Spatial variation of the fish assemblage structure from the upper Rio Paraná floodplain, Brazil, in a dry year.

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ABSTRACT: Spatial variation of the fish assemblage structure from the upper Rio Paraná floodplain, Brazil, in a dry year. Although the upper Rio Paraná floodplain is subjected to impacts generated by hydroelectric plants upstream, studies on fish assemblage reveal its importance to the maintenance of regional biodiversity. The purpose of this study was to analyze the spatial variation in the structure of fish assemblage and to identify processes determining species composition and abundance. Quarterly samples were taken with gill nets in 19 sites during the year 2000. Fish assemblage of three subsystems (Rio Paraná and two tributaries, Baía and Ivinheima) and four categories of biotopes (rivers, channels, connected and disconnected lagoons) were analyzed. No significant differences in richness, diversity and evenness were detected among subsystems and biotopes, in spite of the significant differences detected in abiotic factors among subsystems. On a broad spatial scale, fish assemblage structure of the upper Rio Paraná floodplain was characterized by the dominance of few typical species, unevenly distributed, and influenced by abiotic factors, such as water transparency, dissolved oxygen and pH.
Key-words: neotropical fish; floodplain; fish assemblage structure; abiotic factors.

RESUMO: Variação espacial da estrutura de assembléias de peixes da planície de inundação do alto Rio Paraná, Brasil, num ano seco. Apesar de sujeita aos impactos gerados pelas hidrelétricas a montante, estudos ictiofaunísticos têm reconhecido a importância da planície de inundação do alto rio Paraná na manutenção da biodiversidade regional. O objetivo do presente estudo foi analisar a variação espacial na estrutura das assembléias de peixes e identificar os processos relacionados com a composição e abundância das espécies. Durante o ano de 2000, amostragens trimestrais com redes de espera foram realizadas em 19 estações de coleta, compreendendo três sub-sistemas (rio Paraná e dois tributários, rios Baía e Ivinheima) e quatro categorias de biótopos (rios, canais, lagoas conectadas e desconectadas). Não foram obtidas diferenças significativas na riqueza de espécies, diversidade e eqüitabilidade entre categorias de sub-sistemas e biótopos, a despeito das diferenças significativas verificadas nos fatores abióticos entre os sub-sistemas considerados. Numa ampla escala espacial, a estrutura das assembléias de peixes da planície de inundação do alto Rio Paraná foi caracterizada pela dominância de um pequeno grupo de espécies típicas e influenciada pelos fatores abióticos, como transparência da água, oxigênio dissolvido e pH.
Palavras-chave: peixes neotropicais; planície de inundação; estrutura de assembléias de peixes; fatores abióticos.

Introduction

It is widely recognized that river-floodplain systems have high biotic diversity. Diversity in those systems is related to spatial and temporal heterogeneity and directly influenced by variations of the hydrological cycle (Amoros & Roux, 1988; Junk et al., 1989; Neiff, 1990). Discharge control by hydroelectric plants, with their extensive

contribution to modifications of ecosystems in rivers and flooded areas, has notable consequences on biotic diversity (Sparks, 1995). Severe decreases in population size caused by fail in recruitment (Welcomme, 1979; Gomes & Agostinho, 1997; Vazzoler et al., 1997a), increase in total mortality (Veríssimo, 1994) and local extinction (Veríssimo, 1999) are some consequences of this process. Long periods of drought allied to decrease in lotic stretches as a result of dams have enhanced these effects.

This research focuses on the characterization of the spatial variation in the structure of fish assemblage of the upper Rio Paraná floodplain after two following years of drought and endeavors to detect the factors that determined the observed patterns. The following questions were addressed: i) Is the structure of the fish assemblage, evaluated by certain attributes, spatially variable? ii) Is the structure of the fish assemblage, considering composition and abundance, influenced by variations in abiotic factors?

Material and Methods

Study area, hydrologic and pluviometric regimes, location of the sampling sites

Due to various reservoirs (150 in the basin and four in the main channel), the Rio Paraná (4,695 km long, including 1,870 km within the Brazilian territory) and its tributaries have their flow regulated. The area under analysis lies in the last remaining non-impounded stretch of the Rio Paraná in the Brazilian territory (230 km between the Porto Primavera Dam and the Itaipu Reservoir), characterized by an extensive floodplain on its west side. Nineteen sites, in the Rio Paraná (four sites) and two tributaries, Rio Baía (seven sites) and Rio Ivinheima (eight sites) (herein called subsystems Paraná, Baía and Ivinheima), classified in four habitat categories (herein called biotopes: rivers (three sites), channels (three sites), connected lagoons (nine sites) and disconnected lagoons (four sites) were sampled between the coordinates: 22°20' - 22°80'S and 53°10' - 53°40'W (Fig. 1).

The hydrological regime of the Rio Paraná used to have markedly seasonal variations, with flood (November to May) and dry (June to October) periods (Thomaz et al., 1997). Water connectivity caused by floods promoted the homogeneity of habitats with regard to limnological factors, whereas during the dry period local processes caused evident heterogeneity of biotopes (Thomaz et al., 1992; Agostinho et al., 1995). Decrease in rain amounts and the conclusion of the Porto Primavera Dam, that formed a reservoir with an area of 2,200 km², immediately above, caused a severe decrease in the hydrometric level of the Rio Paraná downstream, during the flood period of 1998 and 1999 (Fig. 2).

Data collection

Samples were taken quarterly, from February to November 2000, with gangs of gill nets (mesh sizes varying from 2.4 to 16 cm opposite knots), set 24 hours, checked at 17h00, 24h00 and 07h00. After identification, individuals were weighted (total weight: Wt; g). Catch per unit effort (CPUE) was used to express data on numerical abundance (number of individuals per 1,000 m² of net in 24 hr; $CPUE_N$) and biomass (kg in 1,000 m² of net in 24 hr; $CPUE_B$).

Abiotic factors recorded when checking gill nets were water temperature (°C), water transparency (Secchi disk; cm), depth (cm), pH (pH meter, DM2), conductivity (conductivity meter Digimed, DM3, μS/cm) and dissolved oxygen (oxygen meter, YSI Yellow Spring, 52CE, mg/l).

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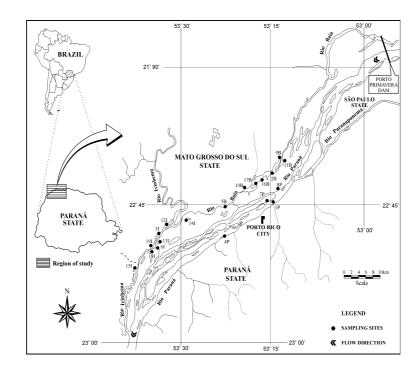Sem título-4   2   25/1/2005, 09:58

Figure 1: Study area and sampling sites (Rivers: 1 (Rio Paraná; RPAR), 2 (Rio Baía; RBAI) and 3 (Rio Ivinheima; RIVI); Channels: 4 (Canal Cortado; CCOR), 5 (Canal Curutuba; CCUR) and 6 (Canal Ipoitã; CIPO); Connected lagoons: 7 (Ressaco do Pau Véio; LPVE), 8 (Lagoa das Garças; LGAR), 9 (Lagoa do Gavião; LGAV), 10 (Lagoa do Guaraná; LGUA), 11 (Lagoa da Onça; LONC), 12 (Lagoa Finado Raimundo; LFRA), 13 (Lagoa dos Patos; LPAT), 14 (Lagoa Sumida; LSUM) and 15 (Lagoa Peroba; LPER); Disconnected lagoons: 16 (Lagoa Pousada das Garças; LPGA), 17 (Lagoa Fechada; LFEC), 18 (Lagoa Ventura; LVEN), 19 (Lagoa Zé do Paco; LZEP)]. P, B and I following the number represent respectively the Paraná, Baía and Ivinheima subsystems.

Data analysis
Spatial variation of the fish assemblage attributes

Species richness (absolute number of species; S), Shannon's Diversity Index (H'), defined as $H' = -\mathbf{S}(ni/N).\log(ni/N)$, where ni=number of individuals of species i, N=total number of individuals (Magurran, 1988), Eveness (E), with $E = H'/\ln(S)$, where H'=Shannon's Diversity Index and S=species richness (Pielou, 1969) were the attributes employed to evaluate the structure of fish assemblage. They were calculated from each sampling site ($CPUE_N$ data matrix) using PC-ORD 3.0 (MacCune & Mefford, 1997). Spatial variation of S, H' and E was tested by unifactorial ANOVA, with subsystems (Paraná, Baía and Ivinheima) and biotopes (rivers, channels, connected and disconnected lagoons) as factors.

Abiotic factors and their relationship with fish assemblage structure

To determine the influence of abiotic factors on fish assemblage structure, multivariate analyses were performed to summarize limnological factors (abiotic factors) and the structure of fish assemblage (biotic data). As temporal variation in abiotic factors is high (Thomaz et al., 1997), averages were obtained for each sample.
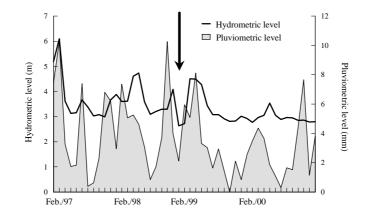
Figure 2: Hydrologic and pluviometric regimes of the Rio Paraná in the municipality of Porto São José. Arrow shows the beginning of Porto Primavera Reservoir filling. Dotted line indicates the period of sampling. Data were given by the National Agency of Electric Energy (ANEEL).

Then, minimum and maximum averages of each site were used in principal components analysis (PCA) (Gauch, 1986) using PC-ORD 3.0 (MacCune & Mefford, 1997), aimed to summarize abiotic data. PCA axes eigenvalues higher than those produced by the Broken-Stick model were retained for interpretation (Jackson, 1993). Spatial variation of limnological factors was tested by unifactorial ANOVAs on the scores of PCA axes retained for interpretation, with subsystems and biotopes as factors.

Detrended correspondence analysis (DCA) was applied to summarize biotic data ($CPUE_N$ data matrix) expecting to identify patterns related to composition and abundance of fish assemblage. Spatial variation was tested by unifactorial ANOVAs on scores of the DCA axes retained for interpretation with subsystems and biotopes as factors. To identify the species that contributed the most in the ordination (DCA), correlations (Pearson) of each species with axes retained for interpretation were generated (the routine of correlation with main matrix; PC-ORD 3.0; MacCune & Mefford, 1997). Since rare species might influence DCA (Palmer, 1993), Kendall's Concordance Coefficient (Siegel, 1975) was applied to assess differences in the rank of dominant species (›80% of total $CPUE_N$) among sampling sites using the same data matrix used in DCA.

Congruency between data matrices of abiotic factors and biotic data (species) was evaluated by correlating the axes of PCA and DCA retained for interpretation. For significant correlations, it was assumed that abiotic factors correlated with the respective PCA axes affected the structure (composition and abundance) of fish assemblage summarized in DCA.

Univariate statistical analyses were performed using the software Statistica™(Statsoft, 1996). Data were transformed when assumptions of normality (Test of Shapiro-Wilk), homocedasticity (Test of Levene) in ANOVA and correlations (Pearson) were not met. Tukey's Test was applied when significant differences were detected between averages. When restriction persisted non-parametric tests (Kruskal-Wallis's and Spearman's Correlation) were employed. Significance level in all tests implies P‹0.05.

Results

During the studied period, seventy three species were collected, distributed into 5 orders and 19 families, classified according to Britski et al. (1999) (Tab. I).

Table I: Total abundance (numeric (CPUE$_N$)) of the fish species in the biotopes of the upper Rio Paraná floodplain during 2000. Biotopes are: R=rivers, C=channels, CL=connected lagoons and DL=disconnected lagoons.

Species	Biotopes			
	R	C	CL	DL
OSTARIOPHYSI				
CHARACIFORMES				
CHARACIDAE				
TETRAGONOPTERINAE				
Bryconamericus stramineus Eigenmann, 1908	0	0	‹0.05	0
Moenkhausia intermedia (Eigenmann, 1908)	16	10	16	70
Astyanax altiparanae Garutti & Britski, 2000	6	4	3	30
Astyanax schubarti Britski, 1964	0	0	1	‹0.05
SALMININAE				
Salminus maxillosus Valenciennes, 1849	0	1	0	0
CYNOPOTAMINAE				
Galeocharax knerii (Steindachner, 1879)	1	‹0.05	0	0
CHARACINAE				
Roeboides paranensis Pignalberi, 1975	11	3	7	37
ACESTRORHYNCHINAE				
Acestrorhynchus lacustris (Reinhardt, 1874)	2	5	5	19
MYLEINAE				
Myloplus cf. tiete (Eigenmann & Norris, 1900)	0	0	‹0.05	0
Metynnis cf. maculatus (Kner, 1860)	‹0.05	0	‹0.05	1
Piaractus mesopotamicus (Holmberg, 1887)	0	0	‹0.05	0
SERRASALMINAE				
Serrasalmus marginatus Valenciennes, 1847	31	29	148	70
Serrasalmus spilopleura Kner, 1860	2	2	5	6
CYNODONTIDAE				
Rhaphiodon vulpinus Agassiz, 1829	16	4	10	‹0.05
PARODONTIDAE				
Apareiodon affinis (Steindachner, 1879)	53	0	0	0
Parodon nasus Kner, 1859	0	‹0.05	0	0
PROCHILODONTIDAE				
Prochilodus lineatus (Valenciennes, 1836)	9	10	8	23
CURIMATIDAE				
Cyphocharax modestus (Fernández-Yépez, 1948)	0	0	1	8
Cyphocharax nagelii Steindachner, 1881	1	0	4	1
Steindachnerina insculpta Fernández-Yépez, 1948	16	7	14	5
ANOSTOMIDAE				
Leporellus vittatus (Valenciennes, 1849)	‹0.05	0	0	0
Leporinus friderici Bloch, 1794	9	5	1	4
Leporinus lacustris Campos, 1945	13	5	27	53
Leporinus obtusidens (Valenciennes, 1847)	4	2	2	4
Leporinus octofasciatus (Steindachner, 1917)	‹0.05	0	0	0
Leporinus sp.	7	3	4	3
Schizodon altoparanae Garavello & Britski, 1990	2	‹0.05	2	2
Schizodon borelli (Boulenger, 1900)	10	32	26	26
Schizodon nasutus Kner, 1859	‹0.05	0	‹0.05	0
ERYTHRINIDAE				
Hoplias aff. malabaricus (Bloch, 1794)	16	18	35	26
Hoplerythrinus unitaeniatus (Spix, 1829)	2	1	8	2
GYMNOTIFORMES				
RHAMPHICHTHYIDAE				
Rhamphichthys rostratus (Linnaeus, 1766)	0	0	2	‹0.05
GYMNOTIDAE				
Gymnotus spp	‹0.05	0	1	3
STERNOPYGIDAE				
Sternopygus macrurus (Schneider, 1801)	‹0.05	0	‹0.05	1
Eigenmannia trilineata Lopez & Castello, 1966	0	‹0.05	2	2
Eigenmannia virescens (Valenciennes, 1847)	0	0	0	‹0.05
SILURIFORMES				
DORADIDAE				
Platydoras armatulus (Valenciennes, 1840)	‹0.05	0	0	0
Pterodoras granulosus (Valenciennes, 1833)	1	0	1	0
Trachydoras paraguayensis (Eigenmann & Ward, 1907)	50	3	38	0
Doras eigenmanni (Boulenger, 1895)	0	0	1	0
AUCHENIPTERIDAE				
Auchenipterus osteomystax (Ribeiro, 1918)	4	1	11	0
Parauchenipterus galeatus (Linnaeus, 1766)	19	8	69	64
AGENEIOSIDAE				
Ageneiosus valenciennesi Bleeker, 1864	0	0	‹0.05	0
PIMELODIDAE				
Hypophthalmus edentatus Spix, 1829	‹0.05	0	1	‹0.05

Rhamdia quelen (Quoy & Gaimard, 1824)	0	0	0	‹0.05
Pimelodella sp. 1	3	0	‹0.05	0
Pimelodella sp. 2	1	0	‹0.05	0
Pimelodus maculatus Lacépède, 1803	5	11	15	2
Iheringichthys labrosus (Kröyer, 1874)	4	2	5	0
Pininampus pirinampu (Spix, 1829)	1	0	‹0.05	0
Hemisorubim platyrhynchos (Valenciennes, 1840)	6	2	6	3
Sorubim lima (Schneider, 1801)	‹0.05	1	‹0.05	0
Pseudoplatystoma corruscans (Agassiz, 1829)	‹0.05	‹0.05	3	5
CALLICHTHYIDAE				
Hoplosternum littorale (Hancock, 1828)	2	0	8	15
LORICARIIDAE				
Loricariichthys platymetopon Isbrücker & Nijssen, 1979	22	24	114	80
Loricariichthys rostratus Reis & Pereira, 2000	0	0	‹0.05	0
Megalancistrus aculeatus (Perugia, 1891)	‹0.05	0	0	0
Rhinelepis strigosa Valenciennes, 1840	0	‹0.05	1	0
Liposarcus anisitsi (Eigenmann & Kennedy, 1903)	2	1	19	11
Hypostomus ancistroides Ihering, 1911	0	‹0.05	1	5
Hypostomus microstomus Weber, 1987	‹0.05	0	0	0
Hypostomus regani (Ihering, 1905)	5	0	0	0
Hypostomus sp. 1	1	1	‹0.05	0
Hypostomus sp. 2	1	‹0.05	0	0
ACANTHOPTERYGII				
PERCIFORMES				
SCIAENIDAE				
Plagioscion squamosissimus (Heckel, 1840)	3	0	3	6
CICHLIDAE				
Satanoperca pappaterra (Heckel, 1840)	0	11	6	1
Crenicichla britskii Kullander, 1982	4	2	2	2
Crenicichla haroldoi Luengo & Britski, 1974	1	0	0	0
Astronotus ocellatus (Cuvier, 1829)	‹0.05	0	2	2
Cichlasoma paranaense Kullander, 1983	1	‹0.05	1	1
Cichla monoculus Spix, 1831	0	2	‹0.05	‹0.05
Cichla sp.	0	0	‹0.05	0
PLEURONECTIFORMES				
ACHIRIDAE				
Catathyridium jenynsii (Günther, 1862)	0	0	‹0.05	‹0.05

Spatial variation of the fish assemblage attributes

Species richness in the Ivinheima (59 species) was higher than the Paraná (56) and Baía (46) subsystems. Although differing in abundance, approximately 21% of species occurred in all biotopes. In fact, H. malabaricus, P. galeatus and S. borelli have been reported in all sampling sites; S. marginatus, L. platymetopon, R. paranensis and P. lineatus have been recorded in at least 17 of them.

Only three species were registered in a single sampling site, as follow, H. regani and A. affinis in a river, and D. eigenmanni in a connected lagoon. In general, connected lagoons were the biotopes with highest species richness and abundance (Tab. I). Species markedly abundant were L. platymetopon in LGAR and T. paraguayensis and S. marginatus in LFRA. Heterogeneity of the relative species abundance among sampling sites reflected in the variation of the diversity index and eveness (Tab. II). Nevertheless, differences were significant neither between subsystems nor between biotopes (Tab. III).

Baía and Ivinheima subsystems had higher mean $CPUE_B$ than the Paraná subsystem (75; 69; 59 respectively) (Tab. II). Highest biomass values were registered in connected (LSUM and LONC) and disconnected (LFEC) lagoons. They contributed together 27% of total biomass.

Abiotic factors and their relationship with fish assemblage structure

Mean values (minimum and maximum) of abiotic factors were, in general, greater in lagoons, except conductivity, which presented greater values in rivers and channels (Tab. IV). In addition the coefficient of variations (Tab. IV) for conductivity and water transparency were greater in rivers and disconnected lagoons, indicating more variation of the abiotic factors in these biotopes.

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Table II: Total abundance (numeric (CPUE$_N$) and biomass (CPUE$_B$)] and attributes of the fish assemblage structure (species richness (S), Shannon's Diversity Index (H') and Eveness (E)) in the 19 sampling sites, grouped by subsystems and biotopes, in the upper Rio Paraná floodplain during 2000. Codes are shown in Fig. 1. Averages (± standard deviation) of values for the subsystems and biotopes.

Codes	Subsystems	Biotopes	Abundance		Attributes		
			CPUE$_N$	CPUE$_B$	S	H'	E
RPAR	Paraná	river	383	23	32	2.35	0.68
RBAI	Baía	river	361	60	28	2.84	0.85
RIVI	Ivinheima	river	367	48	28	2.46	0.74
CCOR	Paraná	channel	317	52	29	2.85	0.85
CCUR	Baía	channel	216	30	24	2.54	0.80
CIPO	Ivinheima	channel	111	24	19	2.46	0.83
LPVE	Paraná	connected lagoon	507	63	32	2.65	0.77
LGAR	Paraná	connected lagoon	603	96	36	2.61	0.73
LGAV	Baía	connected lagoon	231	39	20	2.47	0.83
LGUA	Baía	connected lagoon	645	99	36	2.53	0.71
LONC	Baía	connected lagoon	750	113	33	2.43	0.70
LFRA	Ivinheima	connected lagoon	861	89	36	2.21	0.62
LPAT	Ivinheima	connected lagoon	630	97	33	2.59	0.74
LSUM	Ivinheima	connected lagoon	1011	126	28	1.82	0.55
LPER	Ivinheima	connected lagoon	516	59	32	2.85	0.82
LPGA	Baía	disconnected lagoon	522	72	26	2.37	0.73
LFEC	Baía	disconnected lagoon	883	110	29	2.78	0.82
LVEN	Ivinheima	disconnected lagoon	635	65	28	2.43	0.73
LZEP	Ivinheima	disconnected lagoon	336	45	25	2.64	0.82
	Paraná		452 ±128	59 ±30	32 ±3	2.61 ±0.20	0.75 ±0.07
	Baía		516 ±259	75 ±34	28 ±5	2.57 ±0.18	0.78 ±0.06
	Ivinheima		558 ±292	69 ±33	29 ±5	2.43±0.31	0.73 ±0.10
		river	370 ±11	44 ±15	29 ±2	2.55 ±0.26	0.76 ±0.09
		channel	215 ±103	35 ±15	24 ±5	2.61 ±0.20	0.83±0.02
		connected lagoon	639 ±224	87 ±28	32 ±5	2.46 ±0.30	0.72±0.09
		disconnected lagoon	594 ±229	73 ±27	27 ±2	2.55 ±0.19	0.78±0.05

Table III: Results of unifactorial ANOVAs which evaluated sources of spatial variation (effects) in the attributes of the fish assemblage structure. F = statistics of Fisher; D.F.=degrees of freedom and P=probability of F being higher than that obtained.

Attributes	Effects	F	D.F.	P
Richness (S)	Subsystems	1.02	2;16	0.38
	Biotopes	2.86	3;15	0.07
Diversity (H')	Subsystems	0.90	2;16	0.43
	Biotopes	0.31	3;15	0.82
Eveness (E)	Subsystems	0.51	2;16	0.61
	Biotopes	1.67	3;15	0.22

Table IV: Minimum and maximum averages (coefficient of variation: CV%) of the abiotic factors in the biotopes.

Abiotic factors	Rivers	Channels	Connected lagoons	Disconnected lagoons
Temperature (°C)	17.9-28.1	18.5-28.0	17.3-30.9	17.2-29.8
	(15.3)	(13.2)	(16.4)	(17.4)
Water transparency (cm)	45-226.7	63.3-186.7	35.0-211.7	15-305
	(50.4)	(27.5)	(56.6)	(87.4)
Depth (cm	160-445	120-400	100-425	190-420
	(29.2)	(27.8)	(31.7)	(27.6)
pH	6.0-7.5	6.5-7.4	5.7-7.5	5.8-8.5
	(7.9)	(4.0)	(6.6)	(9.6)
Conductivity (μS/cm)	24.1-67.4	28.4-62.2	26.7-57.0	23.8-47.5
	(34.3)	(19.6)	(22.1)	(23.1)
Dissolved oxygen (mg/l)	3.4-8.5	6.2-8.3	1.7-9.1	3.1-8.7
	(22.0)	(9.3)	(29.6)	(29.4)

Three axes of the PCA explained 74.5% of abiotic factors variation (PC1=34.0%; PC2= 21.3%; PC3=19.2%) (Tab. V). Abiotic factors more correlated with axis 1 (PC1) were maximum water transparency (positive), and minimum dissolved oxygen and pH (negative). Abiotic factors correlated with axis 2 (PC2) were maximum depth (positive), and minimum temperature (negative). Maximum dissolved oxygen was positive correlated with axis 3 (PC3) whereas minimum water transparency was negative (Tab. V).

Table V: Principal components eigenvectors (for each abiotic factor), eigenvalues, Broken-Stick eigenvalues and percent of variance explained by axis 1 (PC1), axis 2 (PC2) and axis 3 (PC3).

Abiotic factors	Rivers	Channels	Connected lagoons	Disconnected lagoons
Temperature (^{0}C)	17.9–28.1	18.5–28.0	17.3–30.9	17.2–29.8
	(15.3)	(13.2)	(16.4)	(17.4)
Water transparency (cm)	45–226.7	63.3–186.7	35.0–211.7	15–305
	(50.4)	(27.5)	(56.6)	(87.4)
Depth (cm)	160-445	120-400	100-425	190–420
	(29.2)	(27.8)	(31.7)	(27.6)
pH	6.0–7.5	6.5–7.4	5.7–7.5	5.8–8.5
	(7.9)	(4.0)	(6.6)	(9.6)
Conductivity (ms/cm)	24.1–67.4	28.4–62.2	26.7–57.0	23.8–47.5
	(34.3)	(19.6)	(22.1)	(23.1)
Dissolved oxygen (mg/l)	3.4–8.5	6.2–8.3	1.7–9.1	3.1–8.7
	(22.0)	(9.3)	(29.6)	(29.4)

Subsystems in PC1 differed significantly (ANOVA; $F_{2;16}$=11.09; P<0.01), specially Baía and Paraná (Tukey Test; P<0.01) and Baía and Ivinheima (Tukey Test; P=0.01), and in PC2 ($F_{2;16}$=9.95; P<0.01), between Paraná and Ivinheima (Tukey Test; P<0.01) (Figs. 3a, c). No significant differences were obtained between the subsystems in PC3 (Fig. 3e). Likewise, there were no significant differences between biotopes in axes 1, 2 and 3 of PCA (Figs. 3b, d, f).
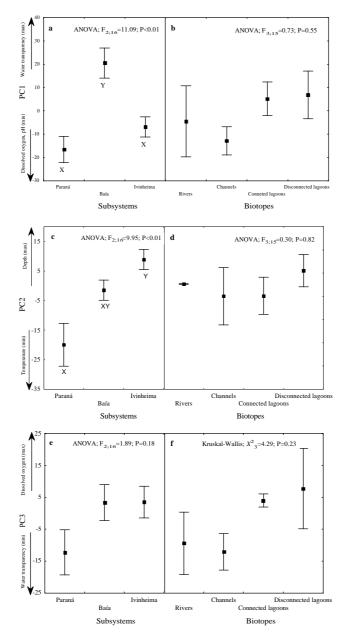
Considering the species data (CPUE$_N$ data matrix), significant differences between subsystems and biotopes have not been registered in DCA axis 1 (eigenvalue=0.54) (Figs. 4a, b), while the axis 2 (eigenvalue=0.27) revealed a certain differentiation among sampling sites (Fig. 4c). This was due to different composition and abundance of fish assemblage. It was obtained spatial differentiation (ANOVA; $F_{2;16}$=10.49; P<0.01) between the Baía and Ivinheima subsystems only (Tukey Test; P<0.01) (Fig. 4c).

Species with positive correlation with DC1 (R>0.88) were characterized by low abundance and caught only in the Rio Paraná (RPAR), such as, A. affinis, C. haroldoi, H. microstomus, H. regani, L. octofasciatus and L. vittatus. On the other hand, species negatively-correlated with axis 1 (R<0.45) were generally abundant and widely caught in lagoons, such as, L. anisitsi, L. platymetopon and S. marginatus. Species positively-correlated with DC2 (R>0.64), such as, H. platyrhynchos, T. paraguayensis and P. pinirampu, were caught mainly in the Rio Ivinheima and in LFRA (connected lagoon), whereas L. lacustris, negatively-correlated (R=-0.64), was abundant in LPGA (disconnected lagoon) (Tab. VI). A high influence of rare species was thus reported. Nonetheless, value of Kendall's Concordance Coefficient (0.19) indicated that abundant species of the upper Rio Paraná floodplain are not distributed evenly among the sampling sites.

Significant correlation occurred only between axis 1 of the PCA and axes 1 (Pearson; R=-0.47; P=0.04) and 2 (Pearson; R=-0.70; P<0.01) of the DCA. This fact suggests congruence between the matrix of abiotic factors and the matrix of biotic data (species). Considering that water transparency, dissolved oxygen and pH were the abiotic factors more correlated with PC1, it is possible to conclude that these factors influenced fish assemblage composition and structure summarized in the DCA.

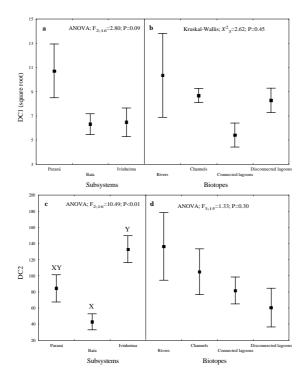**8**   **PETRY, A.C., et al**   Spatial variation of the fish assemblage...

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Figure 3: Averages (± standard error) of the scores from axis 1 (ab), axis 2 (cd) and axis 3 (ef) of the principal components analysis (PCA) for subsystems and biotopes. X and Y indicate mean differences according to the Tukey's Test.

a ANOVA; $F_{2;16}$=2.80; P=0.09

b Kruskal-Wallis; X^2_3=2.62; P=0.45

DC1 (square root)

Paraná Baía Ivinheima

Subsystems

Rivers Channels Connected lagoons Disconnected lagoons

Biotopes

c ANOVA; $F_{2;16}$=10.49; P<0.01

d ANOVA; $F_{3;15}$=1.33; P=0.30

DC2

XY X Y

Paraná Baía Ivinheima

Subsystems

Rivers Channels Connected lagoons Disconnected lagoons

Biotopes

Figure 4: Averages (± standard error) of scores from axis 1 (ab) and axis 2 (cd) of the detrended correspondence analysis (DCA) for the subsystems and biotopes. X and Y indicate mean differences according to the Tukey's Test.

Table VI: Correlation coefficients (Pearson) between abundance (numeric ($CPUE_N$)) of the fish species and axes 1 and 2 of the DCA.

Species	DC1	DC2	Species	DC1	DC2	Species	DC1	DC2
A. affinis	0.88	0.20	H. malabaricus	-0.13	-0.45	P. granulosus	-0.35	0.48
A. altiparanae	0.34	0.13	H. microstomus	0.88	0.20	P. lineatus	-0.05	0.07
A. lacustris	-0.05	-0.49	H. platyrhynchos	-0.15	0.65	P. maculatus	-0.36	-0.01
A. ocellatus	-0.36	-0.45	H. regani	0.88	0.20	P. mesopotamicus	-0.19	0.40
A. osteomystax	-0.23	0.00	H. unitaeniatus	-0.43	-0.54	P. nasus	-0.03	-0.05
A. schubarti	0.06	0.07	Hypostomus sp. 1	0.71	0.14	P. pirinampu	-0.21	0.67
A valenciennesi	-0.23	-0.15	Hypostomus sp. 2	0.87	0.29	P. squamosissimus	0.03	0.32
B. stramineus	0.05	-0.13	I. labrosus	-0.18	0.40	Pimelodella sp. 1	0.78	0.41
C. britskii	-0.06	-0.44	L. anisitsi	-0.46	-0.38	Pimelodella sp. 2	0.79	0.32
C. haroldoi	0.88	0.20	L. friderici	0.52	0.23	R. paranensis	0.33	0.14
C. jenynsii	-0.03	0.38	L. lacustris	-0.36	-0.64	R. quelen	0.00	-0.10
C. modestus	-0.03	-0.41	L. obtusidens	0.09	-0.15	R. rostratus	-0.33	0.09
C. monoculus	-0.08	-0.10	L. octofasciatus	0.88	0.20	R. strigosa	-0.23	0.19
C. nagelii	-0.09	-0.40	L. platymetopon	-0.45	-0.39	R. vulpinus	0.26	0.45
C. paranaense	-0.25	-0.54	L. rostratus	-0.18	-0.30	S. altoparanae	0.21	-0.44
Cichla sp.	0.05	-0.13	L. vittatus	0.88	0.20	S. borelli	-0.01	-0.45
D. eigenmanni	-0.23	0.42	Leporinus sp.	-0.25	0.54	S. insculpta	0.46	-0.07
E. trilineata	0.02	0.11	M. aculeatus	-0.08	0.53	S. lima	0.24	0.32
E. virescens	0.15	0.12	M. cf. maculatus	-0.11	-0.54	S. macrurus	0.02	0.21
G. knerii	0.83	0.33	M. intermedia	0.33	-0.13	S. marginatus	-0.45	0.17
Gymnotus spp	-0.01	-0.23	M. cf. tiete	-0.18	-0.38	S. maxillosus	-0.03	-0.05
H. ancistroides	0.02	-0.09	P. armatulus	-0.08	0.53	S. nasutus	0.69	0.07
H. edentatus	0.38	-0.05	P. corruscans	-0.16	-0.42	S. pappaterra	-0.02	-0.15
H. littorale	-0.21	-0.53	P. galeatus	-0.33	-0.08	S. spilopleura	-0.33	-0.25
						T. paraguayensis	-0.24	0.65

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Discussion

In spite of discharge control by upstream dams, the upper Rio Paraná floodplain has been subjected to variations in water level at least up to the closing of the Porto Primavera flood-gates by the end of 1998 (Agostinho & Zalewski, 1996; Thomaz et al., 1997; Veríssimo, 1999). However, a highly irregular hydrograph, low rainfall and discharge control in the period under analysis have contributed towards a lack of major floods.

When gradient of hydrological connectivity in the transversal axis of the floodplain, direction river-channel/isolated lagoons, is taken into account, it may be inferred that the greatest number of species were captured, on average, in the biotope with intermediary connectivity, or rather, the connected lagoons. However, this result is different from others reported by Agostinho et al. (1997; 2000) in the same area, not only in years of drought but also in years of flood; by Bonetto et al. (1978) in a tributary of the middle Paraná; and by Ward et al. (1999) in the Austrian floodplain of the Danube. In all these studies the rivers had the highest number of species. Differences may be partially explained by the absence of large and medium-sized fish species typical to the river main channel, probably due to the lack of regular floods. The sporadic presence of migratory species, such as H. platyrhynchos, P. maculatus, Leporinus sp. and P. granulosus in the channels and tributaries of the Rio Paraná may have occurred during the displacements towards the upper sections of these stretches. In fact, tributaries are of great importance for the spawning of migratory species (Nakatani et al., 1997; Vazzoler et al., 1997b). Nevertheless, permanent access of fish to connected lagoons favored the occupation of these sites with typically lentic adapted species, such as H. littorale, Gymnotus spp, A. ocellatus and R. rostratus, and with lotic adapted ones, such as P. granulosus, T. paraguayensis and L. friderici.

Lack of floods affecting fish assemblages, reported by Veríssimo (1999) and Agostinho et al. (2001), is also corroborated by this study. Low values of eveness have been observed, especially in lagoons of the upper Rio Paraná floodplain during 1986-1987 and 1996-1997, affecting all biotopes and subsystems. These periods were marked by interruptions and severe decrease in flood intensity (Agostinho et al., 1997; Veríssimo, 1999). Veríssimo (1999) stated that the closure of the Porto Primavera Dam at the end of 1998 affected the water level of the downstream stretch exactly during the spawning period of most species. Therefore, it resulted in recruitment reduction or even fail. It is thus possible that reduced abundance of large and medium-sized species is a result of poor recruitment. One must be however careful in interpreting the absence of spatial variation in species richness, diversity and eveness, since this is greatly due to marked differences in the distribution of the species relative abundance among sampling sites and to a high variability within a particular biotope. Similar results have been reached by Gehrke et al. (1995) who investigated the effects of discharge control on fish communities in Australian rivers.

The flood pulse, considered the main force function in the region (Thomaz et al., 1992), was characteristic for each subsystem. It influenced abiotic factors variation, like the high water transparency of the water column, the smallest concentrations of dissolved oxygen and pH of the sampling sites of the Baía subsystem. Spatial heterogeneity in abiotic factors has also been determined in other studies undertaken in the region (Thomaz et al., 1992; Agostinho et al., 2000). Considering that severe flood causes the homogeneity of environmental conditions in the floodplain biotopes (Thomaz et al., 1997), the spatial distinction for abiotic factors in the subsystems may have been a consequence of changes in the hydrological regime. This may indeed occur since severe flood pulses, absent during the period under analysis, are distinct from one another. Analyzing the main factors related to the structuring of fish assemblage in lentic and lotic systems, Jackson et al. (2001) emphasized pH and dissolved oxygen. Selective pressures on assemblages by

reduced levels of the mentioned factors may result in severe changes in species composition, through a decrease in abundance or even to the elimination of intolerant species. At the same time, the number of individuals of species that are adapted physiologically or anatomically to hypoxia and to relative water acidity remains somewhat unaltered.

A high number of sporadic species, represented by a single specimen during sampling, was the determining factor in the spatial differentiation of the sampling sites. Nevertheless, spatial differentiation pattern among subsystems and biotopes was not so clear, even among the most abundant species. Although only one annual cycle had been evaluated, it appears that heterogeneity in abiotic conditions explains species richness in the region, which, in its turn, affects its distribution and abundance.

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