Feeding ecology of three Astyanax species (Characidae, Tetragonopterinae) from a floodplain lake of Mogi-Gua�� River, Paran� River Basin, Brazil

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Feeding ecology of three *Astyanax* species (Characidae, Tetragonopterinae) from a floodplain lake of Mogi-Guaçú River, Paraná River Basin, Brazil

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Synopsis

The feeding ecology of three characids (*A. fasciatus, A. bimaculatus* and *A. schubarti*) was studied monthly during 1988 in Lake Infernão, a major floodplain lake of the Mogi-Guaçú River in the State of São Paulo. River flooding directly influenced the diet of the omnivorous *A. bimaculatus* and *A. fasciatus* which responded to maximum inundation (March) by consuming predominantly allochthonous insects. In contrast, *A. schubarti* was less influenced by the river flood cycle on qualitative changes in diet and relied basically on aquatic macrophytes and periphytic algae. The importance of zooplankton in the diet of the three species was low, and may be attributed to its low density in the water column (< 1 ind l^{-1}). Ontogenetic diet changes were evident for the three species. For *A. fasciatus* and *A. bimaculatus* the importance of zooplankton was high at the early stages, decreasing with size. *A. schubarti* at younger stages consumed diversified items which gradually decreased quantitatively up to the size class of 65 mm; from this size onwards, the diet became restricted to the consumption of periphytic algae and macrophytes.

Introduction

The South American fish fauna is one of the most diversified in the world, comprising approximately 3000 species (Böhlke et al. 1978), which includes the family Characidae with approximately 400 species (Britski).[1] Within the subfamily Tetragonopterinae of the Characidae, *Astyanax* is one of the most common genera. Eigenmann (1921) recorded 74 species and subspecies, Fowler (1948) more than 50 species and subspecies for Brazilian freshwaters, while Gery (1977) mentioned more than 60 species.

The species herein studied, *Astyanax fasciatus* (Cuvier, 1819) and *Astyanax bimaculatus* (Linnaeus, 1758) have a widespread distribution, occurring from the La Plata basin to Panama and Costa Rica (Godoy 1975, Gery 1977, López 1978).

Astyanax schubarti Britiski 1964[2] has so far been recorded only in the rivers of the State of São Paulo,

[1] Britski, H.A. 1972. Peixes de água doce do Estado de São Paulo; Sistemática. pp. 79–108. *In:* Comissão Interestadual da Bacia Paraná-Uruguai, Poluição e Piscicultura: notas sobre poluição, ictiologia e piscicultura, São Paulo: Faculdade de Saúde Pública da USP e Instituto de Pesca da C.P.R.N.

[2] Britski, H.A. 1964. Sôbre uma nova espécie de *Astyanax* do Rio Mogi-Guassu (Pisces, Characidae). Papéis Avulsos do Departamento de Zoologia, Secretaria da Agricultura de São Paulo 16: 213–215.

being commonly found in the Mogi-Guaçú River coexisting with *A. fasciatus* and *A. bimaculatus* (Nomura 1974). *Astyanax* are relatively small (10–12 cm as adults); they move in schools (Sazima 1984) and are considered of little commercial value, although they have importance as forage species for several predators. In the past few years, different aspects of their biology such as growth, reproduction and feeding have been studied (Nomura 1974, Schroeder-Araujo 1980, Barbieri et al. 1982, Barbosa 1982, Silva 1991, Arcifa et al. 1991). Most of the feeding studies in Brazil, however, have been performed in man-made environments like reservoirs, where the food and feeding habits of the species have probably been altered.

The present study is part of a large scale project (Jataí Project) which is aimed at understanding the role of several oxbow lakes of the Mogi-Guaçú River as well as aspects of the ecology of fish species. Here we present data on the natural food and feeding habitats of such common species as *A. fasciatus, A. bimaculatus* and *A. schubarti* collected monthly during 1988 in Lake Infernão, a floodplain lake of the Mogi-Guaçú River.

Study areas

Lake Infernão is a floodplain lake located within the Jataí Ecological Station (Lat 21°33′, and 21°37′ S, 47°51′ W), Luis Antonio, SP (Fig. 1). It occupies an area of 3.05 ha in the dry season, being 325.0 m long, 96.0 m wide and 4.9 m deep. The dry season is between April and September and the wet season between October and March. Maximum rainfall occurs in January and February (Galvão 1976). Mean annual air temperature is 21.7° C and mean annual rainfall 1433 mm (Toledo-Filho 1984).

The lake remains isolated from the river's main channel during most of the year, connecting with the floodplain during the rainy season. At this time, the rising water of the river promotes inundation of sedges and herbaceous plants, covering the entire floodplain, which also reaches part of the forest located at the northern side of Lake Infernão.

While the Mogi-Guaçú water level fluctuated strongly during 1988, only small variations occurred in lake Infernão, with the exception of March, when the water level increased up to 5.7 m. Maximum rainfall during 1988 occurred in February, and lowest in July and August. Maximum air temperature was registered from September to March, and minimum values in June and July (Fig. 2a, b, c).

The littoral is covered by an extensive belt of submergent and emergent vegetation, composed of *Eichhornia azurea, Scirpus cubensis, Panicum pernambucense, Cabomba* cf. *piauhyensis,* among others. So far twenty six fish species have been recorded (Galetti et al. 1990); predominantly small Tetragonopterinae and iliophagous species such as *Prochilodus lineatus* (*P. scrofa*) and *Steindachnerina insculpta.*

Materials and methods

During 1988 fish were collected monthly, using a cast net, a seine net (mesh size 8 mm) and gillnets (mesh size 15 and 20 mm diagonally stretched) at a fixed station. Specimens were preserved in ice until measured and weighed in the laboratory. Stomachs were isolated and placed in 70% alcohol until analysis.

Gut contents were analysed according to two methods: (1) frequency of occurrence (where the number of stomachs in which a particular item occurs is expressed as a percentage of the total stomachs examined) (Hyslop 1980); (2) points method (Hynes 1950) where gut contents were examined in a counting chamber under a stereomicroscope (25 ×); items were grouped and the area occupied evaluated. The total area of food items was considered the total volume (100%). Calculations were made according to the formula:

$$P_{ij} = \frac{\sum_{x=1}^{N} P_{ix}}{N_j},$$

where P_{ix} is the proportion by volume of item i in the gut of the individual x and N_j is the number of individuals of species j.

Food items were taxonomically determined to the most detailed possible level.

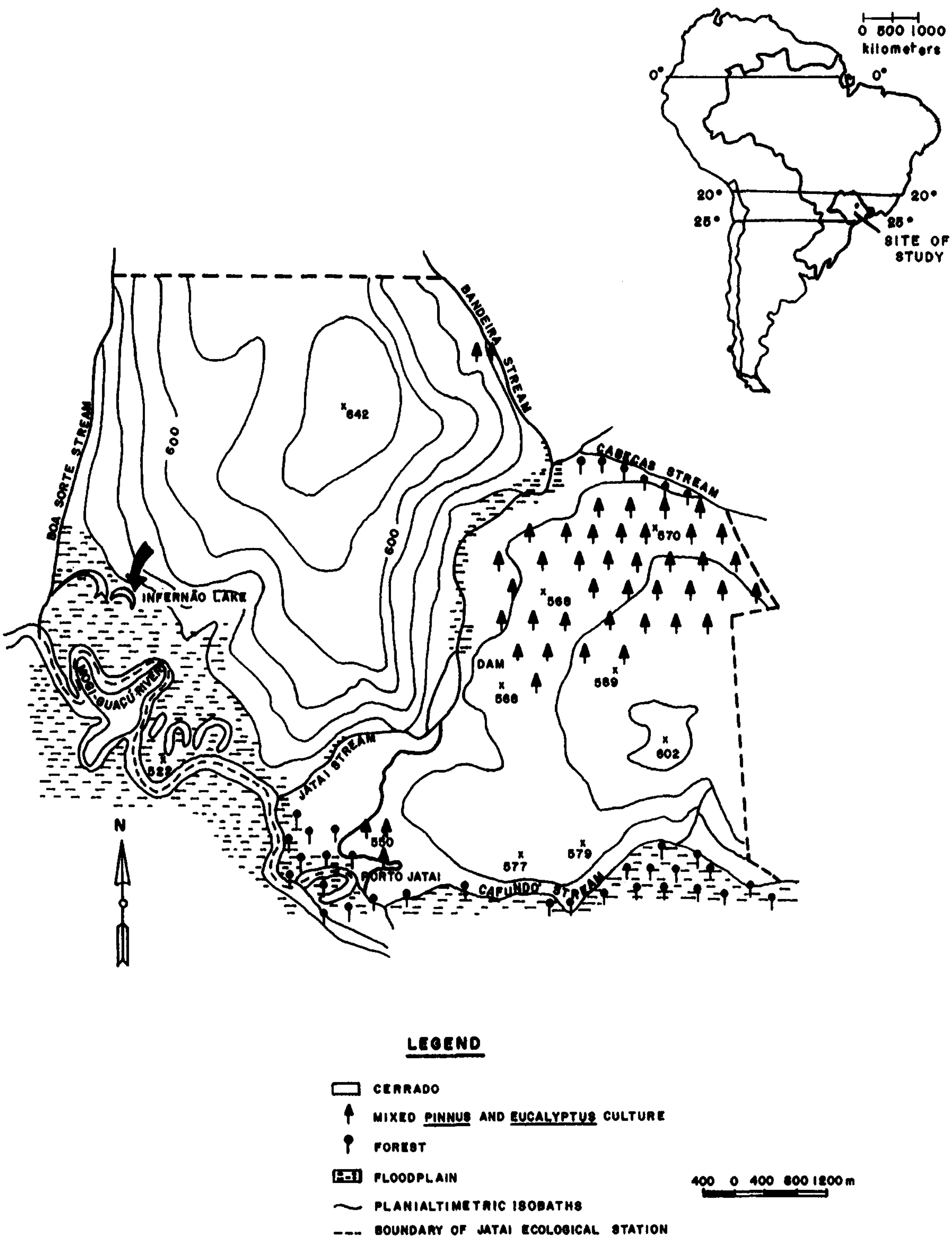
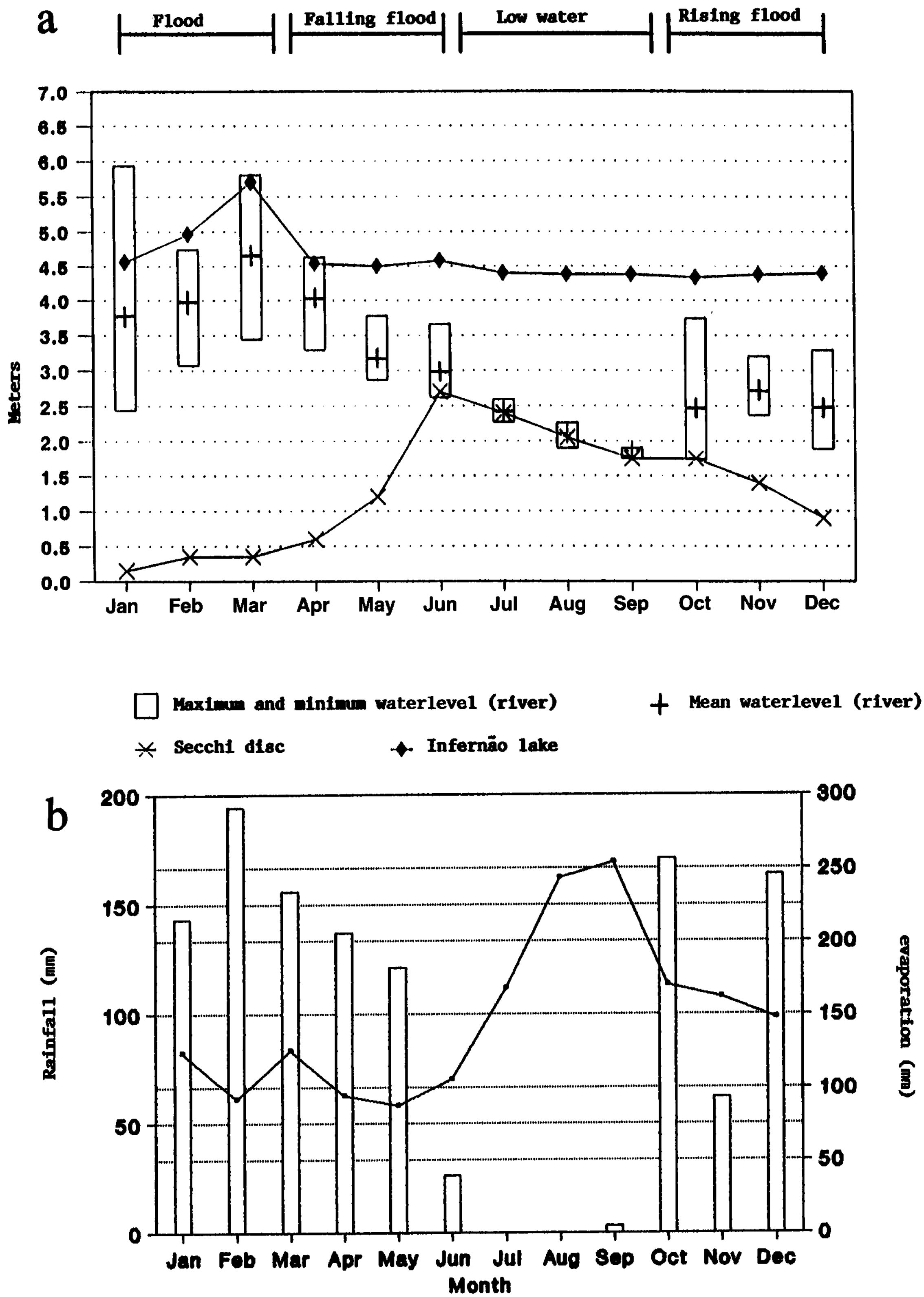


Fig. 1. Location of Jataí Ecological Station in São Paulo State, Brazil, and details showing Mogi-Guaçú River and several oxbow lakes in the floodplain area. Arrow indicates location of Infernão Lake (after Cavalheiro et al. 1990).


a
Flood
Falling flood
Low water
Rising flood
Meters
7.0
6.5
6.0
5.5
5.0
4.5
4.0
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
Jan Feb Mar Apr May Jun Jul Aug Sep Oct Nov Dec
Maximum and minimum waterlevel (river)
Mean waterlevel (river)
Secchi disc
Infernão lake
b
Rainfall (mm)
200
150
100
50
0
evaporation (mm)
300
250
200
150
100
50
0
Jan Feb Mar Apr May Jun Jul Aug Sep Oct Nov Dec
Month

c

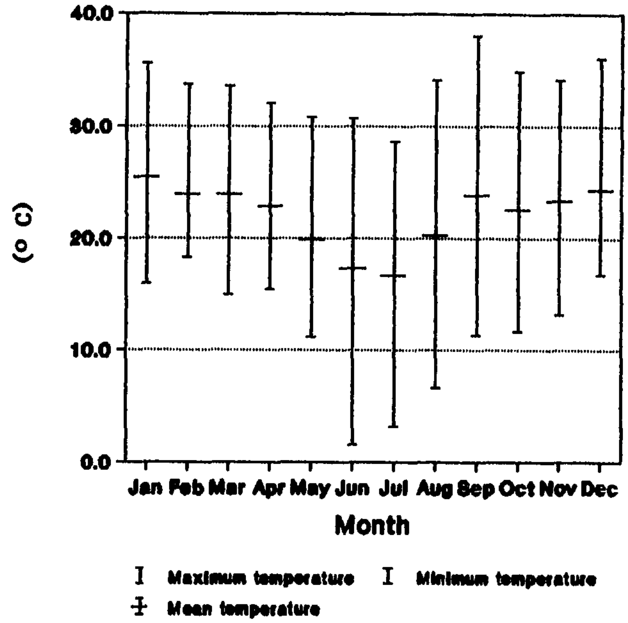


Fig. 2. a – Waterlevel fluctuations of Mogi-Guaçú River and Infernão lake during 1988; b – mean monthly rainfall and evaporation in the same period, c – and maximum, minimum and mean air temperature. Data obtained at DAEE/CTH.

Samples of zooplankton from the region close to the macrophytes were collected monthly utilizing a net 75 cm long, 25 cm in diameter with a mesh of 68 μ. Cladoceran zooplankton were identified, whenever possible, to the level of species and rotifers to the level of genera; Ostracoda and Conchostraca, although not truly euplanktonic were considered as part of the zooplankton. Other limnological data such as water temperature, dissolved oxygen, pH and conductivity were recorded at every sampling and analysed according to Golterman et al. (1969).

Results

General pattern of feeding

Eighty eight specimens of *A. bimaculatus* with total length ranging between 19.1 mm and 82.7 mm were analysed, and although this species showed omnivorous feeding habits, insects dominated. The most representative aquatic insects were Chironomidae and Culicidae larvae as well as larval Diptera. Terrestrial insects were represented predominantly by Hymenoptera (Formicidae), Coleoptera and Diptera adults (Table 1). Algae presented low frequencies of occurrence (< 15.0%).

Ninety four specimens of *A. fasciatus* with total length ranging between 20.0 mm and 62.2 mm were examined. The diet was also omnivorous, with insects representing 30.0% in frequency of occurrence and nearly 60.0% by volume. Coleoptera larvae and Hemiptera nymphs had the highest frequencies of occurrence among aquatic insects, terrestrial groups being represented predominantly by Hymenoptera (Formicidae) and adult Coleoptera (Table 2). Algae occurred in low amounts (< 10%) in volumetric terms.

One hundred and twenty six specimens of *A. schubarti* with total length ranging between 40.7 mm and 89.1 mm were analysed. Their food composition differed markedly from the other two *Astyanax* species, with plant matter (mainly macrophytes) and algae accounting for more than 75% of the volume in this species diet. Food of terrestrial origin was scarce, being consumed only occasionally (Table 3). The predominant algal forms were *Oedogonium* (76.0%), *Eunotia* (54.0%) and *Bulbochaete* (48.0%).

Table 1. Monthly frequency of occurrence (%) of food items from stomachs of *A. bimaculatus*. p = pupae; l = larvae; ad. = adults.

Food categories	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total	%
Aquatic origin														
Animal														
Insecta														
Diptera														
pupae	–	5.9	–	–	11.1	–	12.5	–	–	–	–	–	3	3.4
larvae	–	–	27.3	–	–	–	–	–	–	100.0	–	–	4	4.5
pupary	–	5.9	–	–	–	–	–	–	–	–	–	–	1	1.1
Chironomidae (p)	11.1	5.9	–	7.7	–	–	–	–	–	–	–	–	3	3.4
Chironomidae (l)	–	47.1	–	–	–	–	–	–	–	–	–	–	8	9.1
Ceratopogonidae (l)	–	–	–	–	11.1	–	–	–	–	–	–	–	1	1.1
Chaoboridae (l)	–	11.8	–	–	–	–	–	–	–	–	–	–	2	2.3
Culicidae (l)		11.8	18.2	15.4	–	–	–	–	–	–	–	–	6	6.8
Culicidae (p)	–	–	–	–	–	–	–	–	–	10.0	–	–	1	1.1
Lepidoptera (l)	–	5.9	–	–	–	–	–	–	–	–	–	–	1	1.1
Coleoptera (l)	–	11.8	9.1	–	11.1	–	–	–	–	–	–	–	4	4.5
Psephenidae	–	–	9.1	–	–	–	–	–	–	–	–	–	1	1.1
Hemiptera (n)	–	23.5	–	15.4	–	–	–	–	–	–	–	–	6	6.8
Corixidae (n)	–	5.9	9.1	–	11.1	–	–	–	–	–	–	–	3	3.4
Ephemeroptera (n)	–	5.9	9.1	–	–	–	–	–	–	–	–	–	2	2.3
Collembola	–	35.4	–	7.7	–	–	–	–	–	–	–	–	7	8.0
Odonata (n)	–	23.5	–	–	–	–	–	–	–	–	–	–	4	4.5
Cladocera	–	52.9	–	15.4	22.2	–	–	–	–	–	–	–	13	14.8
Conchostraca	–	35.3	–	–	–	–	–	–	–	–	–	14.3	7	8.0
Ostracoda	11.1	58.8	–	–	11.1	–	–	–	–	–	–	–	12	13.6
Rotifera	–	17.6	–	7.7	–	–	–	–	–	–	–	–	4	4.5
Nematoda	–	5.9	–	7.7	11.1	–	–	–	–	–	–	–	3	3.4
Acarina	22.2	29.4	–	–	11.1	–	–	–	–	–	–	–	8	9.1
Zooplankton (parts)	–	5.9	–	15.4	11.1	–	–	–	–	10.1	–	14.3	6	6.8
Sarcodina	–	11.8	–	7.7	–	–	–	–	–	–	–	–	3	3.4
Osteichthyes	56.7	5.9	9.1	7.7	–	–	12.5	–	–	30.0	–	–	13	14.8
Vegetal														
Vegetal matter	55.6	17.6	9.1	38.5	55.6	100.0	62.5	–	–	40.0	–	57.1	34	38.6
Algae	88.9	35.3	–	23.1	100.0	–	87.5	–	–	40.0	–	85.7	44	50.0
Terrestrial origin								–			–			
Animal								–						
Insecta								–						
Thysanoptera	–	11.8	–	–	–	–	–	–	–	–	–	–	2	2.3
Coleoptera (ad.)	–	5.9	18.2	7.7	–	–	–	–	–	100.0	–	–	5	5.7
Staphylinidae	–	–	18.2	–	–	–	–	–	–	–	–	–	2	2.3
Hymenoptera	–	–	–	–	–	–	–	–	–	50.0	–	–	1	1.1
Diapriidae	–	–	9.1	–	–	–	–	–	–	–	–	–	1	1.1
Formicidae	–	29.4	63.6	7.7	–	–	–	–	–	–	–	–	13	14.8
Homoptera	–	–	9.1	–	–	–	–	–	–	–	–	–	1	1.1
Diptera (ad.)	–	–	36.4	–	–	–	–	–	–	–	–	–	4.	4.5
Isopoda	–	–	9.1	–	–	–	–	–	–	–	–	–	1	1.1
Arachnida		5.9	36.4	–	11.1	–	–	–	–	–	–	–	6	6.8
Unknown origin								–						
Insecta (parts)	55.6	47.1	36.4	61.5	88.9	10.0	75.0	–	100.0	90.0	–	57.1	54	61.4
Organic matter	44.4	35.3	36.4	84.6	88.9	100.0	37.5	–	100.0	40.0	50.0	71.4	48	54.5
Detritus	55.6	29.4	9.1	7.7	–	–	–	–	–		–	–	12	13.6
Number of specimens with food contents	9	17	11	13	9	4	8	–	1	10	2	7	88	

Table 2. Monthly frequency of occurrence (%) of food items from stomachs of *A. fasciatus*. p = pupae; l = larvae; ad. = adults.

Food categories	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total	%
Aquatic origin														
Animal														
Insecta														
Diptera														
pupae	–	–	–	–	10.5	–	–	–	–	–	–	–	2	2.1
Chironomidae (p)	20.0	6.7	–	–	–	–	–	–	–	–	–	–	2	2.1
Chironomidae (l)	–	6.7	–	–	–	–	–	–	–	–	–	–	1	1.1
Culicidae	–	–	25.0	–	–	–	–	–	–	–	–	–	1	1.1
Ceratopogonidae (l)	–	–	–	7.1	–	–	–	–	–	–	–	–	1	1.1
Collembola	20.0	–	–	7.1	–	–	–	–	–	–	–	–	2	2.1
Coleoptera (l)	–	–	25.0	21.4	–	–	–	14.3	–	–	–	–	5	5.3
Hemiptera (n)	–	–	–	–	5.3	–	–	14.3	–	–	–	–	2	2.1
Notonectidae	–	–	7.1	10.5	–	–	–	–	–	–	–	–	3	3.2
Homoptera (n)	–	–	–	–	5.3	–	–	–	–	–	–	–	1	1.1
Neuroptera (l)	–	–	–	7.1	–	–	–	–	–	–	–	–	1	1.1
Nematoda	–	–	–	21.4	5.3	25.0	–	–	–	–	–	–	6	6.4
Cladocera	20.0	–	–	21.4	31.6	–	–	14.3	50.0	–	–	12.5	13	13.8
Rotifera	20.0	6.7	–	21.4	15.8	–	33.3	–	50.0	–	14.3	–	11	11.7
Copepoda	20.0	13.3	–	14.3	10.5	25.0	33.3	–	50.0	16.7	–	–	11.	11.7
Ostracoda	–	6.7	–	28.6	–	–	–	–	–	–	–	–	5	5.3
Conchostraca	–	–	–	7.1	5.3	–	–	–	–	–	–	–	2	2.1
Sarcodina	–	–	–	–	10.5	25.0	–	–	–	–	–	–	3	3.2
Osteichthyes	20.0	6.7	–	–	10.5	–	–	–	–	–	14.3	–	5	5.3
Zooplankton (parts)	20.0	–	–	14.3	21.1	–	–	42.9	50.0	16.7	14.3	12.5	14	14.9
Vegetal														
Vegetal matter	60.0	33.3	–	28.6	26.3	–	33.3	57.1	–	50.0	14.3	87.5	33	35.1
Algae	60.0	53.3	–	71.4	78.9	50.0	–	42.9	100.0	66.7	71.4	87.5	59	62.8
Terrestrial origin														
Animal														
Insecta														
Diptera	–	–	–	7.1	–	–	–	14.3	–	–	–	–	2	2.1
Culicidae	–	–	25.0	–	–	–	–	–	–	–	–	–	1	1.1
Muscoide	–	–	–	–	5.3	–	–	–	–	–	–	–	1	1.1
Coleoptera (ad.)	–	6.7	25.0	7.1	–	–	–	–	–	–	–	–	3	3.2
Hemiptera (ad.)	–	6.7	–	–	–	–	–	–	–	–	–	–	1	1.1
Hymenoptera	–	–	–	7.1	–	–	–	–	–	–	–	–	1	1.1
Formicidae	–	6.7	50.0	–	–	–	–	–	–	6.7	–	–	4	4.3
Chalcidoidea	–	–	25.0	7.1	–	–	–	28.6	–	–	–	–	4	4.3
Thysanoptera	–	–	–	–	–	5.3	–	–	–	–	–	–	1	1.1
Arachnida	–	–	25.0	7.1	–	–	–	28.6	–	–	–	–	4	4.3
Pseudoescorpiones	–	–	25.0	–	–	–	–	–	–	–	–	–	1	1.1
Unknown origin														
Insecta (parts)	20.0	73.3	25.0	100.0	89.5	75.0	100.0	100.0	100.0	100.0	85.7	87.5	78	83.0
Organic matter	60.0	66.7	–	54.3	73.7	50.0	33.3	71.4	100.0	33.3	42.9	62.5	56	59.6
Detritus	100.0	6.7		14.3	5.3	–	–	–	–	–	–	–	9	9.6
Number of specimens with food contents	5	15	4	14	19	4	3	7	2	6	7	8	94	

Seasonal fluctuations

The main differences in limnological conditions in Lake Infernão during 1988 occurred between the wet and dry season. The wet season (October–March) was characterized by high conductivity (48 $\mu S\ cm^{-1}$) and high water temperature (29° C) as well as low oxygen concentrations (85.9% saturation), in contrast to the values registered during the dry season (April–September).

Considering the seasonal variation of food items, a similar pattern was observed between *A. fasciatus* and *A. bimaculatus* (Figs 3, 4). Insects retained their dominant position during the year, showing higher frequencies of occurrence and volume composition

Table 3. Monthly frequency of occurrence (%) of food items from stomachs of *A. schubarti*. p = pupae; l = larvae; ad. = adults; n = nymph.

Food categories	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total	%
Aquatic origin														
Animal														
Insecta														
Diptera														
pupae	–	7.7	–	–	–	–	–	–	–	–	–	–	1	0.8
Chironomidae (p)	–	7.7	–	–	–	7.7	–	–	–	–	–	–	1	0.8
Chironomidae (l)	9.1	7.7	–	–	8.5	7.7	5.0	–	–	–	–	–	6	4.8
Culicidae (l)	–	7.7	–	–	–	–	–	–	–	–	–	–	1	0.8
Ceratopogonidae (l)	–	–	–	5.9	7.7	5.0	–	–	–	–	–	–	3	2.4
Ephemeroptera (n)	4.5	–	–	–	–	–	–	–	–	–	–	–	1	0.8
Odonata (n)	–	–	–	5.9	–	–	–	–	–	–	–	–	1	0.8
Trichoptera (p)	–	–	–	–	–	–	5.0	–	–	–	–	–	1	0.8
Lepidoptera (l)	–	7.7	–	–	–	–	–	–	–	–	–	–	1	0.8
Cladocera	–	7.7	–	–	–	7.7	5.0	33.3	–	–	–	8.3	5	4.0
Rotifera	–	7.7	–	–	–	7.7	–	–	–	–	–	8.3	3	2.4
Copepoda	–	–	–	–	–	23.1	10.0	–	–	–	–	–	5	4.0
Ostracoda	4.5	7.7	–	–	–	–	–	–	–	–	–	–	2	1.6
Conchostraca	4.5	38.5	–	–	–	–	–	–	–	–	–	–	6	4.0
Sarcodina	–	–	–	–	8.3	–	–	–	–	–	–	–	1	0.8
Osteichthyes	18.2	–	25.0	11.8	25.0	–	5.0	–	–	–	100.0	–	13	10.3
Zooplankton (parts)	–	7.7	–	–	–	7.7	33.3	33.3	–	–	–	–	4	3.2
Nematoda	–	7.7	–	–	–	15.4	–	–	–	–	–	–	3	2.4
Acarina	4.5	–	–	–	8.3	–	–	–	–	–	–	–	2	1.6
Mollusca	–	–	12.5	–	–	–	–	–	–	–	–		2	1.6
Vegetal									–		–			
Vegetal matter	27.3	46.2	62.5	70.6	83.3	69.2	65.0	66.7	–	40.0	–	83.3	75	59.5
Algae	86.4	38.5	25.0	100.0	83.3	92.3	80.0	100.0	–	60.0	–	83.3	97	77.0
Terrestrial origin														
Animal														
Insecta														
Diptera (ad.)	–	–	–	5.9	–	5.0	–	–	–	–	–	–	2	1.6
Coleoptera (ad.)	–	–	12.5	–	–	–	–	–	–	–	–	–	1	0.8
Homoptera (ad.)	4.5	–	–	–	–	–	–	–	–	–	–	–	1	0.8
Arachnida	–	–	–	–	–	5.0	–	–	–	–	–	–	1	0.8
Unknown origin														
Insecta (parts)	13.6	23.1	37.5	11.8	16.7	23.1	50.0	33.3	–	40.0	–	16.7	31	24.6
Organic matter	27.3	15.4	37.5	64.7	41.7	46.2	60.0	66.7	–	60.0	100.0	41.7	56	44.4
Detritus	17.3	15.4	25.0	–	8.3	7.7	–	–	–	–	–	8.3	13	10.3
Number of specimens with food contents	22	13	8	17	12	13	20	3	–	5	1	12	126	10.3

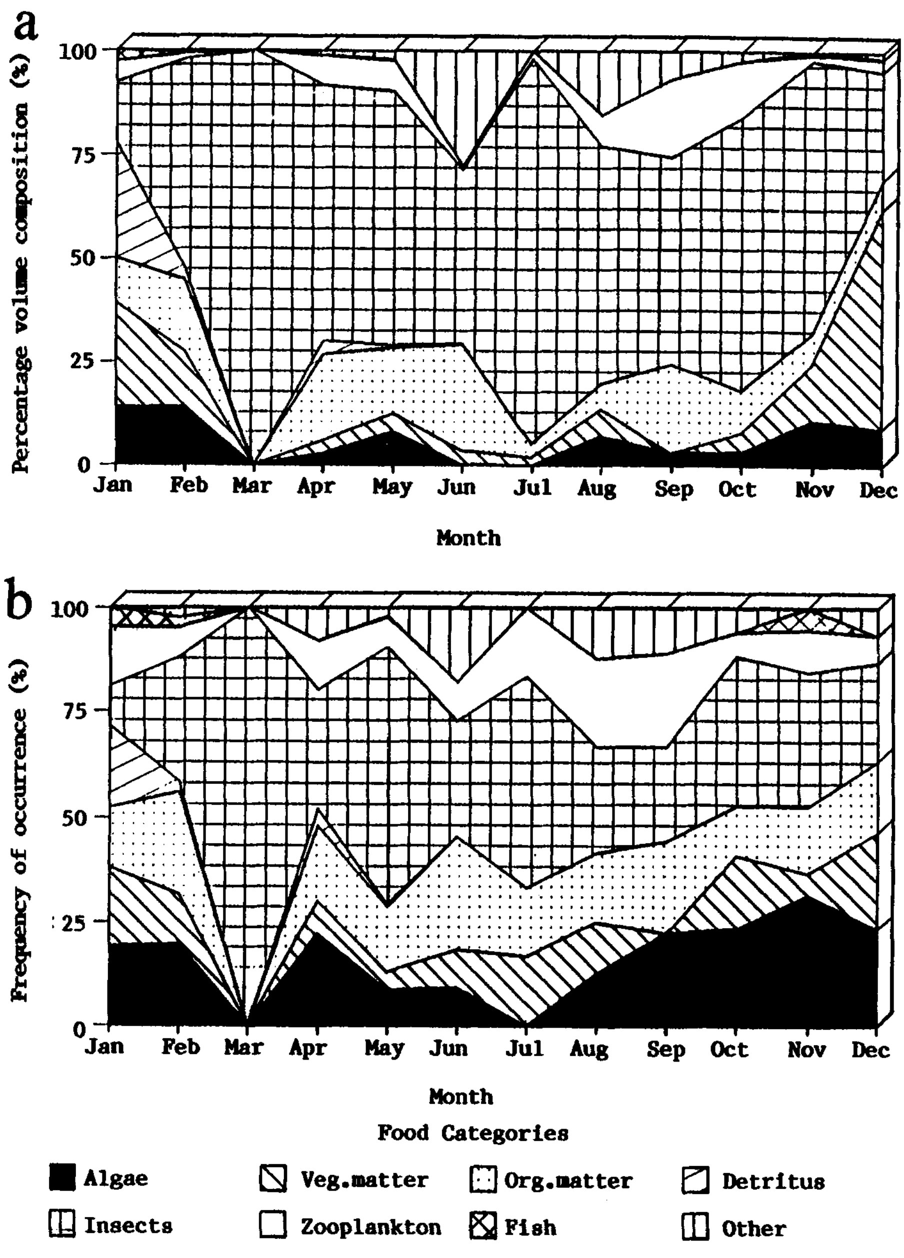


Fig. 3. a – Seasonal variation of volume composition (%), and b – frequency of occurrence (%) of the main food items consumed by *A. fasciatus* during 1988.

in March and October. In March, terrestrial insects dominated as shown in Table 1 and 2.

As for *A. schubarti*, algae and other plant matter were the major food items consumed during the whole year, falling to lower levels at the end of the wet season and the end of the dry season (Fig. 5, Table 3).

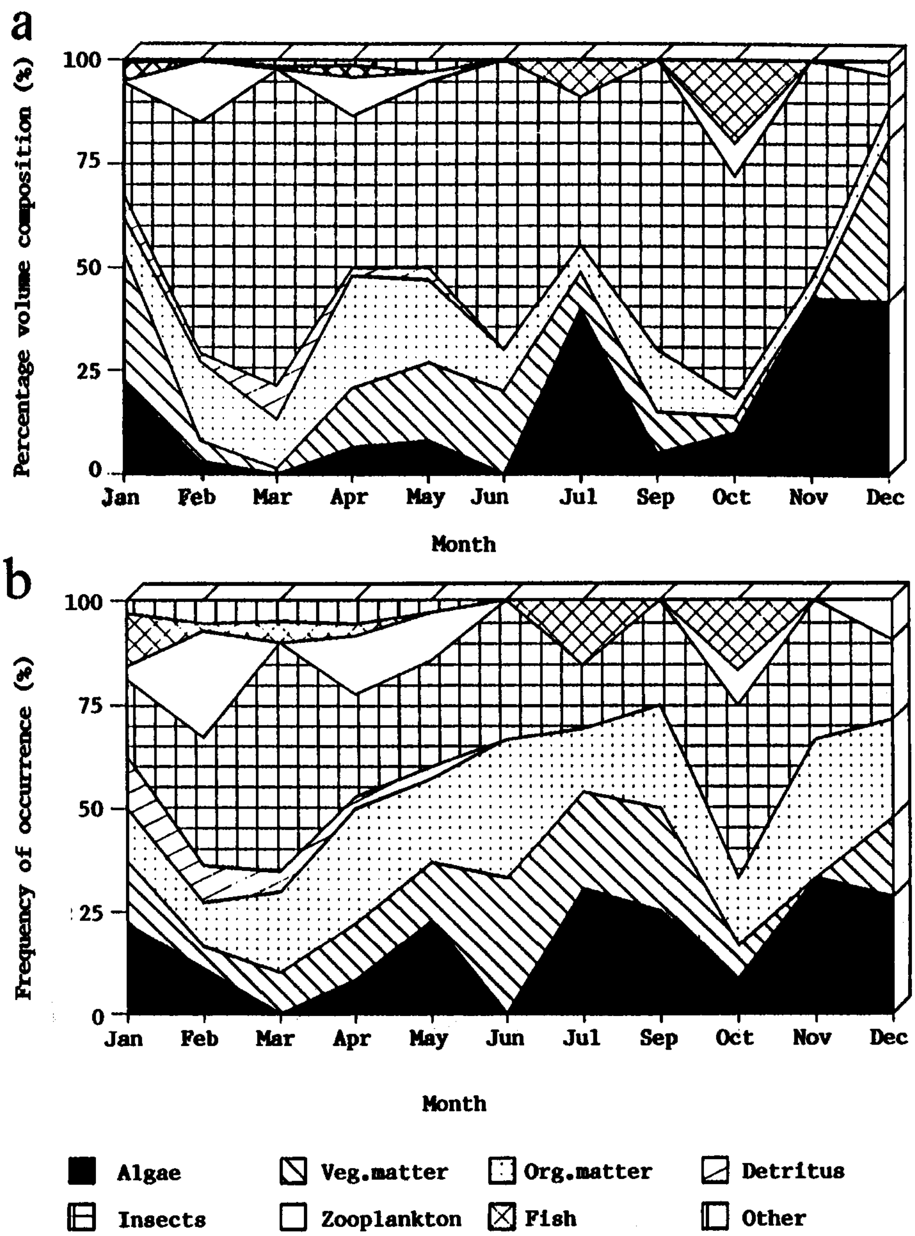


Fig. 4. a – Seasonal variation of volume composition (%) and b – frequency of occurrence (%) of the main food items consumed by *A. bimaculatus* during 1988.

Zooplankton

Densities of zooplankton in the water column of Lake Infernão were very low (< 1 ind l^{-1}). Considering the grouped data for the whole period, zooplankton contributed with values between 3.5 to 12.0% in the diet of the three species.

Cladocera and Copepoda were the main groups consumed by *A. fasciatus* and *A. bimaculatus* while

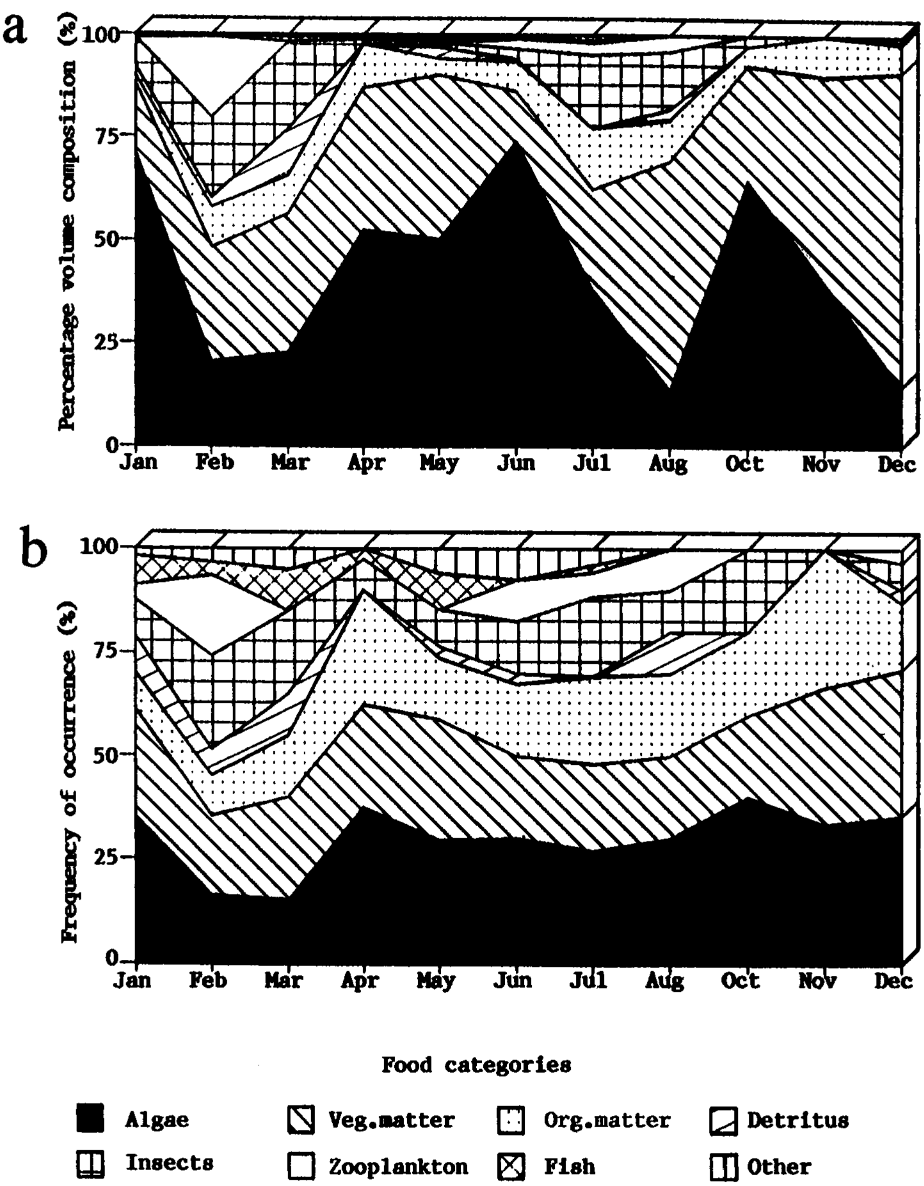


Fig. 5. a – Seasonal variation of volume composition (%) and b – frequency of occurrence (%) of the main food items consumed by *A. schubarti* during 1988.

conchostracans were dominant for *A. schubarti* (Table 4).

The diversity of zooplankton from the water column was very low during the entire year, with the exception of March, when several new species were added (Table 5). The increase of zooplankton diversity in March, however, did not result in a higher consumption of zooplankton by either of the species (Figs 3, 4, 5).

Diet shift with length

Figures 6, 7 and 8 show the variations of the main food categories consumed by specimens of different sizes. Small individuals of *A. fasciatus* showed a greater consumption of zooplankton, insects and 'other items'. With increasing size, plant matter and algae increased in importance.

As for *A. bimaculatus*, zooplankton contributed more than 50.0% of the diet bulk of the smallest individuals (10–20 mm), decreasing in frequency up to the 50–60 mm size class. Fish above this size showed a marked change in feeding, when algae and fish scales appeared in greater proportions.

In the case of *A. schubarti* there were marked differences between individuals in sizes less than 65–70 mm and those above this size. Young fish consumed a broad spectrum of food items while individuals greater than 65–70 mm fed basically algae and vegetal matter, which in volumetric terms accounted for more than 80% of the gut contents.

Discussion

General aspects

From the three *Astyanax* species studied, *A. fasciatus* and *A. bimaculatus* feeding habitats have been investigated more intensively over the last years (Nomura 1974, Godoy 1975, Barbosa 1982, Uieda 1983, Ortaz & Infante 1986, Itaipu Binacional,[3] and Arcifa et al. 1991).

In rivers these two species are omnivorous and exploit similar food resources which include algae, higher plants, insects and fish scales (Godoy 1975, Uieda 1983). In lentic habitats, *A. fasciatus* has been considered zooplanktivorous by Barbosa (1982)

[3] Itaipu Binacional. 1987. Ictiofauna e Biologia Pesqueira. FUEM/SUREMA/Itaipu Binacional, Maringá, 2v.

Table 4. Total number of zooplanktonic organisms consumed by the different fish species.

Groups	Species		
	A. fasciatus	*A. bimaculatus*	*A. schubarti*
Rotifera	15	3	1
Cladocera			
Alona	5	6	–
Biapertura	2	–	–
Bosminopsis	–	–	1
Ceriodaphnia	–	3	–
Chydorus	4	6	3
Diaphanosoma	3	2	1
Disparalona	–	1	–
Graptoleberis	–	–	1
Grimaldina	–	–	–
Ilyocryptus	2	3	4
Leydigiopsis	–	–	–
Macrothrix	–	2	–
Moina		–	–
Oxyurella	–	–	–
Pleuroxus	2	–	2
Simocephalus	19	5	–
Chydoridae (n.i.)	4	6	3
Copepoda			
Cyclopoida	29	10	25
Calanoida	–	6	–
Harapacticoida	–	–	–
Ostracoda	6	15	7
Conchostraca	2	14	39
Number of specimens analysed	94	88	126

and Arcifa et al. (1991), and insectivorous by Schroeder-Araujo 1980, while *A. bimaculatus* is regarded as an omnivorous species which consumes predominantly insects (Godoy 1975, Schroeder-Araujo 1980, Romanini 1989). According to Ortaz & Infante (1986) and Arcifa et al. (1991) *A. bimaculatus* also consumes considerable amounts of zooplankton.

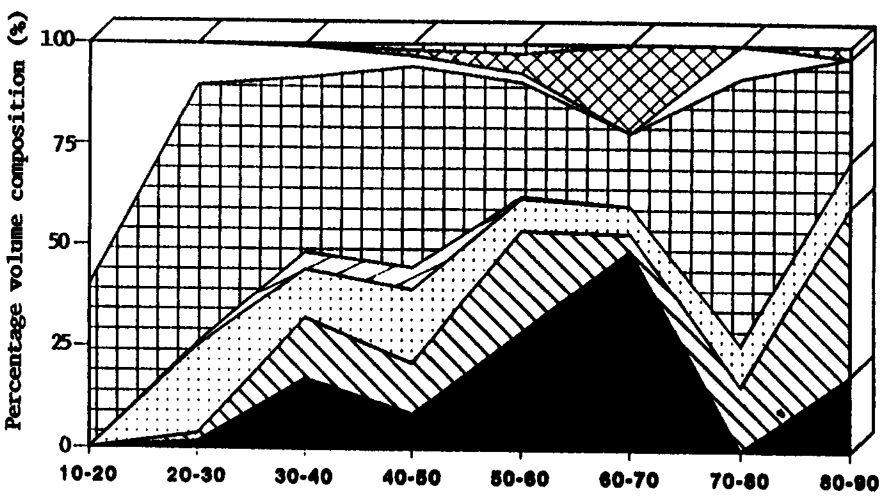
In Lake Infernão both *A. fasciatus* and *A. bimaculatus* consumed basically aquatic and terrestrial insects, a pattern which may be related to the scarcity of items such as zooplankton which occurred in densities below those verified by Frutos and Corrales de Jacobo & Frutos (in Neiff 1990) in oxbow lakes without connection to the Paraná River (10–530 ind. l^{-1} in the dry season and 26–1200 ind. l^{-1} in the wet season, when these lakes were connected to the river).

According to Zaret & Rand (1971), the *Astyanax* show high plasticity in their diet, moving quickly and occupying the surface or the middle region of pools studied in Panamá. This behaviour seems to

Table 5. Zooplanktonic organisms found in the water column of Infernão Lake during 1988. * = presence; ** = abundance; – = absence.

Groups	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Rotifera	**	–	**	–	–	**	–	–	*	–	–	–
Asplanchna sp.	–	–	**	–	–	–	–	–	–	–	–	–
Collotheca sp.	–	–	**	–	–	–	–	–	–	–	–	–
Brachionus falcatus	–	–	**	–	–	–	–	–	–	–	–	–
B. mirus	–	–	**	–	–	–	–	–	–	–	–	–
B. dolabratus	–	–	**	–	–	–	–	–	–	–	–	–
B. patulus macrachantus	–	–	**	*	–	*	*	–	–	–	–	–
Filinia sp.	–	–	*	–	–	–	–	–	–	*	*	–
Keratella tropica	–	–	*	–	–	–	*	–	–	–	–	–
Keratella sp.	–	–	*	–	–	–	*	**	**	*	*	–
Lecane leontina	*	*	*	–	–	–	*	–	–	*	*	–
Lecane sp.	–	–	*	–	–	–	–	–	–	–	–	–
Polyarthra sp.	*	*	*	*	**	*	–	–	–	–	–	–
Trichotria tetractis	–	–	*	–	–	–	–	–	–	–	–	–
Trichocerca sp.	–	–	–	–	–	–	*	–	*	–	*	–
Cladocera												
Bosminopsis deitersi	–	–	*	–	–	–	–	–	–	–	–	–
Ceriodaphnia cornuta cornuta	–	–	**	–	–	–	–	–	–	–	–	–
Ceriodaphnia cornuta rigaudi	–	–	**	–	–	–	–	–	–	–	–	–
Chydorus barroisi	–	–	**	–	–	–	–	–	–	–	–	–
Chydorus sp.	–	–	–	–	–	–	–	–	–	–	*	–
Chydoridae n.i.	–	–	–	–	–	–	*	–	–	–	–	–
Disparalona dadayi	–	–	–	–	–	–	–	–	*	–	*	–
Echinischia sp.	–	–	*	–	–	–	–	–	–	–	–	–
Ilyocryptus	–	–	–	–	–	–	–	–	–	–	*	–
Kurzia cf. *latissima*	–	–	*	–	–	–	–	–	–	–	–	–
Moina sp.	*	–	*	–	–	–	–	–	–	–	–	–
Sarsilatona sp.	–	–	–	–	–	–	–	–	*	–	–	–
Copepoda												
nauplio Cyclopoida	**	–	**	**	**	**	**	**	**	**	**	**
Copepodito Cyclopoida	**	–	**	**	**	**	–	*	**	**	**	**
Paracyclops	–	–	*		–	–	–	–	–	–	–	–
Nematoda	–	–	*		–	*	–		*	–	–	–
Hydracarina	–	–	–	–	–	–	–	–	–	–	–	*
Rhizopoda	–	–	–	–	–	–	–	–	*	–	*	*
Insecta												
Chironomidae larvae	–	–	*	–	–	*	–	–	–	–	–	–

a



b

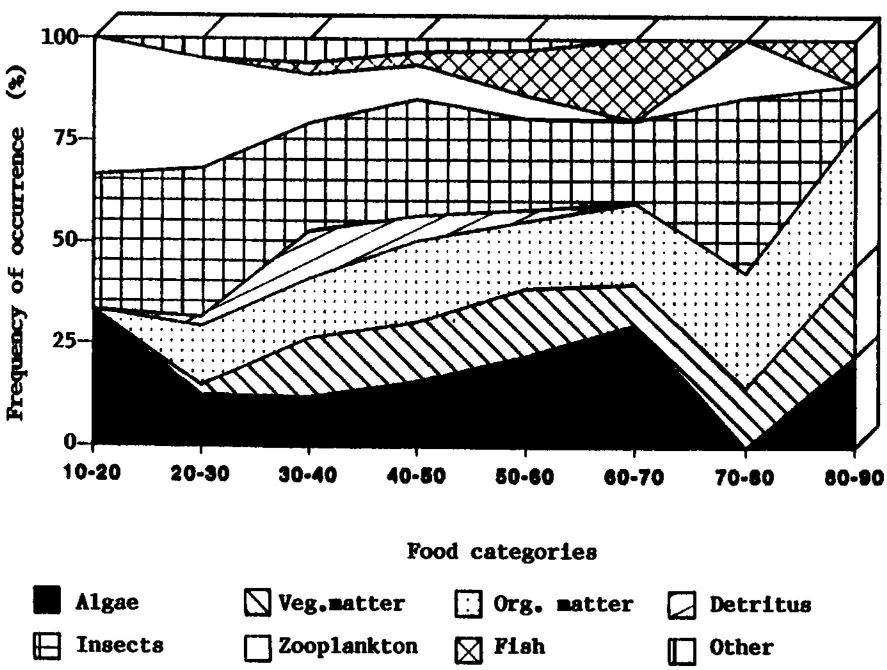


Fig. 6. a – Percentage volume composition and b – frequency of occurrence of the main items consumed by *A. bimaculatus*, according to fish size.

apply both to *A. fasciatus* and *A. bimaculatus* in Lake Infernão, although these species apparently exploit more the littoral region as confirmed by the zooplankton species found in their stomachs (basically littoral forms). The extensive littoral belt occupied by macrophytes in Lake Infernão (Nogueira 1989), may explain the occupation of this habitat by these fish, considering that food items such as periphyton, detritus, insect larvae and zooplankton become abundant in this region. Dense mats of macrophytes are widespread and abundant in tropical floodplains (Welcomme 1985) and may sieve out most of the lakes planktonic production (Hamilton et al. 1990), thus making a rich food source

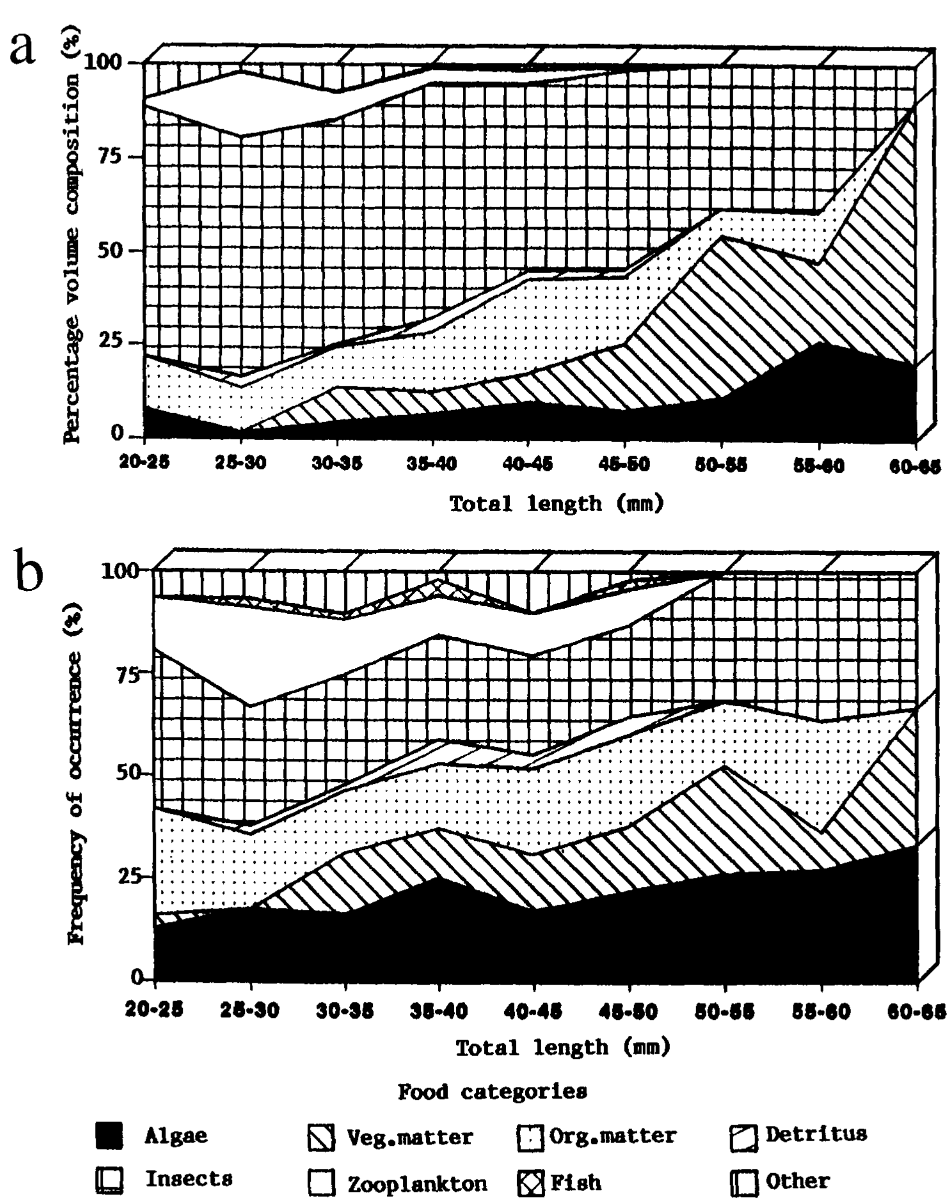


Fig. 7. a – Percentage volume composition and b – frequency of occurrence of the main items consumed by *A. fasciatus*, according to fish size.

available to the abundant invertebrate and fish fauna.

A. schubarti, which has so far only been studied by Godoy (1975) in the Mogi-Guaçú River, was found to consume vegetal matter but was considered omnivorous. In Lake Infernão this species showed food segregation in relation to the other two *Astyanax*, as evidenced by the dietary differences observed, resulting in low food overlap values as shown by Esteves & Galetti (1995) during most of the year.

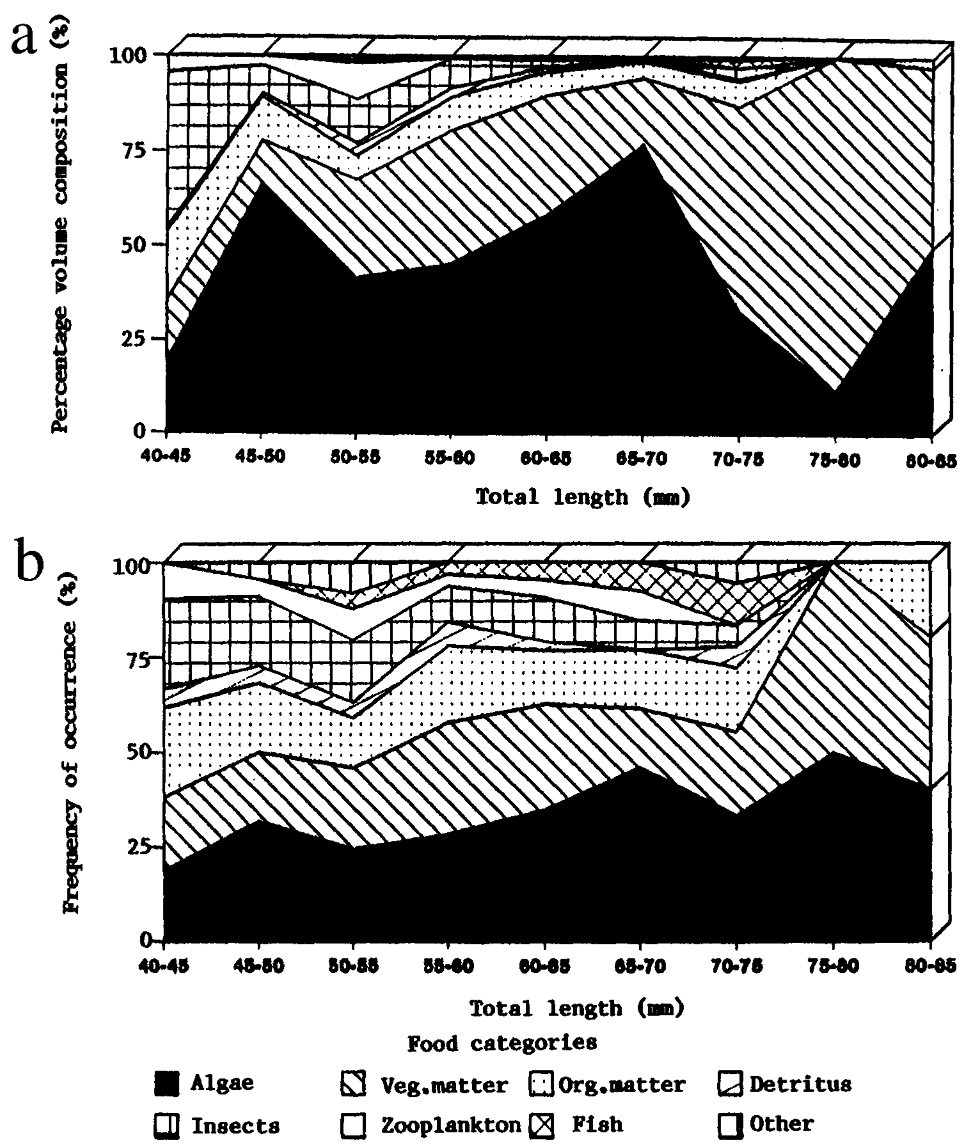


Fig. 8. a – Percentage volume composition and b – frequency of occurrence (b) of the main items consumed by *A. schubarti*, according to fish size.

Seasonal fluctuations

According to Welcomme (1985) the feeding cycle in flood rivers is clearly linked to two factors, firstly the food supply and secondly the population density. Seasonal changes in the habitat affect fishes mainly through qualitative and quantitative changes in available food, though there may be more direct effects such as the opening up of habitats in floodplains, or wind turbulence affecting planktonic larvae (Lowe McConnell 1987).

In Lake Infernão the most pronounced changes in water level occurred at the end of the rainy season in March, when the environment expanded connecting with the river and the gallery forest located at its northern side.

These conditions are reflected in different ways on the potential fish foods: (a) peaks in biomass of periphyton from the aquatic macrophyte *E. azurea*, one being between January and March and one in October when rains started (Schwarzbold et al. 1990); (b) increase in phytoplankton density during the rainy season (Dias Jr. 1990); (c) more intense development in biomass of the macrophyte *E. azurea* during the dry season and of *Scirpus cubensis* during the wet season (Nogueira 1989); (d) small increases in zooplankton abundance and diversity during March.

Considering these seasonal variations, Esteves & Galetti (1995) have shown that there are two periods of more intensive feeding for *A. bimaculatus* and *A. schubarti*, one in February–March (end of the rainy season), and the other in September–October (start of the rains). The qualitative and quantitative changes in feeding during the year observed in this study show a close relationship to these seasonal changes, and coincide with other studies (Goulding 1981, Prejs & Prejs 1987), which showed that most of the species switch diet seasonally in response to the concentrations of their preferred food.

In fact, *A. fasciatus* and *A. bimaculatus* responded quickly to the changes induced by the flood, consuming substantial amounts of allochtonous insects during March. The onset of the rains in September may also have produced an input of terrestrial insects, which the fishes responded to by increasing the intake of this item. It may be suggested that these omnivorous species feed during periods of high food availability as in March in order to accumulate fat for the dry season; on the other hand the start of the rains in September–October seems to produce another increase of food which may be important for the fishes as fat reserves then could have reached a minimum. These aspects would be worth investigating further, in order to confirm this hypothesis.

Other items such as zooplankton also showed seasonal peaks of consumption for *A. fasciatus, A. bimaculatus* and *A. schubarti* (February and September–October). Although no increase in the zooplankton density of the water samples at these periods was observed, it is possible that the scarcity of insects and an increase of the littoral zooplankton forms during the end of the dry season may have favoured a higher intake of this item. The decomposition of macrophytes producing a maximum of detritus at the end of the dry season (Nogueira 1989) may be one of the causes of a zooplankton increase that feed on this source.

The smaller influence of the flood on diet changes of *A. schubarti* probably occurred because this species relied basically on autochtonous food. The greater consumption of algae and vegetal matter by this species during the dry season (June–July) also coincides with the studies of Prejs & Prejs (1987), who found that small Characidae in Venezuela consumed more algae and detritus during the dry season, and Zaret & Rand (1971) who observed that *Astyanax* species studied in Central America relied exclusively on non-insect foods in dry-season pools.

Dietary shifts with fish length

Most of the ontogenetic changes in fish diet are probably accounted for by morphological and maturational changes, particularly the increase in mouth gap and the improvement in locomotory ability. Other factors can also be important including age specific changes in the use of habitats (Schmitt & Holbrook 1984 in Wootton 1990).

In this study, changes in diet according to fish size were apparent for the three species. In both *A fasciatus* and *A. bimaculatus* the importance of zooplankton in the early stages was evident, decreasing gradually according to fish size. It is well known that all fishes in both tropical and temperate regions feed on zooplankton in the early stages (Fernando 1983, Fernando 1994), but there are indications that zooplankton diversity and production in tropical waters is lower than in temperate regions (Burgis & Dunn 1978, Fernando 1980) and may be one of the causes of low fish yields in tropical and equatorial lakes (Fernando 1983).

For *A. bimaculatus*, change in diet of individuals greater than 50 mm was evident, showing a higher percentage of fish scales in the diet. According to Sazima (1983), aggressive encounters between individuals in the school are frequent in *Astyanax bimaculatus* and *Astyanax fasciatus*, which results in the dislodgement of a few fish scales. The occurrence of this food item at restricted size classes for *A. bimaculatus* may be explained by the fact that scale eating seems to be a size-limited behavior, some species ceasing lepidophagy as they grow (Sazima & Uieda 1980 in Sazima 1984).

In the case of *A, schubarti,* smaller individuals (up to 62.0 mm) consumed diversified items including algae attached to macrophytes, while at the size class of 60–70 mm tufts of *Oedogonium* filled the stomachs. Two hypotheses may explain these results: either young and adults are occupying different habitats, or they are deploying different feeding styles.

Considering the latter possibility, it may be suggested that younger fishes of *A. schubarti* are predominantly grazers while older ones are browsers. This hypothesis would explain the more diversified diet at early life, and may represent an important feeding style since more nutritive items of animal origin would be consumed. Behavioral studies in this direction are suggested since they would provide a better understanding of these styles.

Acknowledgements

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