Fish assemblage dynamics in a shallow floodplain lake in the South of Brazil.

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ABSTRACT: Fish assemblage dynamics in a shallow floodplain lake in the South of Brazil. The flood pulse concept suggests that the flood is the principal driving force responsible for the existence, productivity and interactions of the major biota in river floodplain systems. The main goal of this study was to analyze the effects of the floods events and abiotic variables (water temperature, depth, conductivity and transparency) on the fish composition, length, abundance, richness and diversity in a shallow floodplain lake over an annual cycle (2000-2001). Fourteen fish collections were carried out and fishes were sampled using electrofishing equipment. A total of 3,103 individual fish representing 25 species in six families was collected. The Characidae family (12 species) comprised 90.7% of sampled individuals. The fish abundance and richness increased along the annual cycle and the flood events contributed to it. However, the percentage of change on fish numbers and richness was not related with the flood duration. Water temperature, depth, conductivity and transparency influenced fish abundance and richness. The mean length of the six more abundant fish species over the studied annual cycle (representing 91.62% of the total number of collected fishes) was below the estimated length for the first gonadal maturation, showing that the majority of the collected fishes were juveniles. Our results confirm the hypothesis that the floodplains are crucial habitats for the development of juveniles and for the recruitment of the fish assemblages in the South of Brazil.
Key-words: floodplain, flood pulse, fish assemblage, recruitment, Neotropical region.

RESUMO: Dinâmica da comunidade de peixes em uma lagoa rasa associada a uma planície de inundação no Sul do Brasil. O conceito de pulso de inundação sustenta que a inundação é o principal elemento responsável pela organização das comunidades aquáticas em sistemas rio-planície de inundação. O objetivo deste estudo foi analisar o efeito das inundações e de variáveis abióticas (temperatura, profundidade, condutividade e transparência da água) na composição, tamanho, abundância, riqueza e diversidade da ictiofauna em uma lagoa rasa associada a uma planície de inundação ao longo de um ciclo anual (2000-2001). Foram realizadas 14 coletas através de um equipamento de pesca elétrica. Um total de 3.103 peixes distribuídos em 25 espécies e seis famílias foi coletado. A família Characidae (12 espécies) representou 90,7% dos indivíduos amostrados. A abundância e a riqueza de peixes aumentaram ao longo do ciclo anual, sendo que as inundações, provavelmente contribuíram para isto. Entretanto a variação destes parâmetros não esteve correlacionada com a duração das inundações. A temperatura, profundidade, condutividade e transparência da água influenciaram a abundância e a riqueza de peixes. O comprimento médio das seis espécies de peixes mais abundantes (representando 91,62% do número total de indivíduos) esteve abaixo do comprimento estimado para a primeira maturação gonadal, evidenciando que a maioria dos peixes coletados eram juvenis. Nossos resultados sustentam a hipótese de que as planícies de inundação são hábitats cruciais para o desenvolvimento de juvenis e, conseqüentemente, para o recrutamento das assembléias de peixes no Sul do Brasil.
Palavras-chave: planície de inundação, pulso de inundação, assembléia de peixes, recrutamento, região Neotropical.

Introduction

Disturbance has received substantial attention by ecologists mainly because it is a major organizer in many aquatic ecosystems (Sousa, 1984; Grimm & Fisher, 1989). The concept of disturbance in aquatic ecosystems may be defined in terms of the physical event, e.g. intensity, frequency, duration and predictability (Lake, 1990; Poff, 1992) or in terms of the biotic response (Pickett & White, 1985). In this sense, the definition of perturbation proposed by Bender et al. (1984) and Glasby & Underwood (1996) is useful because it describes the combination of cause (disturbance) and effects (response).

In aquatic ecosystems, studies related to disturbance ecology have concentrated efforts in understanding the effects of floods on communities, mainly floods of high intensity (Lake, 2000). The concept of disturbance in aquatic ecosystems is controversial (Benke et al., 1999). While floods in lower courses of the rivers trigger an important ecological interaction between a river channel and the associated floodplain (Junk, 1980), in streams the floods can be characterized as a catastrophic event (Resh et al., 1988).

The flood pulse concept suggests that the flood pulse is the principal driving force responsible for the existence, productivity and interactions of the major biota in river floodplain systems (Junk et al., 1989). Benke et al. (1999) argued that this concept is an extension of the river continuum concept (Vannote et al., 1980), which emphasized longitudinal linkages between downstream and upstream processes but ignored lateral connections between riparian zones. Benke et al. (1999) suggested that the ecological importance of the flood events is far broader than a simple exchange of organic matter between the main channel and the floodplain system. Floods provide a temporary habitat for fishes and other aquatic organisms several times larger than the area of the river channel (Ross & Baker, 1983).

Several studies of fishes in freshwater ecosystems have examined disturbance-related questions, but most of these studies were developed in streams (Ross & Baker, 1983; Harikumar et al., 1994; Rodríguez & Lewis Jr., 1994; Wootton et al., 1996; Maltchik & Medeiros, 2001). Fish populations appear to fluctuate in abundance and species composition from year to year (Starret, 1951), seasonally or over short periods of time, usually associated with floods and drought (Matthews, 1998). In streams, the flood may lead to death of young (Schlosser, 1985; Harvey, 1987) and adult fishes (Toth et al., 1982).

River-floodplain systems are important wetlands in the subtropical region of Brazil. The high heterogeneity of habitats found in these aquatic systems (Luiz et al., 2004) contributes to the high species diversity, especially for fish assemblages (Horne & Goldman, 1994). In the South of Brazil, most of the functional studies in river-floodplain systems was developed in the Upper Paraná River floodplain (Thomaz et al., 1991; Agostinho & Zalewski, 1995; Agostinho et al., 2001; Agostinho et al., 2004). Lake et al. (1986) and Boulton & Lake (1992) argued that longer periods of water flow increase the fish density, and Agostinho et al. (2001) suggests that fish richness increases during the flood events in floodplain systems.

The main goal of this study was to analyze the effects of the flood events and abiotic variables (water temperature, depth, conductivity and transparency) on the fish composition, length, abundance, richness and diversity in a shallow floodplain lake over an annual cycle (2000-2001).

Study area

This study was conducted in a shallow lake associated to a floodplain system in the lower course of the Sinos River in the South of Brazil (Rio Grande do Sul - RS) (Fig. 1). The Sinos River is a seventh order permanent river (Strahler, 1952) of Jacuí/Guaiba catchment. It is 190 km long from its origin at 900 m above sea level, to its confluence with Jacuí River at an elevation of 10 m. The annual precipitation in the Sinos River basin (~ 4,000 km²) ranges from 1,200 to 2,000 mm and is well distributed along the year. The increase in the discharge due to high precipitation originates a series of flood events resulting in the temporary inundation of the floodplain.

Figure 1: The studied floodplain system of the Sinos River (●), located in the South of Brazil (Rio Grande do Sul - RS).

The studied floodplain was approximately 30 ha, and presents several permanent and intermittent shallow lakes, scattered within two different types of vegetation: native woodland and grasslands. During the flood events, the water penetrates into the floodplain system along the different stream reaches. The surface water velocity in the floodplain systems during the flood period is very low. The discharge of Sinos River near the studied floodplain varies between 2.9 and 71 m^3/s (COMITESINOS, 2000).

The studied lake is permanent, irregular and shallow (mean water depth is 20 cm) and it is fed by water from precipitation, runoff and floods from the Sinos River. It has an inundation area of approximately 12,470 m² and is approximately 300 m from the main channel of the Sinos River. During the flood events, the water depth may reach approximately 200 cm in the studied floodplain system. The substratum of the studied lake consists of silt and organic debris. The permanent presence of surface water contributes to the strong development of aquatic macrophyte. Extended beds of Eichhornia azurea and Ludwigia grandiflora cover 95% of the water surface of the studied lake.

Material and methods

Fourteen fish collections were carried out during one annual cycle (from July 2000 to May 2001). Fishes were sampled using an electrofishing equipment of 750V

DC (max. 4A, EFKO). Previous studies showed that electrofishing was an efficient sampling method in fish surveys in the Sinos River (Petry & Schulz, 2001), and it was considered by Severi et al. (1995) a valid technique for qualitative investigations of fish communities because it is less selective when compared to other methods used (Growns et al., 1996).

During the studied annual cycle, diurnal samplings were carried out along a 150 m reach from the margin towards the center of the shallow lake. The sampled area was approximately 150 m². In this transect, the samples were carried out in different microhabitats (distinct types of dominant vegetation and water depth). The time taken for collection was approximately 20 minutes. Only the first collection was developed during the flood event (July 12), and was performed using a boat. All sampled fish were refrigerated in ice and taken to the laboratory for analysis. The collected fish were measured with a caliper to the nearest mm. The size of fish species were classified in small, medium and large following Vazzoler et al. (1997) and Koch et al. (2000). Species richness per collection was the total number of fish species found. The relative fish abundance per collection was represented by the catch-per-unit effort (CPUE - number of fish per 20-min electrofishing). Species diversity was calculated for each collection using Shannon's diversity index (Shannon & Wiener, 1949).

Water temperature and conductivity were measured in situ (one sample in the middle of the shallow lake) using digital water checker equipment (Water test – model 90). Water transparency was measured using a Secchi disk and the water depth was measured with a graduated PVC tube.

Flood duration was the amount of time (number of days) in that the floodplain system remained completely with surface water, and following the Tiner's classification, it was classified as long (between a week and a month) and very long (higher or equal a month). The flood events in the Sinos River basin were classified as frequent (more than fifty floods per 100 years) (Tiner, 1999). Regarding the fish dominance in the studied annual cycle, the species were classified as dominant (100%-30%), common (29%-10%), occasional (9%-1%) and rare (< 1%) (McCullought & Jackson, 1985). The dominance patterns of the fish assemblage were analyzed using specie abundance relationships (Magurran, 1988). The relationships between the variation in the fish abundance, richness and diversity with the flood duration were tested through Pearson correlation's coefficient. Multiple regressions (GLM) were used to determine the influence of the studied abiotic variables on the fish richness, abundance and diversity. To remove the heteroscedasticity, the environmental and biological data were firstly log transformed.

Ordination was performed using PC-ORD 4.2 (McCune & Mefford, 1999). A multivariate analytical approach (Canonical Correspondence Analysis - CCA) was used to examine the relationships between the measured environmental variables and the fish composition and length. Statistical significance of the contribution of each variable to each CCA axis was tested using Monte-Carlo simulation (1,000 iterations) (Ter Braak & Smilauer, 1998). The environmental variables used in CCA ordination were: water temperature, depth, conductivity and transparency. The biological variables were taken from fish species represented by 10 or more individuals found over the studied annual cycle.

Results

The studied shallow lake experienced four floods between July 2000 and May 2001 and the duration of the flood was different for each occasion. Three floods were characterized as long duration (15-19 days) and one as very long duration (> 38 days) (Tab. I). All four floods inundated the studied floodplain of the Sinos River, reaching a maximum depth of 200 cm on the edge of the studied lake (Tab. I). A total of 3,103 individual fish representing 25 species within six families were collected (Tab. II).

Table I: Physical characteristics of studied shallow lake in the South of Brazil along an annual cycle (2000 - 2001).

	12/07*	**27/07**	**10/08**	**24/08**	**08/09**	**25/09***	**02/11**	**09/11**	**22/11**	**06/12**	**08/01**	**11/02***	**01/03**	**22/03**	**19/04**	**28/04***	**31/05**
Days after flood	0	15	29	43	58	0	38	45	58	72	105	0	19	40	68	0	33
Duration of inundation (days)	15	-	-	-	-	38	-	-	-	-	-	19	-	-	-	19	-
Water temperature (°C)	12.7	9.9	15.5	18.6	18.6	-	25.6	27.3	36.4	32.2	31.3	-	30	28	25	-	25.3
Water depth (cm)	200	23.6	21.7	19.4	17.8	200	13.3	10.5	10.3	16.3	13.8	200	20.8	18	20	200	30
Water transparency (cm)	40	40	40	40	40	-	25	15	15	20	20	-	40	15	15	-	20
Water conductivity (µS/cm)	38	49	48	48	36	-	56	56	44	13	24	-	40	40	40	-	54

Flood dates*

Table II: Number of individuals per fish species and classification of fish size according to Vazzoler et al. (1997) and Koch et al. (2000) in the studied shallow lake in the South of Brazil along an annual cycle (2000-2001).

Species	Fish size	12/07	27/07	10/08	24/08	08/09	02/11	09/11	22/11	06/12	08/01	01/03	22/03	19/04	31/05	Total
sp1. Astyanax fasciatus (Cuvier, 1819)	Small	1	21	-	46	21	76	60	107	124	121	178	325	332	87	1,499
sp2. Astyanax bimaculatus (Linnaeus, 1758)	Small	2	9	36	40	53	5	7	11	10	18	11	29	49	7	287
sp3. Astyanax alburnus (Hensel, 1870)	Small	-	4	6	-	-	18	-	22	2	-	11	32	8	20	123
sp4. Astyanax sp. 1	Small	-	-	-	-	-	2	-	2	-	-	6	-	6	4	20
sp5. Astyanax sp. 2	Small	-	-	-	-	-	3	-	-	-	-	3	3	4	-	13
sp6. Phalloceros caudimaculatus (Hensel, 1868)	Small	1	-	-	-	-	1	-	-	-	-	-	-	-	-	2
sp7. Oligosarcus robustus (Menezes, 1969)	Medium	-	1	1	4	2	9	11	10	16	11	-	-	3	1	69
sp8. Hyphessobrycon luetkenii (Boulenger, 1887)	Small	-	-	29	63	52	-	18	21	-	28	81	68	46	75	481
sp9. Hyphessobrycon sp. 1	Small	-	3	5	9	8	17	12	8	15	16	25	43	23	9	193
sp10. Hyphessobrycon sp. 2	Small	-	5	2	-	3	20	-	-	26	-	-	-	-	-	56
sp11. Cyphocharax voga (Hensel, 1870)	Medium	-	6	2	12	7	52	37	39	64	22	6	4	3	6	260
sp12. Cyphocharax sp.	Medium	-	-	-	-	-	-	-	2	-	-	-	2	-	-	4
sp13. Cichlasoma facetum (Jenyns, 1842)	Small	-	2	1	-	1	-	1	1	1	5	-	1	-	-	13
sp14. Cichlasoma portalegrense (Hensel, 1870)	Medium	-	-	-	-	1	3	-	-	-	-	1	4	-	-	9
sp15. Cichlasoma gynogenis	Small	-	-	-	-	-	-	-	-	-	-	-	-	1	1	2
sp16. Hoplias aff. malabaricus (Bloch, 1794)	Large	-	-	1	-	1	-	-	1	-	1	-	-	-	-	4
sp17. Steindachnerina biornata (Braga & Azpelicueta, 1987)	Small	-	-	2	-	-	-	-	-	-	-	-	-	1	-	3
sp18. Pseudocorynopoma doriae (Perugia, 1891)	Small	-	-	-	8	-	15	8	5	1	1	-	-	-	-	38
sp19. Gymnotus carapo (Linnaeus, 1758)	Medium	-	-	-	2	-	1	-	-	-	-	-	-	-	-	3
sp20. Characidium sp.	Small	-	-	-	-	1	-	-	-	-	-	3	-	3	4	11
sp21. Gymnogeophagus rhabdotus (Hensel, 1870)	Small	-	-	-	-	-	-	-	-	-	1	-	-	1	1	3
sp22. Brycanomericus iheringii (Boulenger, 1887)	Small	-	-	-	-	-	-	5	-	-	-	-	-	-	-	5
sp23. Crenicichla lepidota (Heckel, 1840)	Medium	-	-	-	-	-	-	-	-	1	2	-	-	-	-	3
sp24. Crenicichla punctata (Hensel, 1870)	Medium	-	-	-	-	-	-	-	1	-	-	-	-	-	-	1
sp25. Prochilodus lineatus (Valenciennes, 1847)	Large	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1
Richness		3	8	10	8	11	13	9	13	10	11	10	10	14	11	-
Total		4	51	85	184	150	222	159	230	260	226	325	511	481	215	3,103

Most of the species found in the floodplain were classified as small and medium size (92%) (Tab. II). Only two large-size species were sampled over the period of study: Hoplias aff. malabaricus and Prochilodus lineatus. While Astyanax fasciatus was the only species classified as dominant (48.3%), Hyphessobrycon luetkenii was the only species classified as common (15.5%) (Fig. 2). The occasional and rare species represented 92% of the total of collected fishes (Fig. 2). The Characidae family (12 species) comprised 90.7% of sampled individuals (Tab. II).

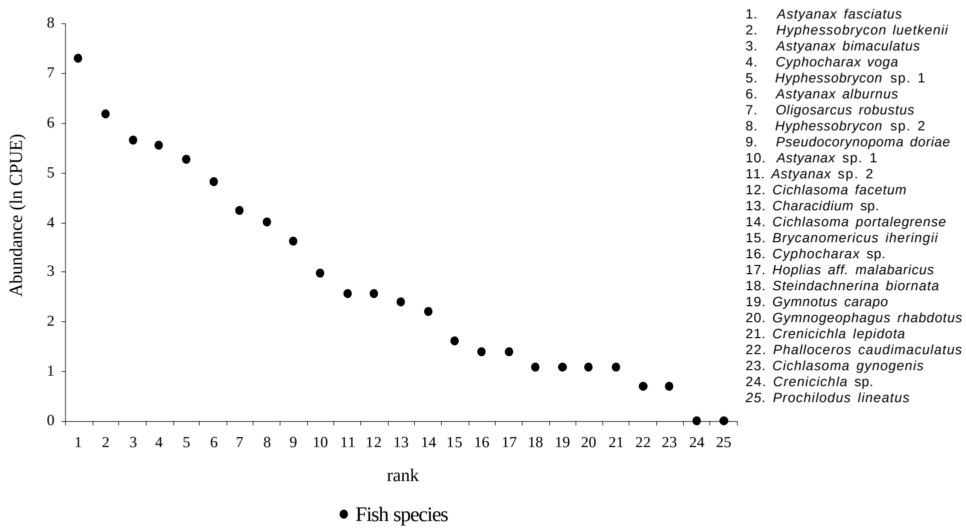

Figure 2: Specie abundance relationship curve in the studied shallow lake along an annual cycle (2000-2001).

The composition of fish species varied during the annual cycle and it was not related only with the flood events (Fig. 3). The physical data of studied shallow lake are shown in Tab. I. The CCA ordination method represents the environmental variables, sampling units and species in relation to their scores on the two main axes of ordination. The CCA determined the influence of the abiotic variables on the composition and length of fish assemblage over the studied annual cycle (Fig. 4).

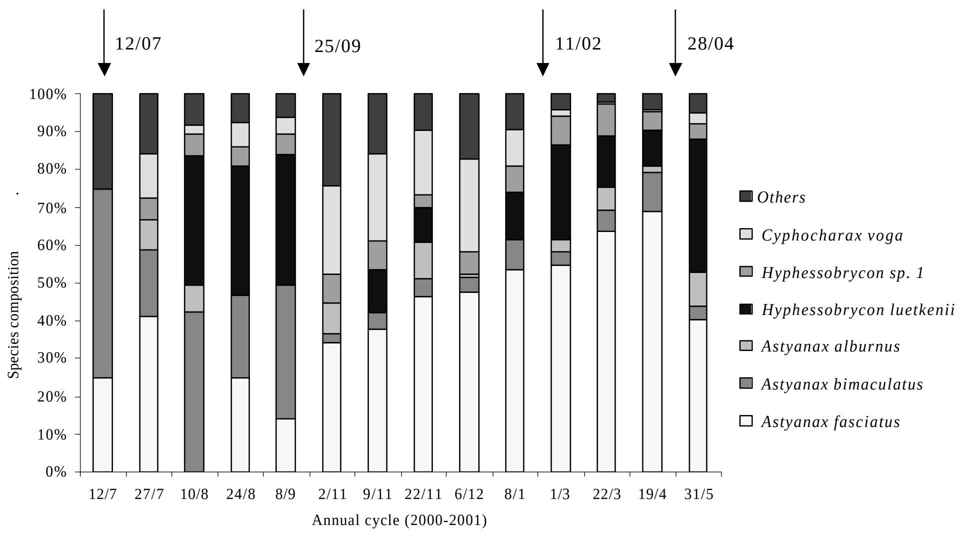

Figure 3: Relative frequency of the dominant species in the studied shallow lake along an annual cycle (2000-2001). Arrow = flood occurrence.

The two first axes explained only 21.4% (14.2% in the axis "1" e 7.2% in the axis "2") of the total variation in the composition and length of the fish assemblage (Tab. III). The Monte-Carlo simulation test (1,000 iterations) showed that the variation in the composition and length of fish assemblage was not related with the water temperature, depth and transparency (P ›0.05) (Fig. 4). However, the smaller individuals of Astyanax fasciatus and Astyanax bimaculatus were associated to collections of the low surface water depth (Fig. 4).

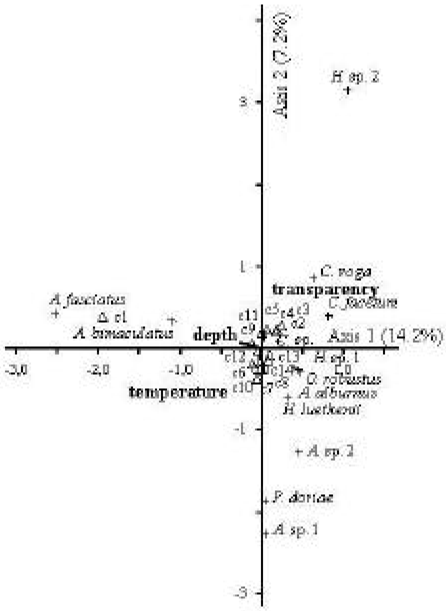

Figure 4: CCA ordination biplot with fish composition (+), collections (") and the studied environmental variables (vectors). c= collections.

Table III: Canonical Correspondence Analysis: summary of results for the first two ordination axes.

	CCA axis	
	1	**2**
CCA: data set (14 collections)		
Eigenvalue	0.088	0.045
Cumulative % variance of taxa	14.2	21.4
Pearson correlation: taxa-environment data	0.922	0.646
Monte Carlo test (p)	0.085	0.818

The relative abundance of fish sampled increased progressively over the 2000-2001 annual cycle (Fig. 5), reaching the highest values during the end of the annual cycle. The abundance was positively influenced by the water temperature and negatively influenced by the water depth, conductivity and transparency (GLM, R^2= 0.714; $F_{4,9}$= 5.612; P= 0.015). The flood events tended to increase the fish abundance, with exception to the last event (April 28). The percentage of change on fish numbers was not related with the flood duration (Pearson, r= 0.531; P= 0.644). The six most abundant fish species over the studied annual cycle (Astyanax fasciatus, Astyanax bimaculatus, Astyanax alburnus, Hyphessobrycon luetkenii, Hyphessobrycon sp. 1 e Cyphocharax voga - with more than 100 individuals) represented 91.62% of the total number of collected fishes. The mean length of these six fish species varied between 25 and 122 mm (Fig. 6).

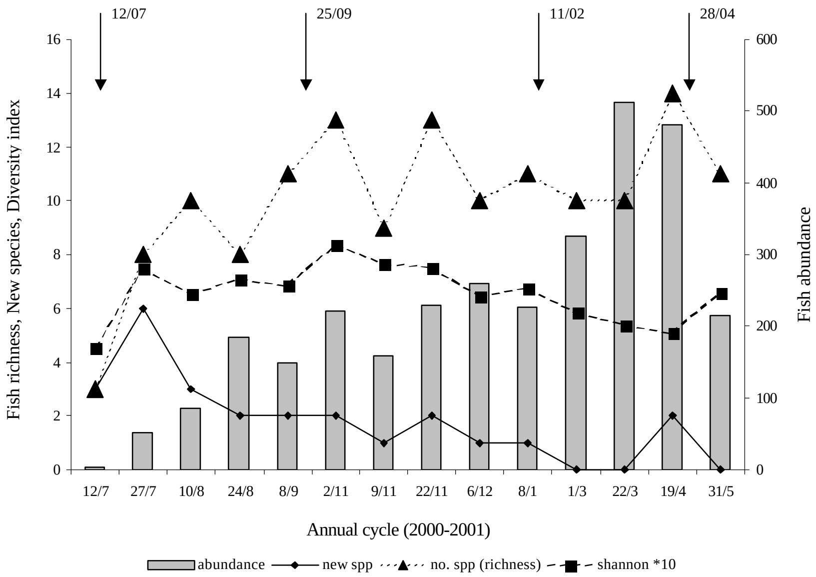

Figure 5: Abundance, new species, richness and diversity of fish community in the studied shallow lake along an annual cycle (2000-2001). Arrow = flood occurrence.

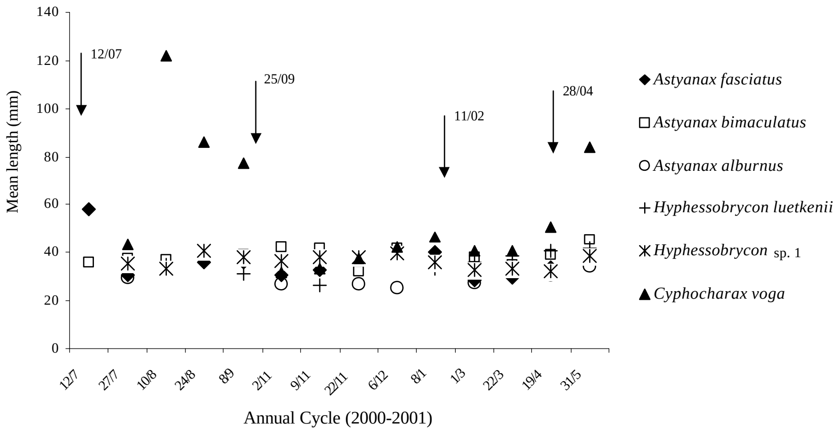

Figure 6: Mean length of the six most abundant fish species (represented by the species with more than 100 individuals) in the studied shallow lake along an annual cycle (2000-2001). Arrow = flood occurrence.

The fish richness tended to increase along the annual cycle and the mean values pooled for the periods after inundation were progressively higher (Fig. 5). However, the flood events influenced differently the total fish richness (Fig. 5) and it was not related with the flood duration (Pearson, r= 0.910; P= 0.272). The number of new species per collection was higher during the beginning of the annual cycle, and more than half of the species found were captured before the second flood (Fig. 5). The fish richness was positively influenced by the water conductivity and negatively influenced by the water temperature, depth and transparency (GLM, R^2= 0.756; $F_{4,9}$=6.970; P= 0.008).

The diversity of fish also increased slightly during the beginning of the annual cycle reaching the highest values after the flood with the highest duration but started to decrease after the second inundation (Fig. 5). This result may be related to the higher number of fish captured (mainly Astyanax fasciatus) during the second half of the annual cycle. The percentage of change of the fish diversity was not related with the flood duration (Pearson, r= 0.338; P= 0.781). The water depth influence negatively on fish diversity (R^2= 0.441; $F_{1,12}$=9.454; P= 0.01), however, the water temperature (R^2= 0.113; $F_{1,12}$= 1.528; P= 0.240), conductivity (R^2= 0.071; $F_{1,12}$= 0.916; P= 0.357) and transparency (R^2= 0.001; $F_{1,12}$= 0.012; P= 0.916) did not influence the fish diversity.

Discussion

Junk et al. (1989) demonstrated the importance of floods on the structure and functioning of the floodplain systems. Agostinho et al. (2001) observed that the floods positively influence the fish richness in floodplain systems and Júlio Jr. et al. (2000) maintained that floods allow the movement of fish communities within its favorite habitats in the river-floodplain system. In our study, fish abundance and richness increased along the annual cycle and the floods events contributed to it. This increase may be a consequence of the fish input from the main channel during the inundation events and of the dragging of eggs and larvae of various fish species that use those lakes to go through their development (Júlio Jr. et al., 2000; Nakatani et al., 2004). The fish dispersion among nearby wetlands within the studied floodplain is another possibility, due to the fact that the six most abundant fish species that were of small and medium size, presented sedentary habitat or realized small-scale migrations. However these hypotheses should be tested through radiotelemetry studies. Junk et al. (1989) maintain that the flood pulse is the key factor in the organization of the aquatic communities from floodplains. This hypothesis is often supported by researchers who investigate such environments (Thomaz et al., 1997).

The abiotic variables (water temperature, conductivity, depth, and transparency) also influenced fish abundance and richness over the studied annual cycle. According to Thomaz et al. (1997), river-floodplain systems in tropical regions show a noticeable time variation of physical, chemical and biological factors as a reaction to the flood events. Considering the causal interaction among the abiotic variables and the flood pulses it is hard to identify the determinant factor in the fish assemblage variation over the investigating time period in the floodplain.

Water level fluctuation is a complex variable, which encompasses several attributes (intensity, frequency and duration). According to Agostinho et al. (2001), the assemblage composition of fish communities in wetland systems is influenced by the flood regime. In this study, no relation was observed (positive or negative) between duration of flood and variation in the richness and abundance of fishes. The lack of any relationships may have been influenced by the low number of events or because the majority of the floods which occurred were of long duration.

Our study showed that none of the measured environmental variables could account for the variation in the composition and length of fish assemblage. However, the slight variation in the mean length of the fish community over the studied annual cycle could have led to that outcome. It was noticed that the smaller individuals of Astyanax fasciatus and Astyanax bimaculatus were associated with the collections of low water depth. According to Silva (1994), in a lacustrine environment longer fish dwell in deeper habitats, and only once in a while they look for marginal regions for feeding and reproduction, and smaller individuals try to remain in more shallow waters where they probably do not undergone the action of predators.

Medeiros & Maltchik (2001a,b) pointed out that, although the floods hindered the establishment of dominant species in a tropical semiarid stream, during the discontinuous surface water flow some fish species became dominant in these systems. Throughout this study the inundations did not impede the establishment of dominant species as e.g. Astyanax fasciatus, Astyanax bimaculatus and Hyphessobrycon luetkenii. This result can be due to the fact that the dominant species found are characteristic of lentic systems. Vazzoler et al. (1997) regarded that small-sized sedentary fish species use the lentic environments of floodplain systems to complete their life cycles.

Floodplains and rivers have a high level of biological integrity (Agostinho & Zalewski, 1996). Flood events seasonally connect large extensions of the terrestrial environments to the nearby water bodies, increasing the availability of food, suitable habitats for reproduction, growth rates and competition in fish communities (Ross & Baker, 1983; Agostinho et al., 2001; Graaf, 2003). The mean length of the six most abundant fish species was below the estimated length for the first gonadal maturation, indicating that the majority of the collected fishes were juveniles (Fontoura et al., 1993; Hartz & Barbieri, 1994; Vazzoler et al., 1997). Vazzoler et al. (1997) noticed that 70% of the individuals found in the floodplain of the Upper Paraná River were juveniles that occupied mainly the lentic environments of those systems. According to Paiva (1982), floodplains are recognized as natural nurseries for several fish species. Along the flood events, eggs and larvae of different fish species can be driven to those lakes where more chances for their development due to better conditions of food and shelter can be found (Júlio Jr. et al., 2000).

Our results confirm the hypothesis that floodplain water bodies are crucial habitats for the development of the juveniles and for the recruitment of the fish assemblages (Agostinho & Zalewski, 1996; Molls, 1999; Grift et al., 2001). The failure of a flood event would probably result in a strong negative impact on the fish reproductive activity in this region.

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