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Diet seasonality and food overlap of the fish assemblage in a pantanal pond

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We assessed the trophic structure of the fish fauna in Sinhá Mariana pond, Mato Grosso State, from March 2000 to February 2001. The aim was to determine the feeding patterns of the fish species during the rainy and dry seasons. The diets of 26 species (1,294 stomach contents) were determined by the volumetric method. Insects and fish were the most important food resources: insects were the dominant food of 23% and 27% of the species, respectively, in the rainy and dry season, and fish was the dominant item for 31% of the species in both seasons. Cluster analysis (Euclidean Distance) identified seven trophic guilds in the rainy season (detritivores, herbivores, insectivores, lepidophages, omnivores, piscivores and planktivores), and five trophic guilds in the dry season (detritivores, insectivores, lepidophages, omnivores and piscivores). The smallest mean values of diet breadth were observed for the specialist guilds (detritivores, lepidophages and piscivores), in both seasons. The widest means for diet breadth were observed for the omnivores, regardless of the season. In general, there was no seasonal variation in feeding overlap among the species studied. At the community level, diet overlap values between species were low (< 0.4) for 80% of the pairs in each season, suggesting wide partitioning of the food resource. The fish assemblage showed a tendency toward trophic specialization, regardless of the season, although several species changed their diets. We might consider two non-excludent hypothesis: that there is no pattern on the use of seasonal food resources and/or probably there are several patterns, because each one is based on characteristics of the studied site and the taxonomic composition of the resident species.

Neste trabalho foi avaliada a estrutura trófica da ictiofauna na baía Sinhá Mariana (MT), no período de março de 2000 a fevereiro de 2001, com o objetivo de detectar qual o padrão alimentar exibido pelos peixes, durante as estações chuvosa e seca. A dieta de 26 espécies (1.294 estômagos) foi avaliada pelo método volumétrico. Insetos e peixes foram os itens mais consumidos pela maioria das espécies, sendo que o primeiro foi alimento dominante para 23% e 27% das espécies, respectivamente, na cheia e na seca e o segundo para 31% das espécies em ambas as estações. Através da análise de agrupamento (Distância Euclidiana) foram identificadas sete guildas tróficas na cheia (detritívora, herbívora, insetívora, lepidófaga, omnívora, piscívora e planctívora) e cinco na seca (detritívora, insetívora, lepidófaga, omnívora e piscívora). Os menores valores médios de amplitude de nicho trófico foram verificados para as guildas constituídas por espécies especialistas (detritívora, lepidófaga e piscívora), em ambos os períodos. Em oposição, as maiores médias foram observadas para a guilda omnívora, independente do período. Em geral, não houve variação sazonal na sobreposição alimentar das espécies. Em nível de comunidade, os coeficientes de sobreposição alimentar foram baixos (< 0,4) para cerca de 80% das espécies para cada período, indicando ampla partição de recursos alimentares. A assembléia de peixes mostrou tendência à especialização trófica, independente da estação considerada e apenas algumas espécies mudaram suas dietas. Assim, é possível considerar duas hipóteses: que não existe um padrão sazonal no uso dos recursos alimentares e/ou que provavelmente existam vários padrões, uma vez que cada um deles é baseado nas características do ambiente estudado e na composição taxonômica das espécies residentes.

Key words: Fishes, Feeding overlap, Seasonal analysis, Pond.

Introduction

Studies of feeding in fish assemblages in a particular site allows us to recognize distinctive trophic guilds, and also make inferences about their structure, the degree of importance of the different trophic levels and the relationships among their components. In regard to trophic relationships among Neotropical fishes, one of the major challenges is to understand the ecological mechanisms by which a large number of species are able to coexist in the same community and the manner in which resources are shared (Esteves & Galetti, 1994). Studies in several freshwater environments (Goulding, 1980; Prejs & Prejs, 1987; Olurin *et al*., 1991; Hahn *et al*., 2004; Mérona & Mérona, 2004; Pouilly *et al*., 2003, 2004, 2006) have shown that the same food resource may be shared by numerous fish species, and that each species may successively exploit several different sources during the year. Although trophic segregation has been indicated as the main mechanism structuring fish assemblages

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(Pianka, 1969; Ross, 1986), this may vary according to sites conditions such as seasonality (Bouton *et al*., 1997).

Neotropical freshwater ecosystems undergo cyclic changes in response to alternating wet and dry seasons. These changes affect the food resources for the fish fauna, and according to several researchers (Araújo-Lima *et al*., 1995; Winemiller & Jepsen, 1998; Lowe-McConnell, 1999; Yamamoto, 2004; Hahn *et al*., 2004) may modify the trophic spectrum and the feeding rhythm of the fish, influencing the trophic relationships among species. Esteves & Aranha (1999) noted that studies of the effects of hydrological changes on fish assemblages may elucidate qualitative and quantitative changes in the diet for different species resident in the site.

In spite of the search for answers to interpret the different patterns observed in studies conducted in tropical regions, there is no agreement on seasonal effects (hydrological cycle) on the organization of fish assemblages. Lowe-McConnell's (1964) studies on the Rupununi River (British Guiana) pioneered in reporting on cyclical alterations in trophic organization of fishes. According to Lowe-McConnell, the fish fauna in general showed more specialized diets during the high-water season when foods are varied, and lower food overlap values were recorded among species in this period. Prejs & Prejs (1987) reported high food overlap in the dry season for fish communities in Venezuelan rivers, as did Meschiatti (1995) for marginal ponds of the Mogi-Guaçu River, São Paulo, Brazil. Other studies conducted on the Machado and Negro rivers in Amazonas, Brazil, gave similar results (Goulding, 1980; Goulding *et al*., 1988). On the other hand, Zaret & Rand (1971) observed reduced diet overlaps between species during the dry season in Panamanian streams, which they attributed to a shortage in food resources. Conversely, Mérona & Mérona (2004) pointed out that there was no difference in mean overlap for the Rei Lake (Amazonas) fish fauna between seasons. Whereas individual species exhibited diet changes between the wet and dry seasons, there was no general pattern of seasonal change within feeding guilds.

In this context, the main objective of the present study was to examine seasonal patterns (hydrological cycle) of diet among fish species of the Sinhá Mariana pond in Mato Grosso State, to estimate the potential for trophic interactions within the local assemblages. Our question was: do the fish act as more trophic specialists in the rainy season when food sources are plentiful, or in the dry season when the opposite situation obtains?

Material and Methods

Study area. Sinhá Mariana pond (locally called a "baía"or bay) is part of an enormous complex of ponds and várzeas in the Pantanal wetland, Mato Grosso State, Brazil. This pond belongs to the Cuiabá River basin and is located near the Barão de Melgaço district (16º20.3'S, 55º54.2'W) (Fig. 1). The Cuiabá River basin covers approximately 9,365 km², comprising the Cerrado and Pantanal regions of the Mato Grosso State. This pond is located in a relief plain, in a fluvial-lacustrine plain in the middle flood area (Franco & Pinheiro 1982). The bottom is mainly sandy, and the mean depth during the study period was 1.55 m. This region is characterized by complex seasonal dynamics in function of the hydrological cycle (rainy and dry season).

Fish collections. Fish were collected from March 2000 through February 2001, using gill nets with different mesh sizes (24 to 140 mm between opposite knots) and seining (50 m length and 0.5 cm mesh). Nets were left in the water for 24 hours, with inspections at 8:00, 17:00 and 22:00. The seines were operated during the day (8:00 hours) and at night (22:00 hours). All individuals were measured (standard length, cm) and weighed (total weight, g). The stomach contents were fixed in 10% formalin. Representative specimens of all species were deposited in the Núcleo de Pesquisas em Limnologia, Ictiologia e Aqüicultura (Nupélia - NUP), Universidade Estadual de Maringá, Paraná State).

All analyses were conducted considering the hydrological cycle: the rainy season as occurring in March, April, November and December 2000, and January and February 2001; and the dry season as from May to October 2000. These periods were defined with respect to the water level of the Cuiabá River (Fig. 2).

Diet analysis and trophic classification. The diets of 26 species were based on all stomachs with food, when at least four individuals of a species were caught in each period. The food items were identified under optical and stereoscopic microscopes, and were grouped in eight taxonomic and/or ecological categories to facilitate the interpretation of the guilds at the inter-specific level (Pouilly *et al*., 2006) and for general comparisons: insects (Chironomidae, other Diptera, Coleoptera, Ephemeroptera, Hymenoptera, Hemiptera, Isoptera, Trichoptera and insect remains), crustaceans (Decapoda), microcrustaceans (Cladocera, Copepoda, Ostracoda and Conchostraca), other invertebrates (Testacea, Rotifera, Nematoda, Oligochaeta, Gastropoda, Bivalvia, Araneae, Acarina), fish (Characiformes, Clupeiformes, Gymnotiformes, Siluriformes, Synbranchiformes, Perciformes and fish remains), scales (without other fish remains), plants (leaves, fruits/seeds, algae) and detritus/sediment (including all kinds of material from the bottom, organic film, mud, sand and sponge spicules).

Stomach contents were analyzed by the volumetric method; *i.e.*, the total volume of a food item taken by the fish population is given as a percentage of the total volume of all stomach contents (Hyslop, 1980), using graduated test tubes, and a glass counting plate (Hellawell & Abel, 1971). Food items were determined to the most detailed taxonomic level possible.

Fish diets were compared and grouped by cluster analysis (UPGMA algorithm) on the Euclidian Distance matrix derived from relative volume (eight taxonomic and/or ecological categories) *versus* fish species. The pattern of similarity in the diets was described for each season. To perform this analysis we used the program Statistic 7.0.

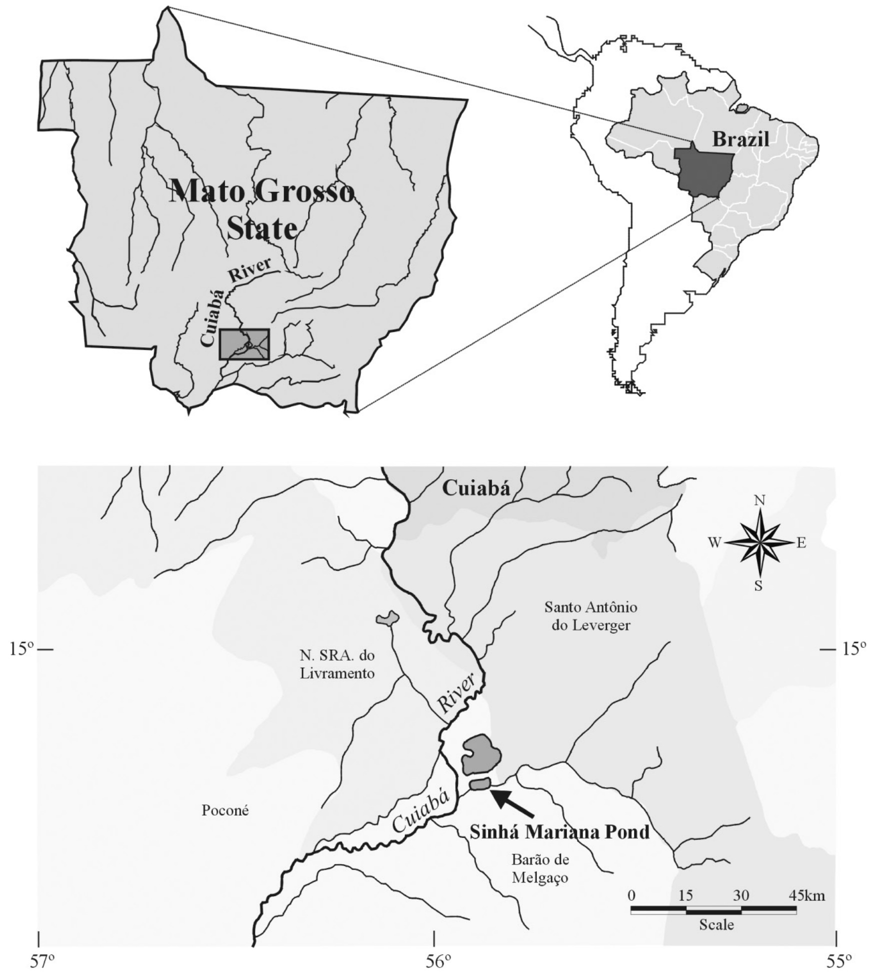

Fig. 1. Studied area showing the Sinhá Mariana pond (Mato Grosso State, Brazil).

Dietary specialization. In order to show the relative level of dietary specialization of the species, the diet breath of a given species or guild was calculated using Levin's measure (Krebs, 1999), with volume value data. Hurlbert's formula (1978) was applied to standardize the trophic niche measure (ranging from 0 to 1), according to the formula:

$$Bi = \frac{1}{(n-1)}\left(\frac{1}{(\sum_j p_{ij}^2)} - 1\right)$$

where: Ba = Levin's standardized index for predator i; p_{ij}= proportion of diet of predator i that is made up of prey j; n= total number of food resources. Breath niche values were arbitrarily set at the following levels: high (> 0.6), intermediate (0.4 - 0.6) or low (<0.4).

To test the assumptions, the Shapiro-Wilk test for normality and the Levene test for equality of variance were performed (Shapiro & Wilk, 1965). Data were tested by Student's t test to verify differences between rainy and dry seasons (Statistica 7.1 - www.statsoft.com).

Feeding overlap. Feeding overlap was measured for each hydrological season using the Pianka Index (1973), according to the formula:

$$O_{jk} = \frac{\sum_i^n p_{ij} p_{ik}}{\sqrt{\sum_i^n p_{ij}^2 \sum_i^n p_{ik}^2}}$$

where: O_{jk} = Pianka's measure of niche overlap index between j and k species; p_{ij} = proportion resource i of the total resources used by species j; pik = proportion resource i of the total resources used by species k; n = total number of resource states.

Overlap values were arbitrarily set at the following levels: high (> 0.6), intermediate (0.4 - 0.6) or low (<0.4) (Grossman, 1986). This index assumes prey to be equally available to all predators (Reinthal, 1990).

We used a null model to evaluate the significance of Pianka's index for each hydrological season (Inger & Colwell, 1977; Juliano & Lawton, 1990; Winemiller & Pianka, 1990; Tokeshi, 1999). In this null model, the observed percent of food category values were randomized 10,000 times within each period, and for each randomization a Pianka's index was calculated. The P-value for the observed index was estimated as the proportion of randomized index greater than the observed one. The null model analysis was computed using EcoSim 7.0 (Gotelli & Entsminger, 2006).

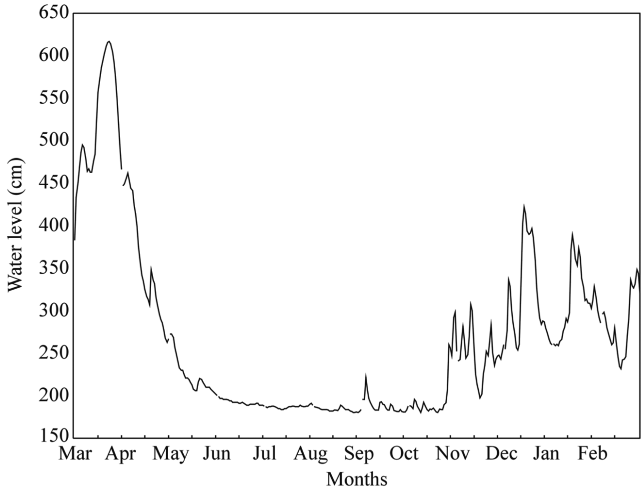

Fig. 2. Water level in the in the studied region, Sinhá Mariana pond, Mato Grosso State, Brazil, from March/2000 to February/2001, showing the wet and dry seasons. These dates were provided by Agência Nacional de Águas (ANA).

Results

A total of 1,294 fish belonging to 26 species, 24 genera, 12 families and three orders were consistently caught at the study site. These species occurred in both hydrological seasons (rainy and dry) and provided enough stomach-content data (at least four individuals) to conduct all the analyses (Table 1).

Diet and trophic guilds. Stomach content analysis showed that 24 food items were consumed by the fish fauna. Insects and fish were the most exploited resources by the majority of the fish species. Insects were the main food of 23% of the fish in the rainy season and 27% of the fish in the dry season. Fish were the dominant prey of 31% of the species in both periods. Detritus/sediment was prominent in the stomach contents of 15% of the species in both periods; microcrustaceans were preferred food only for *Moenkhausia dichroura*, and scales only for *Roeboides prognatus*. Plants occurred in the diet of nine and ten species in the rainy and dry seasons respectively, but were the preferred food of 11% of the fish species in the rainy season (Tables 2 and 3).

Cluster analysis based on diet composition (Tables 2 and 3) showed seven and five major trophic guilds (Fig. 3) in the rainy and dry seasons respectively.

Detritivores: four and six fish species, in the rainy and dry seasons respectively, largely consumed organic detritus and sediments, showing bottom-dwelling behavior. *Prochilodus lineatus, Hypostomus boulengeri, Pterygoplichthys ambrosettii,* and *Psectrogaster curviventris* fed on detritus in both seasons, showing low breadth niche (B = 0.15).

Herbivores: this trophic guild occurred only in the rainy season, and was represented by *Astyanax abramis, Loricaria* sp. 1 and *Trachydoras paraguayensis*. In their stomach contents, fruits and seeds (volume > 60%) predominated, with small portions of leaves and algae (filamentous, unicellular and colonials). These species showed low breadth niche (B = 0.15).

Omnivores: three species in the rainy season and four species in the dry season showed mixed diets composed of animal food items (microcrustaceans, insects and fish), vegetable food items (leaves, fruits, seeds and algae) in addition to detritus, in

Table 1. Fish species list included in this study. Sinhá Mariana pond. Mato Grosso State. Brazil (March/2000 to February/2001). CD = Code of the species used in figure 3; VS = Voucher specimens; SA = Number of stomach contents analyzed; SL = Standard Length range (cm).

ORDER/Family/Species	CD	VS	Rainy Period		Dry period	
			SA	SL	SA	SL
OSTEICHTHYES						
CHARACIFORMES						
Acestrorhynchidae						
Acestrorhynchus pantaneiro	Apan	Nup 874	8	5-24	25	9.4-24.5
Characidae						
Aphyocharax anisitsi	Aani	Nup 2149	5	1.6-4.3	14	1.8-3
Aphyocharax dentatus	Aden	Nup 956	39	2 - 5.5	60	2-5.7
Astyanax abramis	Aabr	Nup 2130	8	2.5-5.1	22	3.1-7.2
Bryconamericus exodon	Bexo	Nup 3551	5	1.4-3.6	21	1.5-4.1
Hemigrammus marginatus	Hmar	Nup 1977	4	1 - 3.4	9	1.3-2.9
Moenkhausia dichroura	Mdic	Nup 3259	20	1.3-7.2	23	1.7-7
Pygocentrus nattereri	Pnat	Nup 3330	50	2.5 - 27	18	12.5-28.5
Roeboides affinis	Raff	Nup 2169	10	2.9-10.5	41	3.2-10
Salminus brasiliensis	Sbra	Nup 3270	5	10-42.5	6	17.5-41.5
Serrasalmus marginatus	Smar	Nup 3393	17	1.6-24.6	4	4-21.5
Triportheus nematurus	Tnem	Nup 921	16	3.6-18.5	66	6.5-17
Curimatidae						
Psectrogaster curviventris	Pcur	Nup 1007	8	5.3-15.5	37	5.1 - 21
Cynodontidae						
Rhaphiodon vulpinus	Rvul	Nup 880	7	30.5- 53.5	5	27.5-50.5
Parodontidae						
Apareiodon affinis	Aaff	Nup 3436	27	0.9-6.9	12	2.1-6.6
Prochilodontidae						
Prochilodus lineatus	Plin	Nup 2254	15	6.5-37.5	11	8.6-33.5
PERCIFORMES						
Sciaenidae						
Pachyurus bonariensis	Pbon	Nup 3364	156	1-17.5	57	0.9-17.5
Plagioscion ternetzi	Pter	Nup 3006	31	0.7-35	13	6.5-34.5
SILURIFORMES						
Auchenipteridae						
Auchenipterus osteomystax	Aost	Nup 1932	12	15-21.5	21	11-21
Doradidae						
Trachydoras paraguayensis	Tpag	Nup 4539	47	2-11.7	53	2.7-12.3
Heptapteridae						
Pimelodella gracilis	Pigr	Nup 202	10	3.6-9	92	3.6-8.2
Loricariidae						
Loricaria sp. 1	Lor1	Nup 1048	5	4.5-28.5	6	11.5 - 25
Hypostomus boulengeri	Hbou	Nup 3542	12	11.3-21.5	13	9.8-21.5
Pterygoplichthys ambrosettii	Pamb	Nup 2115	11	21.5-34	4	17-33.5
Pimelodidae						
Pimelodus argenteus	Parg	Nup 2135	28	2-33.5	38	5.3-17.5
Pimelodus maculatus	Pmac	Nup 4142	27	6-21	40	5.4-20

Table 2. Diet composition (volume) of the fish species in the Sinhá Mariana pond during the rainy season. The numbers in bold indicate the main food items (values ³ 50%),* values < 0.1. The marked lines show the sum of the organisms inside of each taxonomic category.

Species / Items	*A. abramis*	*A. affinis*	*A. anisitsi*	*A. dentatus*	*A. osteomystax*	*A. pantaneiro*	*B. exodon*	*H. boulengeri*	*H. marginatus*	*Loricaria* sp.1	*M. dichroura*	*P. ambrosettii*	*P. argenteus*	*P. .bonariensis*	*P. curviventris*	*P. gracilis*	*P. lineatus*	*P. maculatus*	*P. nattereri*	*P. ternetzi*	*R. affinis*	*R.. vulpinus*	*S. marginatus*	*S. brasiliensis*	*T. nematurus*	*T. paraguayensis*
Insects	32.2		88.1	4.6	99		89.6		60	10.6			10.8	98.2	0.1	25.4	0.6	5.1		*	0.1		6.6		77.6	10.7
Chironomidae			2.9	0.3	*		44.8		25	0.7			0.5	61	0.1	1.1	*	*		*	0.1		*		*	0.9
Diptera	0.4		58.8	0.1	33.1		14.9						*	0.1		0.2		*		*					*	*
Coleoptera	20			0.3	5								*	0.1		1		0.2					0.3		1.8	
Ephemeroptera				0.8	46.5				15				9.2	36.6		13		0.1					6.3		47.2	0.1
Hymenoptera	11.8			0.5	2.4								0.1			0.1	*	*							4.2	
Hemiptera			8.8	2.4	0.1		7.5							0.3		0.1							*		24.3	0.1
Trichoptera										9.9				0.1				0.1		*					*	9.3
Insect remains			17.6	0.2	11.9		22.4		20				2.2			9.9	0.6	4.6								0.3
Crustaceans											2.3							4.7	0.4	2.4						
Microcrustaceans	0.4	36.5	2.9	8.3	1		7.5	0.7	20		95	7.5	0.7	0.7	4.4	0.5	4.7	*		*			*		19.9	4.7
Other Invert.		2.4	2.9	0.01			1.5						*			3.7		0.6		0.2					2.4	2.9
Fishes				86.7		100							38.5	0.4		67.4		31.5	98.8	97	1.2	100	93	100		
Characiformes				86.4		70										67.4			25.6	16.4		2.6	33	70.9		
Clupeiformes						28.9																				
Gymnotiformes																			0.2	36.2		25.8				
Siluriformes														0.4					7.2	12.7			13.8			
Synbranchiformes																						28.8				
Perciformes																			13.1	29.3						
Fish remains				0.3		1.1							38.5					31.5	52.7	2.4	1.2	42.9	46.2	29.1		
Scales				0.2							0.1		13			1.2	0.1	0.9			98.6		0.3		*	4
Plants	67.5	24.5						8.1		80.2		15.2	26.5	0.8	9.3	0.6	13.4	33.3	0.9	0.4			*		0.2	65.6
Leaves		2.4											0.1	0.8			5.6	2.8	0.9	0.3			*		0.2	
Fruits/seeds	67.5									80.1			26.4			0.5		30.2		*						65.2
Algae		22.1						8.1		0.1		15.2	*		9.3	0.1	7.8	0.3							*	0.4
Detritus		36.7	5.9	0.3			1.5	91.2	20	9.3	2.7	77.3	9.4	*	86.2	1.2	81.1	24					*		*	12.1

similar proportions. This guild did not show the same species composition in the rainy and dry seasons, except for *Pimelodus argenteus* which showed an omnivorous feeding habit during the entire study period (B = 0.48 and B = 0.56 respectively in the rainy and dry seasons). Although *Moenkhausia dichroura* showed a preference for microcrustaceans (diet volume > 60% in both periods), it belongs to this guild in the dry season because it consumed 14% insects, 12% detritus and 11% plants (B = 0.32). The values for diet breadth for this guild were the highest compared to the other guilds, regardless of the hydrological season (B = 0.51 and B = 0.41 respectively in the rainy and dry seasons).

Insectivores: six and seven species belonged to this trophic guild in the rainy and dry seasons, respectively. Aquatic insect larvae (Chironomidae, Ephemeroptera and Trichoptera) were the most important food items for the greater part of the species. However, *Loricaria* sp.1 and *Aphyocharax anisitsi* consumed preferentially terrestrial Coleoptera and indeterminate insect remains, respectively, in the dry season. *Auchenipterus osteomystax, Bryconamericus exodon, Pachyurus bonariensis,* and *Triportheus nematurus* occurred in both seasons, and showed B = 0.08 in the rainy season and B = 0.11 in the dry season.

Planktivores: this trophic guild was represented only by *M. dichroura*, during the rainy season. This species consumed mainly zooplankton (volume = 95%), principally Cladocera and Copepoda, showing low breadth niche (B = 0.03).

Lepidophages: although scales were found in the stomach contents of several species, only for *Roeboides affinis* this source was important in the diet (volume > 90%), in both season (B = 0.01 and 0.03 respectively, in the rainy and dry seasons).

Piscivores: eight and seven species, respectively, in the rainy and dry seasons consumed fish (volume between 50 and 100%). *Acestrorhynchus pantaneiro, Plagioscion ternetzi, Raphiodon vulpinus, Salminus brasiliensis*, and the piranhas *Serrasalmus marginatus* and *Pygocentrus nattereri* were essentially piscivorous during the study period (volume of prey fish > 95%). The niche breadth values ranged between 0.03 and 0.07, respectively in the rainy and dry seasons.

Table 3. Diet composition (volume) of the fish species in the Sinhá Mariana pond during the dry season. The numbers in bold indicate the main food items (values ³ 50%), * values < 0.1. The marked lines show the sum of the organisms inside of each taxonomic category.

SpeciesItems	*A. abramis*	*A. affinis*	*A. anisitsi*	*A. dentatus*	*A. osteomystax*	*A. pantaneiro*	*B. exodon*	*H. boulengeri*	*H. marginatus*	*Loricaria* sp.1	*M. dichroura*	*P. ambrosettii*	*P. argenteus*	*P. bonariensis*	*P. curviventris*	*P. gracilis*	*P. lineatus*	*P. maculatus*	*P. natteri*	*P. ternetzi*	*R. affinis*	*R. vulpinus*	*S. marginatus*	*S. brasiliensis*	*T. nematurus*	*T. paraguayensis*
Insects	72.2	1.1	57.1	32.7	84.8		86.3		0.2	61.4	13.9		18.4	100		13.5	0.02	4.6			3.3				86.1	18.5
Chironomidae	0.8	1.1	8.6	5.4			36.7			9	7.4		0.2	30.8		4.5		0.6			*				0.1	1.6
Diptera			3.2	0.3	31.5		2.8						0.1			3.6		0.03			*				*	0.1
Coleoptera	5.6		4.3	2.6	2.3		8.9			20.3	6.2		3.2			0.2	*	1.5							5.4	0.4
Ephemeroptera	55.1		2.2	23.3	47.4								10.1	69.2		3.1		0.04			3.2				17.9	2.2
Hymenoptera	10.7		2.2	0.1	0.2		1.4		*				*			0.1		0.01							*	*
Hemiptera			4.3	0.5							0.3					0.1									0.1	
Isoptera				0.2			2.4																		61.7	
Trichoptera							30.6		0.1	32.1			0.1			0.8		0.01							*	13.6
Insect remains			32.3	0.3	3.4		3.5		0.1		*		4.7			1.1		2.47							0.9	0.6
Crustaceans				14.7		0.24							27.6			44.1		6.29						5.2	0.8	
Microcrustaceans	*	3.2		35.1	15.1		2.6	0.1	0.2		62.6		*		*	0.01	0.6	0.02							*	13.1
Other Invert.	0.1		25.8	0.5			7.3	*	*	1.7			*		0.5	0.3									0.7	16.2
Fishes	3.3			15.7		99.8	2.4		73.4				10.4			15.4		50.3	100	100		100	99.4	94.7		
Characiformes				12.8		44.4	2.4											2.52	33.1	58		69.1	22.1	9.7		
Gymnotiformes						14.8														6.2						
Siluriformes									73.4											6.2			44.2	32.8		
Perciformes						7.6													5.7							
Fish remains	3.3			2.9		33							10.4			15.4		47.8	61.2	29.7		30.9	33.1	52.2		
Scales	7.9			0.4					2.8		*		4.2			5.9	*	13.7			96.7				*	1
Plants	16.5	49.9		0.5				2.1	0.3	3.4	11.1	13.1	23.6		4.1	9.6	29.8	9.4			*		*		9.9	7.5
Leaves	1.3										0.4		4		0.8	0.1	15.4	3.54			*				3.1	
Fruits/seeds	15.1			0.5						3.4	5.5		19.5			9.5		5.82							6.8	5.9
Algae	0.1	49.9						2.1	0.3		5.2	13.1			3.3		14.4	0.07					*			1.6
Detritus	*	45.8	17.2	0.4			1.4	97.8	23.2	33.6	12.3	86.9	15.8		95.3	11.3	69.6	15.7					0.6		2.3	43.6

The diet breadth values for each species in the rainy and dry seasons are shown in the Fig. 4. Some individual species showed different breadth niche values (*A. abramis, A. affinis, A. anisitsi, A. dentatus, A. osteomystax, H. marginatus, M. dichroura, P. gracilis*, and *T. paraguayensis*) between rainy and dry season. However, according to the t test, there was no evidence that the means between the species' diets in the two hydrological seasons were different ($t = 0.64$ and $p = 0.52$) (Fig. 5).

Feeding overlap. The feeding overlap values for each hydrological season were significantly greater than expected ($p < 0.05$), suggesting that these values were not random, and hence indicated a biological process.

In regard to the general feeding overlap calculated for the all species pairs, there was no difference between the hydrological seasons. Considering the entire assemblage in the Sinhá Mariana pond, the mean overlap among diets was low (< 0.4) for about 80% of species pairs in each period, showing a high degree of food partitioning (Fig. 6). High values (> 0.6) were observed for 10.4% and 12.0% of the species pairs, in the rainy and dry seasons respectively. During the rains, these high values were found because species pairs shared mainly detritus/sediment, insects, fruit/seeds, microcrustaceans and fish. Similarly, during the dry season, detritus/sediment, insects, microcrustaceans, crustaceans and fish were common foods for several species pairs (Tables 2 and 3).

Discussion

The region studied is located in the upper part of the Pantanal floodplain, and supports a high diversity of fishes (Súarez *et al*., 2001; Súarez *et al*., 2004). During the sampling period, 144 fish species were caught; however, most of them occurred rarely or only seasonally. Twenty-six species co-occurred in both hydrological seasons, and these species were considered as the resident fish assemblages in the Sinhá Mariana pond. In general the fish fauna was composed of small and middle-sized species with standard lengths up to 30 cm, except for *Salminus brasiliensis, Rhaphiodon vulpinus, Prochilodus lineatus, Plagioscion ternetzi* and *Pterygoplichthys ambrosettii*, which reached lengths of more than 40 cm.

The wide diversity of food types exploited by the fish in Sinhá Mariana pond evidenced that these fish are repre-

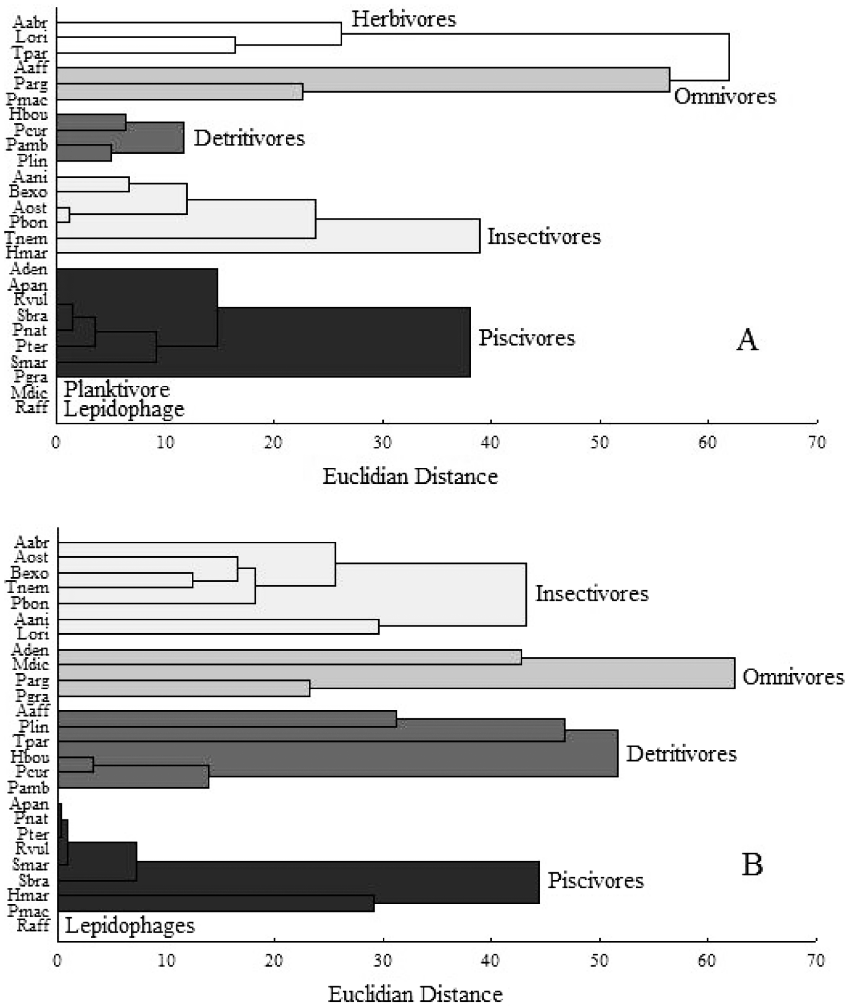

Fig. 3. Dendrogram of diet similarity of the fish assemblage in the Sinhá Mariana pond (Mato Grosso State, Brazil) showing the trophic guilds during rainy (A) and dry (B) seasons. Abbreviations of the species names are showing in table 1.

sentatives of all consumer trophic levels. However, at the community level, it was possible to conclude that the most of the energy supporting the fish fauna was derived from insects and fish, since individual species widely consumed both food resources.

Crowder & Cooper (1982) suggested that because of high capture rates when prey is plentiful, the feeding niche breadth of a predator will be narrowest when food in a particular site is abundant. Although the fish species included more than one kind of food in its diet, the highest dominance by a single food item suggests their abundance in the environment, besides may indicate food active selection.

The trophic guilds, in general, were composed of few species, indicating a more or less uniform distribution of food resource exploitation among the fishes. This finding suggests that these fish species are avoiding trophic competition (Angel & Ojeda, 2001), whereas it is most probable that the fish fauna of Sinhá Mariana pond optimized the food resources available, as described by Jacksic (1981) and Hahn & Fugi (2007).

With respect to the structure of the guilds, it was possible to perceive different tendencies in accordance with seasonality. It is expected that fish will show a high degree of diet change, as a result of changes in the river flow regime (Marçal-Simabuku & Peret, 2002; Hahn & Fugi, 2007). In fact, in Sinhá Mariana pond the herbivore and planktivore guilds occurred only in the rainy season, probably because of input of allochthonous plant material for the former guild and the increase of zooplankton, due to the enrichment of nutrients, typical of the rainy season (Esteves, 1988) for the second guild. Several species changed their trophic positions during the study period. *Aphyocharax dentatus* and *Pimelodella gracilis* acted as piscivores during the rainy season, when they consumed a high proportion of characid juveniles; whereas during the dry season their diets were omnivorous, including aquatic insects, crustaceans and other items. A similar picture was observed for *Astyanax abramis, Loricaria* sp. 1 and *Trachydoras paraguayensis*, which were insectivores during the dry season and changed to herbivores in the rainy season. *Apareiodon affinis*, which was detritivorous during the dry season, showed an omnivorous habit in the rainy season, when it consumed similar propor-

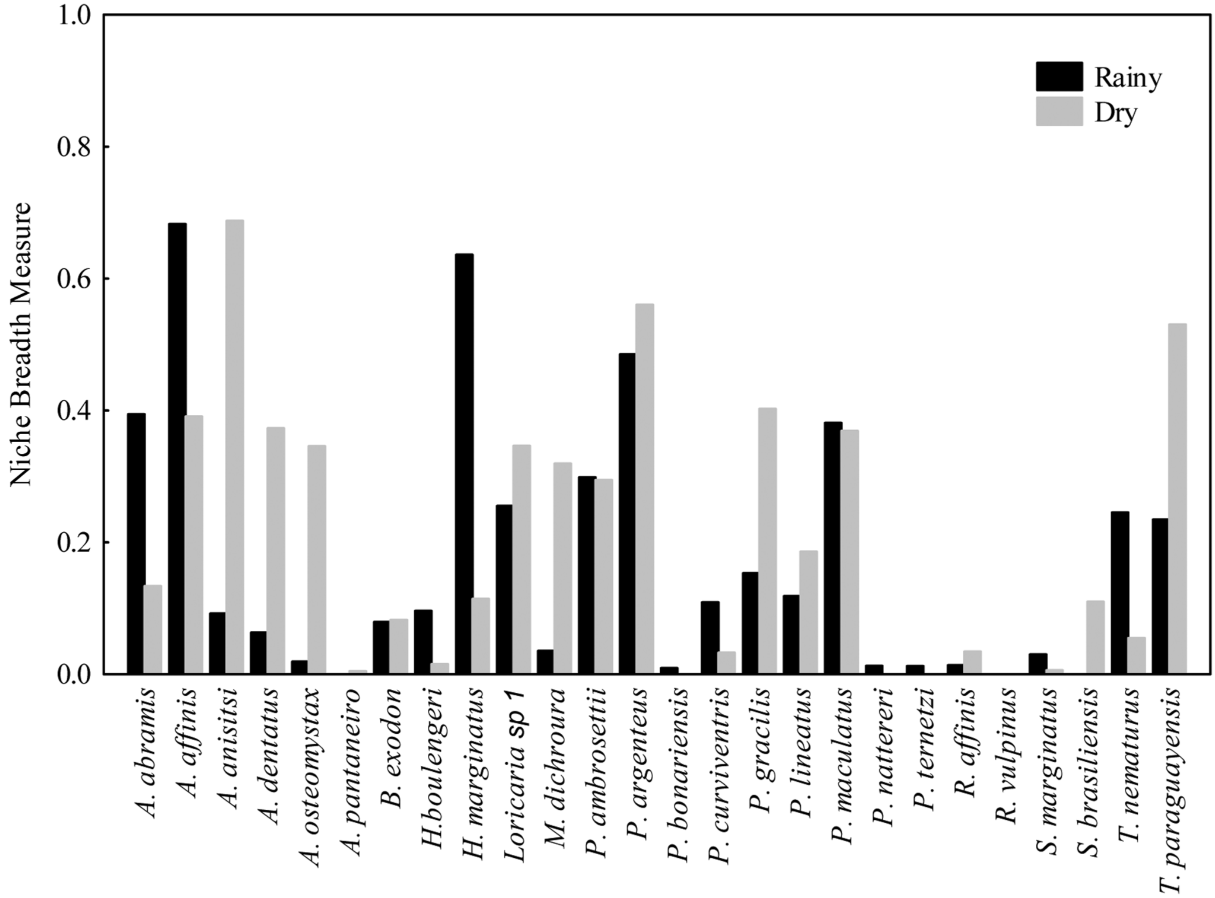

Fig. 4. Niche breadth values to fish assemblage in the Sinhá Mariana pond (Mato Grosso State, Brazil) using Levin's standardized index, during rainy and dry seasons.

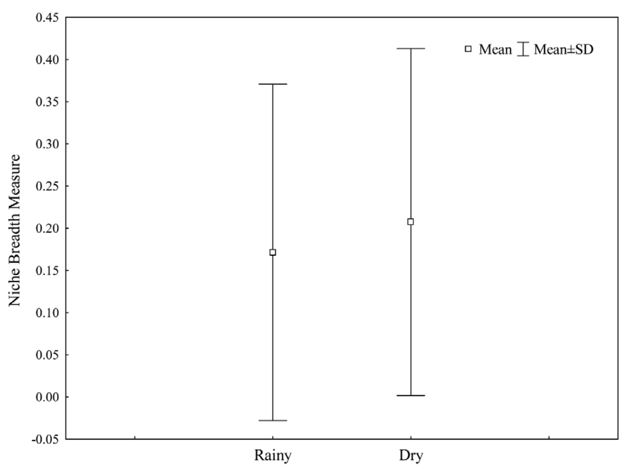

Fig. 5. Values of trophic niche breadth (mean ± standard error) of fish species in the Sinhá Mariana pond (Mato Grosso State, Brazil) during rainy and dry seasons.

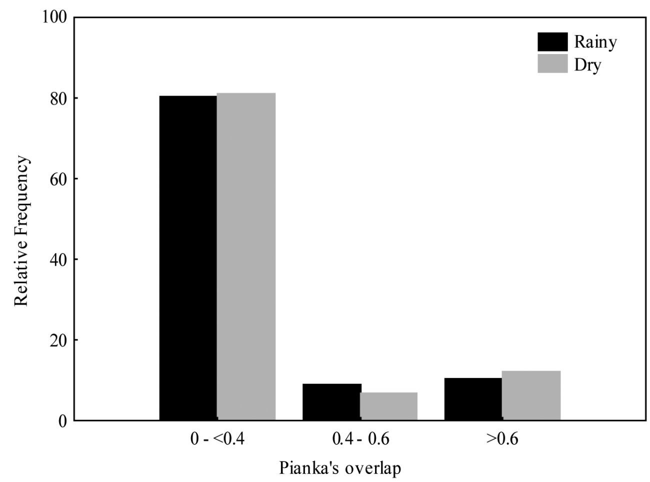

Fig. 6. Overlaps values distribution among fish diet in the Sinhá Mariana pond (Mato Grosso State, Brazil) using Pianka's index, during rainy and dry seasons.

tions of microcrustaceans, plants and detritus/sediment. The other species remained in the same guilds regardless of the season, showing some degree of trophic specialization. These included members of the piscivore guild, composed of *Acestrorhynchus pantaneiro, Rhaphiodon vulpinus, Pygocentrus nattereri, Salminus brasiliensis* and *Serrasalmus marginatus*; the detritivore guild, represented by *Hypostomus boulengeri, Psectrogaster curviventris, Prochilodus lineatus,* and *Pterygoplichthys ambrosettii*; and finally the lepidophages guild, formed by only one species, *Roeboides affinis*.

The analysis of feeding overlap showed that resource partitioning was well defined, with low overlap overall (values < 0.4) at the community level in both seasons. This observation contrasts with the literature data, which have shown high values in the dry season as a function of the shortage in food resources, and low values in the rainy season when food resources are abundant (Lowe-McConnell, 1964; Goulding, 1980; Prejs & Prejs, 1987; Goulding *et al*., 1988). In the present study, this pattern was due to the fact that most combination pairs belonged to species of different trophic guilds. Then, high values of interspecific diet overlaps (> 0.6) were observed among species belonging to the same trophic guild, which showed slight seasonality. The intermediate values were obtained mainly between pairs of species that consumed more than one type of food resource (with dominance of one of them); whereas pairs of piscivores and detritivores showed the highest values of diet overlap (with narrow diets).

Despite the wide diversity of food resources exploited by all the species studied, the trophic organization in guilds, the low individual niche breadth values, the small number of omnivorous species and the low interspecific overlap values all suggest a tendency toward trophic specialization in this assemblage. However, we note that the fact of the species being specialists does not imply that they are subject to evolutionary restraints (for example, regarding morphology), and therefore according to Lowe-McConnell (1999), specialization is not adaptive in assemblages that exploit ephemeral resources, such as in the Sinhá Mariana pond, where some resources occur or are available only seasonally.

In conclusion, this study showed that the trophic structure of the fish fauna and their seasonal dynamics had a singular characteristic, probably due to feeding specificity of the majority of the species. This is an unusual situation in tropical freshwater environments, where most fishes are generalist feeders (Wootton, 1990; Matthews, 1998; Lowe-McConnell, 1999; Hahn *et al*., 2004).

The fish assemblage showed a tendency toward trophic specialization, regardless of the season; only some species changed their diets. We might consider two non-excludent hypothesis: that there is no pattern on the use of seasonal food resources and/or probably there are several patterns, because each one is based on characteristics of the site and the taxonomic composition of the resident species.

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