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Food resource used by small-sized fish in macrophyte patches in ponds of the upper Paraná river floodplain

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ABSTRACT. This study analyzed the diet of seven small-sized fish species (Characidae) and assessed their use of food resources. The species were collected in 2001 from nine ponds with aquatic macrophytes in the Paraná river floodplain, Brazil. *Astyanax altiparanae*, *Astyanax fasciatus*, *Hemigrammus marginatus* and *Moenkhausia intermedia* consumed aquatic and terrestrial insects. *Bryconomericus stramineus* and *Moenkhausia sanctaefilomenae* co-dominantly ate insects and microcrustaceans, whereas *Hyphessobrycon eques* had microcrustaceans as their most important food resource. Overlapping feeding coefficients varied from intermediate (0.4-0.6) to low (< 0.4) for the majority of the combination pairs. A high mean intestinal length was verified for *A. altiparanae* and *A. fasciatus*, while a smaller mean was found for *H. eques*. When comparing all these results, it is possible to conclude that the species were partially segregated by the trophic niche dimension. Thus, the co-existence and higher abundance of these small fish in the shoreline of the ponds is explained by high feeding adaptability, absence of specializations in the feeding tract (except intestinal length) and the wide food supply provided by aquatic macrophytes.

Key words: *Astyanax*, *Bryconamericus*, *Hemigrammus*, *Hyphessobrycon*, *Moenkhausia*, diet.

RESUMO. Uso do alimento por peixes de pequeno porte associados às macrófitas aquáticas em lagoas da planície de inundação do alto rio Paraná. Uso do alimento por peixes de pequeno porte associados a macrófitas aquáticas em lagoas da planície de inundação do alto rio Paraná. Nesse estudo foi investigada a dieta de sete espécies de peixes de pequeno porte (Characidae), em nove lagoas providas de macrófitas aquáticas, da planície aluvial do alto rio Paraná, Brasil, no ano de 2001. *Astyanax altiparanae, Astyanax fasciatus, Hemigrammus marginatus* e *Moenkhausia intermedia* consumiram insetos aquáticos e terrestres; para *Bryconomericus stramineus* e *Moenkhausia sanctaefilomenae* houve co-dominância de insetos aquáticos e microcrustáceos na dieta, enquanto que *Hyphessobrycon eques* explorou predominantemente microcrustáceos. Os valores de sobreposição alimentar variaram de intermediário (0,4-0,6) a baixos (< 0,4) para a maioria dos pares de espécies. Com relação ao comprimento do intestino constatou-se a maior média ajustada para *A. altiparanae* e *A. fasciatus* e a menor para *H. eques.* Todos esses resultados analisados conjuntamente permitem inferir que a dimensão de nicho trófico segregou parcialmente essas espécies. E ainda que, a co-existência e elevada abundância desses pequenos peixes nas regiões marginais das lagoas é proporcionada pela alta adaptabilidade trófica, pela ausência de especializações no trato digestivo (exceto para o comprimento do intestino) e pelo amplo suprimento alimentar fornecido pelas macrófitas aquáticas.

Palavras-chave: *Astyanax*, *Bryconamericus*, *Hemigrammus*, *Hyphessobrycon*, *Moenkhausia*, dieta.

Introduction

Trophic segregation has been considered the most important mechanism in food resource partitioning in fish assemblages (ROSS, 1986). Food partitioning is a tactic in which the food resource is subdivided into parts to reflect the feeding propensities of various species, and according to Gerking (1994) it may be conceived as an efficient way to exploit the total food resource in a habitat. Thus, one of the major challenges of Neotropical fish ecology is to understand the ecological mechanisms through which large numbers of species are able to coexist in the same community, and the manner in which resources are shared (ESTEVES; GALETTI, 1995).

Several species show a divergence of characters when in sympatry by minimizing the effects of the interspecific competition (PIANKA, 1982). Thus, congener and/or sympatric fish species have shown distinct behavior (AGOSTINHO et al., 2003) and distinct morphological attributes to ingest food (DELARIVA; AGOSTINHO, 2001; FUGI et al., 2001; RUSSO et al., 2004). These attributes include position, size and shape of mouth and teeth, type of gill rake, and intestinal length (WOOTTON, 1990). Therefore, investigations in feeding habits in connection with the comparative trophic morphology are useful to elucidate the dynamics of the ecosystem and the occupation of habitat by fish. According to Fryer and Iles (1972), intestinal length is clearly related to the trophic status of the species. Its length is ordered in the following way: carnivores < omnivores < herbivores < detritivores.

In this paper we present data on the diet of seven small-sized coexisting fishes (Characidae) in ponds largely colonized by aquatic macrophytes of the upper Paraná river floodplain. These plants indirectly influence fish feeding, as they serve as substrate for the development of several organisms such as periphytic algae (RODRIGUES et al., 2003; RODRIGUES; BICUDO, 2004) and invertebrates (testate amoebae, rotifers, insects, microcrustaceans, oligochaetes, mollusks) (LANSAC-TÔHA et al., 2003; TAKEDA et al., 2003), and affect the balance of forage efficiency of predator with refuge needs for prey (HARREL; DIBBLE, 2001). However, the role of macrophytes in the ecology of neotropical fish fauna is still poorly understood (AGOSTINHO et al., 2007). There are few studies evaluating the effect of macrophytes on fish assemblage in the Paraná river floodplain, and previous studies in this floodplain investigated on fish assemblage structure (DELARIVA et al., 1994; AGOSTINHO et al., 2007), while studies about feeding ecology of these small fish are scarce. Hahn and Loureiro-Crippa (2006) analyzed the diet and trophic morphology of two species of fish associated with aquatic macrophytes in this floodplain.

It has been assumed that these species segregate food resources to a certain extent, since they exhibit an opportunistic diet (PELICICE; AGOSTINHO, 2006; CASATTI; CASTRO, 2006) and because the aquatic macrophytes provide wide food availability (CARPENTER; LODGE, 1986; DIBBLE et al., 1996; PELICICE; AGOSTINHO, 2006; THOMAZ et al., 2008). Thus, this study was designed to investigate interspecific variations in food resource utilization by these sympatric populations within this microhabitat (macrophyte patches).

Material and methods

The studied area is a remainder of the Paraná river floodplain and is located in the Protected Area of Islands and *várzeas* of the Paraná river (Brazil). The upper Paraná river floodplain is located between two reservoirs and it is immediately downstream from the Porto Primavera Dam and about 200 km upstream of the beginning of the Itaipu Reservoir. This area is 230 km in length, 20 km wide and contains several ponds, channels and rivers.

Samples were carried out in nine ponds that were associated to three rivers in this floodplain: the Ivinheima river (22°49'S and 53°33'W – Capivara, Jacaré and Cervo Ponds), the Baía river (22°43'S and 53°18'W – Traíra and Aurélio Ponds) and the Paraná river (22°43'S and 53°11'W – Pousada, Clara, Genipapo and Osmar Ponds) (Figure 1). All ponds had aquatic macrophytes along their shorelines during the study period. The most frequent species of aquatic macrophytes found were: *Eichhornia azurea*, *E. crassipes*, *Polygonum ferrugineum*, *P. punctatum* and *Salvinia* spp. (SANTOS; THOMAZ, 2007).

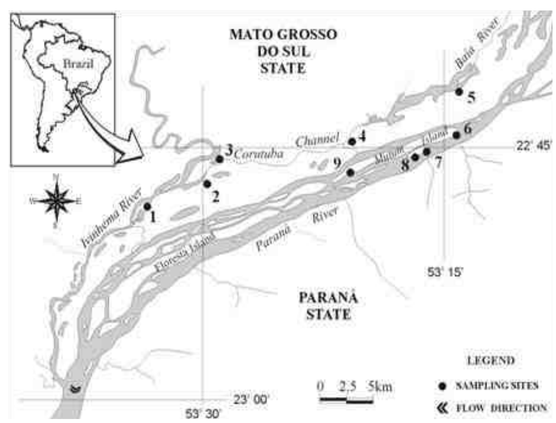

Figure 1. Study area showing the nine ponds of the Upper Paraná river floodplain, Paraná State, Brazil: 1. Capivara, 2. Jacaré, 3. Cervo, 4. Traíra, 5. Aurélio, 6. Pousada, 7. Clara, 8. Genipapo, and 9. Osmar.

The seven species of small-sized fish species that coexisted in the nine ponds included in this study were: *Astyanax altiparanae* (Garutti; Britski, 2000) (28-106 mm SL); *Astyanax fasciatus* (Cuvier, 1819) (38-76 mm SL); *Bryconamericus stramineus* Eigenmann 1908 (18-45 mm SL); *Hemigrammus marginatus* Ellis, 1911 (23-49 mm SL); *Hyphessobrycon eques* (Steindachner, 1882) (12-34 mm SL); *Moenkhausia intermedia* Eigenmann, 1908 (19-68 mm SL) and *Moenkhausia sanctaefilomenae* (Steindachner, 1907) (14-46 mm SL). Voucher specimens were deposited in the Fish Collection of the Núcleo de Pesquisas em Limnologia, Ictiologia e Aqüicultura (Nupélia – Universidade Estadual de Maringá, Paraná State).

Samples were taken in February, May, August and November 2001, in each one of the nine ponds, totalizing 36 samples. During the sampling, seining (50 m length and 0.5 cm mesh) was used along the shoreline near to macrophyte patches. After being caught, all fish were identified and measured (standard length – SL) and their stomachs with content were fixed in 10% formalin.

Stomach contents were analyzed by volumetric method (the proportion by volume of each item is expressed as a percentage of all examined individuals, for each species) (HYSLOP, 1980), using graduated test tubes and a counting glass plate (HELLAWELL; ABEL, 1971). Item identifications were made to the lowest possible taxonomic level.

To verify the concordance of the fish feeding data (data conformity) among the ponds to all species, the Kendall concordance coefficient (W) (SIEGAL, 1975) was applied after calculating the volume percentage of each food item to each species. The association among variables (ponds) was measured. This proceeding is according to Peretti and Andrian (2004) and was applied since it was impossible to consider spatial variations, because the number of individuals was insufficient within each pond.

A multivariate ordination technique (GAUCH JR., 1982) was used to summarize the diet matrix (SHELDOM; MEFFE, 1993). The program PC-ORD (McCUNE; MEFFORD, 1997) was used for this analysis.

To complement the DCA ordinations of diet similarity, conventional diet overlap indices were calculated between all species pairs (PELHAM et al., 2001). Overlapping feeding was measured using the Schoener Index (SCHOENER, 1970) based on percentage volume data, according to the formula:

$$\alpha = 1 - 0.5 \left(\sum_{x=i}^{n} |P_{xi} - P_{xy}| \right) \quad (1)$$

where:

n = number of prey;

P_{xi} = proportion of food item i in the diet of species x;

P_{xy} = proportion of food item i in the diet of species y.

Overlapping feeding coefficients were arbitrarily considered 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).

Intestinal length was obtained for 30 individuals of each species. Covariance analysis (Ancova) was applied to test differences in intestinal length among species, using SL as a co-variable (HUITEMA, 1980); all were log transformed to linearize relationships. Adjusted mean intestinal lengths were compared using Scheffe's test when statistical significance was observed.

All statistical analysis was conducted by the Statistic Program for Windows, version 7.1 (STATSOFT, 2005).

Results

Kendall's coefficient (W = 0.59106 and p < 0.001) did not identify significant differences among the food items ingested by fish in the nine ponds. Therefore, they were treated as one single ecological situation. A total of 4,092 fish were collected, and these species represented 35% of the total (1,270 individuals).

Diet composition

The stomach content of 529 individuals was analyzed. The diet was composed mainly of aquatic and terrestrial insects and microcrustaceans. Among the aquatic insects, Chironomidae, Chaoboridae and other Diptera larvae predominated. Among the terrestrial insects, Hymenoptera predominated, and among the microcrustaceans, Cladocera and Copepoda were found most frequently. For *A. altiparanae, A. fasciatus, H. marginatus* and *M. intermedia*, insects were the most important food items, however, the origin of the food was different among them. In the diet of *A. altiparanae* and *M. intermedia* there was a co-dominance of terrestrial insects (Hymenoptera) and aquatic insects (Chironomidae). In the diet of *A. fasciatus*, aquatic insects (mainly Diptera) represented 60% of the diet. For *H. marginatus*, Hymenoptera was the most important food item representing 70% of its diet. However, plants were also an important food item for *A. altiparanae, A. fasciatus*, and *M. intermedia*. A mixture of aquatic insects and microcrustaceans was consumed by *Bryconomericus stramineus* and *M. sanctaefilomenae* and these two items together contributed to 50% and 71% of the diet of each species, respectively. *Hyphessobrycon eques* had a different diet, consuming predominantly microcrustaceans (77% of its diet) (Table 1).

Table 1. Feeding resources (% total volume) used by small-sized fishes in ponds of the upper Paraná river floodplain, Paraná State, Brazil. Numbers in boldface indicate values > 10%.

Items/Species	*A.alt*	*A.fas*	*B.str*	*H.mar*	*H.equ*	*M.int*	*M.san*
Number analyzed	178	20	14	17	65	19	216
Autochthonous							
Rotífera	0.09	0.19	0.01	1.00	2.89	0.02	0.06
Bryozoa	1.19			0.30		0.07	0.05
Copepoda	3.54	0.51	**12.98**	0.90	**42.66**	4.37	**11.25**
Cladocera	2.83	0.57	**14.79**	1.99	**33.98**	2.62	**19.70**
Ostracoda	0.01		0.07		0.72		0.01
Chironomidae	**20.41**	**13.27**	**20.12**	1.00	1.45	**11.37**	6.15
Chaoboridae	0.13	6.32	7.07	0.10	0.58	5.64	**21.82**
Outros Díptera	4.13	**32.85**	0.72	1.00	0.72	4.15	**17.96**
Coleoptera	4.38	6.95	1.08	4.98	1.37	1.90	
Ephemeroptera	0.13	0.63	0.07	1.99		0.02	
*Algae	**11.90**	4.99	**26.54**	6.97	**10.77**	9.51	**11.42**
Allochthonous							
Hymenoptera	**24.67**	**13.27**	7.07	**70.65**	0.07	**29.52**	0.75
Coleoptera	3.07	0.06	1.80	0.80	0.14	2.19	0.41
Hemiptera	0.40	0.63	0.09				0.20
Ephemeroptera	0.24		2.02		0.14		0.11
Lepidoptera	2.50						0.01
Odonata	1.01	5.05	0.07	0.10	0.07		0.08
Oligochaeta	0.73	0.44	0.40	1.99	1.08	0.39	0.02
Arachnida	1.30		0.11		0.36		0.27
Unidentified							
Plants	**17.06**	**13.90**		3.98	1.58	**28.21**	9.7
Detritus	0.29	0.38	4.98	2.29	1.37		0.02

*unicelular and filamentous algae.

Diet similarity

The DCA analyses were used to summarize the interspecific variation of the diet and three trophic groups were formed (Figure 2A).

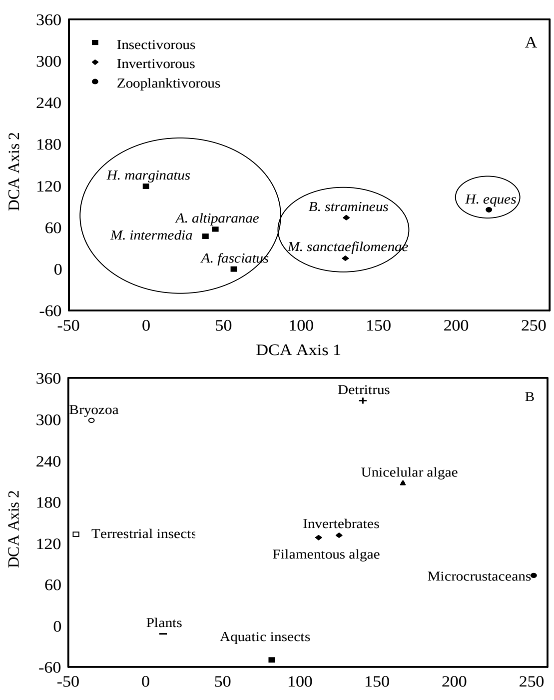

Figure 2. Ordination of the small-sized fishes (A) and of the feeding resources (B) in ponds of the Paraná river floodplain, Paraná State, Brazil.

The first axis of the DCA (eigenvalues = 0.45) was retained for interpretation because it showed eigenvalues greater than 0.20. Positioned in the lower scores and consuming mainly terrestrial and aquatic insects and plants are: *A. altiparanae, A. fasciatus, M. intermedia*, and *H. marginatus*. The only species with higher scores is *H. eques*, which consumed microcrustaceans predominantly (Figure 2A and B). In the intermediate scores are *B. stramineus* and *M. sanctaefilomenae*, which consumed aquatic insects, microcrustaceans and filamentous algae (Figure 2A and B).

Overlapping feeding coefficients varied from intermediate (0.4-0.6 in 52.4% of the pairs) to low (< 0.4 in 42.8%) for the majority of the combination pairs. Species that had the most similar diets were *A. altiparanae* and *M. intermedia* (0.78), while *H. eques* had the lowest values when compared with the other species (Table 2).

Table 2. Diet similarity among small-sized fishes in ponds of the upper Paraná river floodplain. Numbers in boldface indicate values > 0.60. Aalt = *A. altiparanae,* Afas = *A. fasciatus* Bstr = *B. stramineus*, Hmar = *H. marginatus*, Hequ = *H. eques,* M.int = *M. intermedia* and Msan = *M. sanctaefilomenae*.

	Afãs	Bstr	Hmar	Hequ	Mint	Msan
Aalt	0.38	0.50	0.47	0.24	**0.78**	0.40
Afãs		0.36	0.32	0.13	0.57	0.47
Bstr			0.23	0.45	0.45	0.53
Hmar				0.18	0.49	0.17
Hequ					0.22	0.47
Mint						0.43

Intestinal length

A significant interaction between standard length and species ($F_{6.333}$ = 11.44; p < 0.0001) indicated that relationships between body ($F_{7.333}$ = 84.89; p < 0.0001) and intestinal length ($F_{6.333}$ = 13.87; p < 0.0001) differ among species. The highest intestinal length values were verified for *A. altiparanae* and *A. fasciatus*, while *H. eques* showed the lowest mean (Figure 3). The comparison means test indicated that intestinal length is different between *A. altiparanae* and *A. fasciatus*, and both species also had significant differences when compared to the other species. Significant differences also were found between *H. eques* and *B. stramineus*; *H. eques* and *M. intermedia*; and *H. eques* and *M. sactaefilomenae*. *Bryconamericus stramineus*, *H. marginatus*, *M. intermedia* and *M. sanctaefilomenae* showed no significant differences in relation to intestinal length.

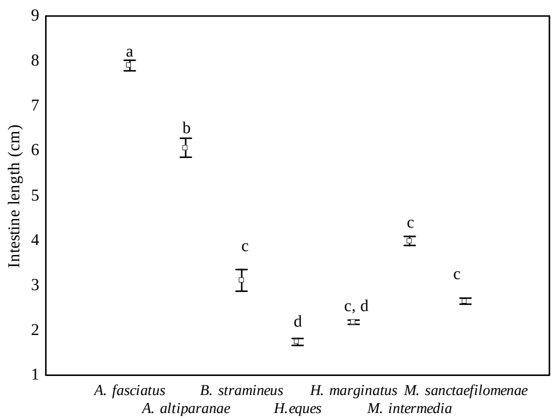

Figure 3. Adjusted means and standard error of intestinal length of the small-sized fishes in ponds of the upper Paraná river floodplain. (Post-hoc Scheffé test, p < 0,05). Distinct characters (a, b, c, d) shows significant differences.

Discussion

The high predation on insects and microcrustaceans by the fishes studied suggests that these arthropods support the high density of small-sized fish in the ponds of the upper Paraná river. Autochthonous resources were the most exploited by the species, and certainly aquatic macrophytes provide these foods. In the Lake Monte Alegre (São Paulo State) 8 fish species associated with macrophytes consumed mainly aquatic insects, microcrustaceans and rotifers, the most abundant invertebrates associated with macrophytes in this Lake (MESCHIATTI; ARCIFA, 2002). Small-sized fish that inhabit bank of macrophytes in the Rosana Reservoir (State of São Paulo) feed on autochthonous items (algae, microcrustaceans and aquatic insects), showed the aquatic macrophytes serve as an important foraging micro-habitat for these species (CASATTI et al., 2003). Terrestrial insects were recorded in the stomachs of all species but were the main food only for *H. marginatus*, which consumed mainly Hymenoptera. It is probable that these invertebrates are abundant and available especially during rainy periods. However, the year 2001 was characterized as a dry year and might have contributed to the small importance of these invertebrates for most of the fish species studied. Russo et al. (2004) showed that terrestrial insects were most important to small fish diet during rainy period. Microcrustaceans were recorded in high densities in samplings made concurrently with this study (LANSAC-TÔHA et al., 2004) and were an important food item (mainly Copepoda e Cladocera) for three species: *B. stramineus, M. sanctaefilomenae* and especially to *H. eques*. Ostracoda, Cladocera, and Copepoda were the main food items consumed for fishes associated with patches of *Egeria* spp. in Rosana reservoir (PELICICE; AGOSTINHO, 2006).

In general, feeding ecology studies about coexistent species stress the importance of detailed analyses of each one because small trophic requirements can be responsible for living in a common environment (YAMAOKA, 1991). Thus, discrete differences in the preferred food in the habitat explored (HORI, 1987) and in the temporal resources used (PELICICE; AGOSTINHO, 2006) lead to favorable conditions for coexistence. In spite of results showing that the fish studied exploited several common food resources, the species were partially segregated by the trophic niche dimension. The intermediate and low food overlap among these species also confirms their trophic segregation. Pelicice and Agostinho (2006) observed that, in general, small fish had interespecific low overlapping feeding and suggest that individuals are feeding in an opportunistic way among macrophyte patches, probably in response to the most abundant resources.

Although these species are generalists and/or opportunists and are dependent upon the resources offered by the environment, when in simpatry, these small fish use the main feeding source in different ways. *Hyphessobrycon eques* is the species that differs of the others species, eating mainly microcrustaceans, indicative of its zooplanktivorous habit. In the Rosana Reservoir (Southeastern Brazil), this species was characterized as invertivorous, consuming insect larvae and microcrustaceans (CASATTI et al., 2003). However, in another study carried out in this same reservoir, this species was zooplanktivorous (PELICICE; AGOSTINHO, 2006).

These fish do not show any clear differences in the shape of the structures associated with food intake or other apparent structural modifications in the mouth, teeth and gill rackers (data not shown). However, differences in intestinal length were seen among the species. Morphological patterns related to feeding markedly reflect the diet of a fish (FUGI et al., 2001; DELARIVA; AGOSTINHO, 2001). The long intestinal length of *A. altiparanae* and *A. fasciatus* may be an adaptation for consuming plants when these resources are available in the environment. In fact, plants were recorded in the diet of both species (see Table 1). In addition, plants have also been recorded in the stomach contents of both species in several other ecosystems (CASSEMIRO et al., 2002; RUSSO et al., 2004; HAHN et al., 2004). In the other species, especially *H. eques*, the short intestinal length may reflect their carnivorous diet. Graciolli et al. (2003) pointed out that the lack of a consistent phylogeny for many groups, such as the Tetragonopterinae, is still an obstacle for understanding whether feeding habits are a consequence of the evolution of these fish or of the environment.

In conclusion, this study showed that the co-existence and higher abundance of these small-sized fish living in the shorelines of the ponds are explained by high feeding adaptability, absence of specializations in the feeding tract and wide food supply provided by aquatic macrophyte habitats. According to Géry (1977), the Tetragonopterinae fish are the most successful taxon of caracideans and they dominate almost all the Neotropical biotopes. Thus, it is probable that the ecological features considered above are the key to understanding the great success of these fish species in Neotropical freshwaters.

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