	14.9 (13.5)	0.5 (0.4)
Hyphessobrycon eques	0.5 (0.2)	16.7 (9.8)	1.8 (0.4)	3.2 (1.5)	0.1 (*)	8.0 (4.4)	11.5 (5.9)	6.3 (3.4)
Hyphessobrycon sp.	-	-	-	-	-	-	13.8 (2.9)	-
Moenkhausia intermedia	18.1 (48.8)	9.7 (33.7)	-	35.8 (14.2)	-	37.2 (26.9)	5.7 (21.3)	10.5 (16.1)
Moenkhausia sanctaefilomenae	-	5.2 (5.4)	12.2 (5.9)	28.0 (15.6)	4.3 (1.4)	46.1 (44.6)	1.1(0.8)	91.0 (89.5)
Aphyocharax anisitsi	6.9 (4.5)	9.0 (8.1)	0.7 (0.2)	13.5 (4.6)	0.4 (0.1)	36.5 (13.6)	0.5 (0.3)	9.3 (4.8)
Aphyocharax sp.	0.7 (0.4)	3.0 (2.0)	0.6 (0.3)	3.4 (0.4)	3.1 (0.9)	3.6 (0.8)	4.6 (4.2)	0.5 (0.2)
Serrapinnus notomelas	7.1 (3.9)	209.3(116.1)	5.8 (1.7)	17.5 (6.8)	0.9 (0.2)	137.0 (48.0)	13.8 (5.3)	186.7 (87.9)
Serrapinnus sp. 1	2.1 (0.5)	55.8 (19.5)	-	0.3 (0.1)	-	0.2 (0.1)	0.1 (*)	9.8 (3.0)
Serrapinnus sp. 2	1.9 (1.0)	40.9 (17.6)	1.2 (0.3)	5.3 (1.4)	-	1.4 (1.3)	5.1 (1.9)	39.9 (13.6)
Odontostilbe sp.	0.1 (*)	6.2 (4.9)	0.1 (*)	0.7(0.1)	0.1 (*)	1.4 (0.3)	-	-
Salminus brasiliensis	-	-	-	-	-	* (1.3)	-	-
Roeboides paranensis	1.5 (1.0)	7.0 (16.1)	0.1 (0.1)	6.2 (6.8)	-	6.0 (6.4)	1.3 (0.8)	18.8 (44.2)
Acestrorhynchus lacustris	-	0.8 (26.2)	- 1	0.3 (13.3)	-	0.3 (8.0)	0.5 (0.7)	1.1 (27.8)
Metynnis cf. maculatus	0.1 (*)	-	-	-	* (2.4)	-	- 1	
Myleus tiete	-	-	0.1 (*)	-		-	-	-
Serrasalmus marginatus	0.8 (0.2)	0.5(1.9)	0.1 (*)	0.4(1.4)	-	0.1(0.3)	0.5 (6.1)	0.5(1.0)
Serrasalmus maculatus	-	-	-	0.1 (1.4)	-	0.1 (16.7)	-	-
Characidium aff. zebra	-	0.3 (0.2)	0.1 (*)	- 1	0.2 (*)	0.6 (0.1)	0.4 (0.2)	1.8 (0.8)
Characidium sp.	-	0.2 (0.2)	- ` `	-	- 1	- 1	- 1	0.2(0.1)
Apareiodon affinis	-	0.1 (*)	1.4 (0.4)	-	-	* (0.1)	2.3 (0.3)	0.2(0.1)
Prochilodus lineatus	-	0.1 (23.1)	-	* (27.5)	-	-	-	0.1 (6.4)
Steindachnerina insculpta	0.4 (5.8)	5.0 (53.6)	2.9 (2.0)	17.8 (56.3)	4.0 (4.1)	132.9(177.4)	11.5 (59.6)	87.6 (464.5)
Cyphocharax modestus	-	0.4 (7.6)	-	1.5 (65.6)	-	- 1	-	-
Cyphocharax nagelii	-	-	-	-	-	1.2 (2.5)	-	0.1 (0.5)
Leporinus friderici	0.4 (13.6)	0.2 (3.8)	-	-	-	-	-	-
Leporinus lacustris	-	* (3.6)	-	0.1 (5.2)	-	-	0.1 (0.6)	1.6 (20.5)
Leporinus obtusidens	-	* (1.6)	-	-	-	-	-	0.1 (0.4)
Leporinus sp.	-	* (1.9)	-	-	-	0.1 (21.7)	-	-
Schizodon borellii	-	0.1 (5.5)	0.2 (0.1)	0.6 (20.0)	-	-	-	-
Pyrrhulina australis	* (*)	0.3 (0.1)	0.2 (*)	0.1 (*)	-	0.3 (0.1)	0.1 (*)	0.8 (0.1)
Hoplias aff. malabaricus	0.3 (22.5)	1.4 (158.4)	0.1 (3.9)	0.5 (31.1)	0.1 (0.6)	0.1 (11.2)	1.4 (21.8)	0.9 (139.9)
Hoplerythrinus unitaeniatus	-	0.3 (48.3)	-	* (*)	-	0.1 (14.9)	-	-
Gymnotiformes								
Gymnotus spp.	-	* (0.4)	-	-	-	-	-	-
<i>Eigenmannia</i> sp.	* (0.1)	0.2 (0.5)	-	* (*)	-	-	-	0.1 (0.8)
Siluriformes								
Parauchenipterus galeatus	-	-	-	-	-	* (0.4)	-	-
Pimelodella sp.		0.2 (1.7)	-	0.8 (0.5)	-	3.9 (4.4)	-	6.6 (20.6)
Pimelodus maculatus	0.1 (17.1)	-	-	0.3 (0.3)	-	-	-	
Hoplosternum littorale	-	-	-	1.2 (0.7)	-	* (6.2)	-	0.3 (15.7)
Liposarcus anisitsi	-	0.2 (*)	-	* (32.0)	-	-	0.1 (50.9)	-
Loricariichthys platymetopon	0.1 (0.6)	7.1 (39.1)	0.3 (5.0)	1.5 (28.0)	* (0.9)	1.1 (13.3)	-	3.0 (133.7)
Loricariichthys sp.	-	-	0.1 (1.4)	-	-	-	-	-
Cyprinodontiformes	6 4 (I)							
Rivulus sp.	0.1 (*)	-	-	-	-	-	-	-
Perciformes								
Plagioscion squamosissimus	0.1 (0.1)	-	-	-	-	-	-	-
Astronotus ocellatus	-	2.1(0.9)	-	* (10.4)	-	-	-	0.1 (48.6)
Cichla monoculus	-	0.1(0.3)	-	0.2 (4.4)	-	-	-	-
Cichlasoma paranaense	-	0.7 (3.9)	-	* (*)	0.1 (*)	0.3 (17.7)	0.1(0.1)	0.3 (0.4)
Crenicichla britskii	-	-	0.1 (0.1)	-	- (0.1)	-	0.1 (0.6)	-
Satanoperca pappaterra	0.8 (4.2)	3.1 (39.4)	0.9 (11.9)	1.0 (18.1)	0.6 (25.3)	-	3.5 (60.5)	3.2 (1.5)
Laetacara sp.	-	0.1 (0.1)	-	0.4 (0.3)	0.1 (*)	-	-	-
Synbranchiformes		بەر بەر						
Synbranchus marmoratus	-	* (*)	-	-	-	-	-	-
Pleuronectiformes	0.1 (0.0)		0.1 (0.2)					
Catathyridium jenynsii	0.1(0.2)	-	0.1(0.3)	-	-	-	-	-

Winemiller, K. O., S. Tarim, D. Shormann & J. B. Cotner. 2000. Fish assemblage structure in relation to environmental variation among Brazos River oxbow lakes. Transactions of the American Fisheries Society, 129: 451-468.