Diet and Dietary Overlap of Three Sympatric Fish Species in Lakes of the Upper Paraná River Floodplain

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ABSTRACT

For a dietary study, specimens of Astyanax bimaculatus, Astyanax schubarti, and Moenkhausia intermedia were caught monthly with seines-nets in six lakes (Pau Veio, Porto Rico, Três Amigos, Mutum, Pontal, and Canal do Meio), on the floodplain of the Upper Paraná River, from March 1992 through February 1993. We analyzed stomach contents of 599 A. bimaculatus, 293 A. schubarti, and 394 M. intermedia, by the Occurrence and Points methods, combined in the Alimentary Index (AI). This analysis revealed that these species have broad dietary spectra. A. bimaculatus was an omnivore, with a tendency toward herbivory-insectivory. In most of the lakes it consumed terrestrial insects, followed by higher plants and microcrustaceans. A. schubarti was an omnivore, consuming the same type of items in the different lakes, in different proportions depending on the locality. M. intermedia was a planktophage, feeding mainly on cladocerans (more than 50%) in all the lakes except for Pontal, where higher plants were predominant (45.1%). Although A. bimaculatus and A. schubarti consumed similar items in the different localities, detrended correspondence analysis (DCA) showed distinct segregation among the three species in all lakes studied.

Key words: Astyanax bimaculatus, Astyanax schubarti, Moenkhausia intermedia, diet.

INTRODUCTION

The lambari-guaçu or tambiú, Astyanax bimaculatus (Linnaeus, 1758), the yellow-tailed lambari, Astyanax schubarti (Britski, 1964), and the piqui, Moenkhausia intermedia (Eigenmann, 1908) are very abundant sympatric species on Paraná River floodplain the Upper (FUEM.PADCT/CIAMB, 1995). Although they have no relevant economic value, they are fodder species, important in the diet of piscivores generally, and medium- to large-sized individuals are much exploited in the commercial fishery of the region.

The study of dietary habits of fishes is essential for understanding their functional role in an ecosystem. Mendelson (1975) hypothesized that food, a limiting factor, is fundamental in studies of interspecies competition in fish populations. In such cases, individuals which have similar habit and morphology may compete with each other when they occur in the same area. However, species which coexist in nature may be segregated along many resource dimensions, such as food, time, and various aspects of the habitat such as refuges, light, temperature, and current velocity in the rivers, among others. These factors correspond to three main axes: habitat, food, and time, along which segregation takes place (Pianka, 1969).

The lakes covered in this study loose contact with the river during the dry season. This confines a large quantity of fish, which then undergo stressful biotic and abiotic conditions. As the water level drops, the assemblages of fish remaining in the puddles are subject to extreme physical and chemical conditions, and their density is drastically increased, heightening intra- and interspecies competitive pressures.

In this investigation, we describe the diet of three sympatric species (*A. bimaculatus, A. schubarti*, and *M. intermedia*), with emphasis principally on the spatial changes in the diet, and diet overlap.

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STUDY AREA

The region studied is located on islands in the Paraná River, Municipality of Porto Rico in the northeastern part of the State of Paraná. In this stretch, the river varies in width to a maximum of 14 km and has an extensive floodplain, especially on its right bank. We considered six lakes (Fig. 1): Pau Veio, Porto Rico, Três Amigos, Mutum, Pontal, and Canal do Meio.

MATERIALS AND METHODS

Collections of fish were made monthly from March 1992 through February 1993 in the six lakes. Seines-nets (20 m long and 1 cm stretched mesh) were used. After being netted, the specimens were measured, weighed, and fixed in 4% formol for extraction of the viscera.

In the laboratory, the stomach of 599 specimens of *A. bimaculatus* (Ls = 1.58-17.10 cm); 239 *A. schubarti* (Ls = 1.90-6.12 cm), and 394 *M. intermedia* (Ls = 1.60-6.21 cm) were analyzed by the frequency of occurrence and points methods (Hynes, 1950; Hyslop, 1980) combined in the Alimentary Index (AI) (Kawakami & Vazzoler, 1980), expressed in percentage.

The diet of the fish was described for all individuals, including all food items and the "major groups" consumed. The main items were grouped as : Testacea = Arcella and Difflugia; Microcrustaceans = Cladocera, Copepoda, Ostracoda, and Conchostraca; Aquatic Insects = insect larvae and aquatic Hemiptera; Terrestrial Insects = winged insects; Fish Remains = fins, scales, and fragments; Higher Plants = monocotyledons and dicotyledons; Algae = unicellular and filamentous algae; and Other = Rotifera. Acarina. Nematoda. Arachnida. Bivalvia, Isopoda.

The patterns of similarity between the diets of the three species were identified by detrended correspondence analysis (DCA) (Gauch, Jr., 1982). For this analysis, we combined data on the items consumed by the specimens of the three species x six localities.



Figure1. Collection locations in Porto Rico town, Paraná State, Brazil.

RESULTS

Astyanax bimaculatus

A total of 41 items were recorded in the diet of this species (Table I). Of these, insect remained (wings, legs, and fragments of terrestrial insects) predominated (23.1%),followed bv monocotyledons (leaves and seeds of grasses) (20.3%), cladocerans (14.2%), and plant detritus (plant remains in advanced stages of decomposition) (11.2%). The broad and diversified dietary spectrum of this species allowed us to characterize it as an omnivore. This could best be seen when the items were grouped in "major groups". In this case, terrestrial insects (28.9%) and higher plants (28.2%) were the most representative groups in the diet.

Table I. Relative frequency of the Alimentary Index (AI%) of the food consumed by *A.bim=Astyanax bimaculatus* (599), *A.sch=Astyanax schubarti* (293), and *M.int=Moenkhausia intermedia* (394), caught in floodplain lakes of the Upper Paraná River.

ITEMS	A.him	A.sch	M.int
-	AI (%)	AI (%)	AI (%)
Testacea	3.9	8.5	0.9
Arcella	0.03	0.01	0.01
Difflugia	4.98	10.47	1.10
Nematoda	0.04	0.04	0.03
Rotifera	0.01	0.01	-
Brvozoa	1.26	1.59	0.08
Acarina	0.16	0.05	0.01
Bivalvia	0.01	0.01	-
Gastropoda	0.01	-	-
Microcrustaceans	16.2	11.8	54.3
Cladocera	14.17	10.63	56.95
Copepoda	5.73	2.35	3.18
Conchostraca	0.24	0.02	0.23
Ostracoda	0.04	0.07	0.01
Decapoda	0.01	_	-
Arachnida	0.03	-	-
Isopoda	0.01	-	-
Aquatic insects	9.9	15.4	3.8
Chaoboridae	0.01	0.05	0.01
Chironomidae	6.18	6.54	1.78
Coleoptera adult	0.13	-	-
Coleoptera larva	0.09	0.19	0.01
Diptera larva	0.04	0.03	0.09
Ephemeroptera larva	0.01	_	_
Hemiptera aquatic	0.84	0.89	0.25
Lepidoptera larva	0.01	-	-
Odonata larva	0.01	-	0.01
Terrestrial insects	28.9	15.1	3.8
Collembola	0.01	-	-
Diptera adult	0.21	-	-
Ephemeroptera adult	0.03	0.25	0.79
Hemiptera terrestrial	0.17	0.05	0.02
Hymenoptera	0.02	-	0.03
Homoptera	0.01	0.01	-
Isoptera	0.07	0.04	0.01
Neuroptera	-	-	0.01
Odonata adult	0.06	0.05	-
Orthoptera	-	0.01	-
Plecoptera	-	0.03	-
Insect remains	23.17	11.71	12.32
Shrimp	-	-	0.01
Fish remains	3.6	1.9	-
Scales	2.57	2.37	0.01
Fish remains	0.85	0.05	0.09
Algae	3.3	4.5	-
Unicellular algae	0.01	0.01	-
Filamentous algae	3.89	5.01	0.01
Higher plants	28.2	32.0	10.5
Monocotyledons	20.33	31.53	7.28
Dicotyledons	11.27	4.91	0.84
Organic detritus	3.04	10.99	14.82
Inorganic detritus	0.24	0.03	0.01

Considering the spatial variations in the diet (Fig. 2), note that in general, terrestrial insects participated prominently in Pau Veio, Porto Rico, Três Amigos, and Canal do Meio Lakes. In Mutum Lake, the predominant item was higher plants, with 44.8% of the AI. In Pontal Lake, microcrustaceans predominated with approximately 45.0% of the AI.



Figure 2. Relative frequency (AI%) of food items in the diet of *Astyanax bimaculatus*, in floodplain lakes of the Upper Paraná River. A-Testacea; B-Bryozoa; C-Microcrustaceans; D-Aquatic insects; E-Terrestrial insects; F-Higher plants; G-Organic detritus; H-Fish remains; I-Algae and J-Other.

Astyanax schubarti

The diet of this species was composed of 32 items (Table I). The main items in order of importance were: monocotyledons (31.5%), insect remains (11.7%), organic detritus (11.0%), cladocerans (10.6%), and *Difflugia* (10.5%). As for "major groups", higher plants stood out with 32.0%, followed by aquatic insects (15.4%), terrestrial insects (15.1%), and microcrustaceans (11.8%), demonstrating the omnivorous habit of this species.

There were considerable changes in the utilization of food, within the same lake and between different lakes (Fig. 3). In Canal do Meio Lake, Testacea stood out (31.9%); in Mutum, organic detritus (37.3%); in Pau Veio, higher plants (48.3%); in Pontal,

microcrustaceans (48.7%); in Porto Rico, aquatic insects (42.0%); and in Três Amigos, algae represented 38.0% of the AI. Therefore, there was no uniform spatial pattern in the diet of this species.



Figure 3. Relative frequency (AI%) of food items in the diet of *Astyanax schubarti*, in floodplain lakes of the Upper Paraná River. A-Testacea; B-Bryozoa; C-Microcrustaceans; D-Aquatic insects; E-Terrestrial insects; F-Higher plants; G-Organic detritus; H-Fish remains; I-Algae and J-Other.

Moenkhausia intermedia

Although this species included 29 items in its diet, few of them were prominent and most were recorded in very low proportions (Table I). The items most consumed were cladocerans (57.0%), organic detritus (14.8%), and insect remains (12.3%). Considering the "major groups" of food, microcrustaceans represented 54.3% of the AI, followed by terrestrial insects (17.2%), organic detritus (12.0%), and higher plants (10.5%), showing that this species tended to feed on zooplankton.

The spatial analysis (Fig. 4) showed that except for Pontal Lake, where higher plants were the most consumed item, microcrustaceans were the predominant food in the stomachs, principally in Mutum where they made up 99.3% of the AI.



Figure 4. Relative frequency (AI%) of food items in the diet of *Moenkhausia intermedia*, in floodplain lakes of the Upper Paraná River. A-Testacea; C-Microcrustaceans; D-Aquatic insects; E-Terrestrial insects; F-Higher plants; G-Organic detritus and J-Other.

Diet overlap

Correspondence analysis revealed a distinct segregation of the species in the different lakes (Fig. 5). Axis 1 of the DCA divided the species into two groups, indicating microhabitat separation. The first group with the lowest scores was represented by A. bimaculatus and A. schubarti, and the second by M. intermedia. Axis 2 of the DCA divided the species of the same genus into two other groups, A bimaculatus with the highest scores, and A. schubarti with the lowest. However, the diet of these species was very similar in Canal do Meio and Pau Veio Lakes.

DISCUSSION

According to Gerking (1994), areconsidered specialists fish species which have marked trophic adaptations. The three species studied here, mainly *A. bimaculatus* and *A. schubarti*, which are considered generalists because of their wide food spectrum, probably lack such adaptations. *M. intermedia*, which has a more

restricted, specific diet, may possess more developed mechanisms for selection, which were not investigated in this study.



Figure 5. Correspondence analysis of dietary similarity of *Astyanax bimaculatus, Astyanax schubarti*, and *Moenkhausia intermedia*, in floodplain lakes of the Upper Paraná River. CM-Canal do Meio; Mut-Mutum; PV-Pau Veio; Pon-Pontal; PR-Porto Rico and TA-Três Amigos.

A. bimaculatus was considered omnivorous with a tendency toward herbivory-insectivory. In an oxbow lake of the Mogi-Guaçú River, State of São Paulo, this species was categorized in the same terms by Meschiatti (1995). Other investigators have suggested that this species is omnivorous, in different bodies of water (Nomura, 1975; Oliveros, 1980; Arcifa & Meschiatti, 1993). Although A. bimaculatus fed predominantly on plants and insects in the lakes studied, microcrustaceans also constituted a relatively significant resource. Ortaz & Infante (1986) commented that these organisms (mainly cladocerans and copepods) were numerically important for this species.

The fact that the diet of *A. bimaculatus* ranged from detritus and benthic organisms to terrestrial insects and surface plants indicated its capability to exploit all compartments of the water column. We point out, however, that some of the lakes are shallow during certain times of year, which facilitates this shift.

A. schubarti was characterized as an omnivore because of the fact that it incorporated a similar proportion of food items originating from animals (several kinds) and plants in its diet. In the Mogi-Guaçú River, Esteves (1996) mentioned that this species differed from congeners in having a more specialized feeding habit, consuming a large quantity of plants. Meschiatti (1995), studying the food of this species in an oxbow lake of the Mogi-Guaçú, State of São Paulo, characterized it as an herbivore-insectivore.

M. intermedia had a diet constituted basically of microcrustaceans, which were identified as planktonic species. Maldonado (1983), studying their gill rakers in lentic environments of the Riachuelo basin, Argentina, observed that this was a filter-feeding species. However, this behavior was observed in juveniles, while insects were the main component of the diet of adults.

Esteves (1994) and Meschiatti (1995) characterized this species as an omnivore in oxbow lakes of the Mogi-Guaçú River, although Esteves commented on the predominance of copepods among the microcrustaceans consumed.

Although the six lakes showed different characteristics in relation to various physical and chemical parameters, Pau Veio and Porto Rico Lakes were, according to Okada (1995), the most similar. However, this similarity was not reflected in the diet of the species of these localities. Therefore, apparently the environment did not interfere with feeding, and no clear-cut spatial pattern was observed for the three species in the different lakes.

It is believed that the main factor is the availability and abundance of the different food items. Wootton (1990) commented that fish were good samplers, and that stomach contents were a good parameter to evaluate food availability in the environment. In this sense, the fact that microcrustaceans constituted a predominant food only in Pontal Lake for *A. bimaculatus* and *A. schubarti*, suggested that these organisms were abundant in this

environment. On the other hand, for *M*. *intermedia* which used microcrustaceans as the main resource in nearly all the lakes, microcrustaceans were of secondary importance in Pontal Lake, possibly as a function of the intensive predation of the former two species.

Correspondence analysis (similarity) corroborated the results obtained. *M. intermedia* had the most distinct diet, showing little overlap with that of the lambaris. These, on the other hand, consumed similar items, but showed low dietary overlap in the different lakes. This provided evidence that although the items are qualitatively similar, their proportions differ in the diets of both species. This analysis also showed that the three species were segregated, even in different lakes, i.e. environment did not appear to be a limiting factor in food choice.

Gerking (1994) commented that some studies have shown that feeding habit did not sufficiently segregate the species into compartments within the habitat, over time. Because of the seasonality of the floodplain, and the stressful periods to which the lakes are subject, competition between species appears inevitable. A. schubarti and M. intermedia disappear during the dry season. It was possible that one of the factors influencing this disappearance, besides predation, was reduction in the food supply which leads to intense competition for food among these species and others which were not investigated in this study.

Because of the absence of individuals of A. schubarti and M. intermedia from the catches during the dry season in most of the lakes, seasonal analyses were not performed. In view of this, the dominance of A. bimaculatus during the most stressful phases of the drought period becomes evident. Agostinho et al. (1997) found that in temporary lakes of the Paraná River floodplain, A. schubarti was completely eliminated during the dry period, while its congener A. bimaculatus was always found in the final catches, even in large numbers. Agostinho et al (1997) explained this phenomenon as a function of the coloration of both species, laying stress on the light color of A. schubarti which contrasts with the organic detritus of the bottom sediment, making it easy prey. A. bimaculatus, as a result of the umeral and peduncular-caudal spots, has a better possibility for camouflage and predator avoidance. Agostinho *et al.* (1997) also observed the early disappearance of *M. intermedia* from the catches during the drying phases. Agostinho *et al* (1997) also referred to the dominance of *A. bimaculatus* in puddles in the final phase of drying, and thus in drastic conditions as to dissolved oxygen content, pH, and electrical conductivity.

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RESUMO

Para estudo da dieta foram capturados mensalmente exemplares de Astvanax bimaculatus, Astyanax schubarti e Moenkhausia intermedia com redes de arraste, em seis lagoas (Pau Velho, Porto Rico, Três Amigos, Mutum, Pontal e Canal do Meio), na planície de inundação do alto rio Paraná, de março/92 a fevereiro/93. Foram analisados 599 conteúdos gástricos de A. bimaculatus, 293 de A. schubarti e 394 de M. intermedia, pelos métodos de Ocorrência e Pontos, combinados no Índice Alimentar (IAi). Tal análise revelou que estas espécies apresentam amplo espectro alimentar. A. bimaculatus foi caracterizada como onívora com tendência a herbivoria-insetivoria. consumindo, na maioria das lagoas, insetos terrestres, seguidos de vegetal superior e microcrustáceos. A. schubarti foi caracterizada como onívora, consumindo os mesmos tipos de itens nas diferentes lagoas, com proporções distintas, dependendo do local. M. intermedia foi caracterizada como planctófaga, alimentando-se principalmente de Cladocera (mais de 50%) em todas as lagoas, exceto na Pontal, onde vegetal superior se sobressaiu (com 45,1%). Embora A. bimaculatus e A. schubarti tenham consumido itens semelhantes nos

diferentes locais, a análise de correspondência destendenciada (DCA) evidencia uma nítida segregação entre as três espécies em todas as lagoas estudadas.

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