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Astyanax paranae Eigenmann, 1914 (Characiformes: Characidae) in the Alagados Reservoir, Paraná, Brazil: diet composition and variation

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Aspects of the feeding ecology of a small characin, *Astyanax paranae*, were studied during 1996/1997 and 1998/1999 in the Alagados Reservoir, Paraná, Brazil (25º01'50.0" S; 050º03'41.9" W). Fishes were quarterly captured from the reservoir's riverine and lacustrine zones and stomachs contents of 711 adult individuals were analyzed by volumetric method. Species' feeding spectrum and spatial, temporal and sexual variations on diet were evaluated. Data matrix was summarized by detrented correspondence analysis (DCA) and the axes scores from DCA were used as variables in one-way ANOVA of null models to test diet variations. *Astyanax paranae* fed on detritus/sediment, plant matter, algae and aquatic and terrestrial invertebrates. The time-space prevalence of detritus/sediment and plant matter on diet characterized the feeding habit as detritivorous tending to herbivory. Significant differences on food items proportions occurred between the sampling months and sampling sites and were related to resources availability, characterizing the species trophic opportunism.

Aspectos da ecologia alimentar de um pequeno caracídeo, *Astyanax paranae*, foram estudados durante 1996/1997 e 1998/1999 no reservatório de Alagados, Paraná, Brasil (25º01'50,0" S; 50º03'41,9" W). Os peixes foram capturados trimestralmente nas zonas fluvial e lacustre do reservatório e os conteúdos gástricos de 711 espécimes adultos foram analisados através do método volumétrico. Foram avaliados o espectro alimentar da espécie e alterações espaciais, temporais e entre os sexos na dieta. A matriz de dados foi sumarizada através da análise de correspondência com remoção do efeito do arco (DCA) e os escores dos eixos resultantes da DCA utilizados como variáveis em análises de variância (ANOVA) unifatoriais de modelos nulos para testar diferenças na dieta. *Astyanax paranae* consumiu detrito/sedimento, vegetais, algas e invertebrados aquáticos e terrestres. O predomínio espaço-temporal de detrito/sedimento e vegetais na dieta indicou hábito alimentar detritívoro com tendência a herbivoria. Diferenças significativas na proporção dos itens alimentares ocorreram entre os meses e locais amostrados, tendo sido relacionadas à disponibilidade dos recursos, caracterizando o oportunismo trófico da espécie.

Key words: Fish, Feeding, Dam, Detritivory, Freshwater.

Introduction

Astyanax paranae is a small characin known as Lambari-do-rabo-vermelho. The species is commonly found in the Upper rio Paraná basin (Garutti & Britski, 2000), showing a distribution restricted to small tributaries, preferably dwelling headwaters stretches (Godoy, 1975; Garutti & Britski, 2000; Benedito-Cecilio *et al*., 2004). It was characterized as a short life cycle species (Barbieri, 1992a), with predominantly omnivorous feeding habit (Ferreira, 2004) and presenting sexual dimorphism, being the females more robust than the males (Eigenmann, 1914; Godoy, 1975). The meristic characters regarding the identification of *A. paranae* can be found in Garutti & Britski (2000).

In spite of its adaptation to lotic environments, ichthyofaunistic surveys reported the occurrence of *A. paranae* also in reservoirs presenting expressive population abundance in impoundments of the rio Piquiri basin in the Paraná State (Luiz *et al*., 2005). The proliferation of *Astyanax* species in Brazilian reservoirs is a commonly mentioned fact (Castro & Arcifa, 1987; Arcifa *et al*., 1988; Agostinho *et al*., 1997; Fugi, 1998), and attributes such as capacity of reproduction in lentic environments and a wide feeding spectrum were related to this fish group success in reservoirs colonization (Castro & Arcifa,

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1987; Agostinho *et al*., 1999). Consequently, the knowledge of which food resources are predominantly maintaining fish populations and possible variations in their diet can be considered the initial step to understand the processes involved in the establishment of fish species in reservoirs. In the specific case of the Alagados Reservoir, previous studies pointed out *A. paranae* as the dominant among eight captured species (Luiz, 2000) and characterized its feeding habit as detritivorous (Abelha, 2001). Considering that survival, growth and reproduction of fishes depend on the amount of energy and nutrients generated by the feeding activity (Wootton, 1999), the indication of population abundance among *Astyanax* species maintained through the use of an unusual food resource raised the need of a new research perspective.

Therefore, in this study it is evaluated the feeding spectrum, feeding habit, time-space and sex variation in the diet of *Astyanax paranae* at Alagados Reservoir, Paraná State, Brazil.

Material and Methods

Study site. The Alagados Reservoir is located in the second plateau of the Paraná State (Maack, 2002) (25º01'50.0"S; 50º03'41.9"W), close to the cities of Ponta Grossa and Castro (type locality of *A. paranae* - Garutti & Britski, 2000). Alagados is a small reservoir (area of 7.1 Km^2), closed in 1945, showing a narrow and prolonged morphometry (Fig. 1), originated from the damming of the rio Pitangui for hydropower and water supply use (COPEL, 1999). The reservoir's drainage area has being intensively used for agriculture and cattle-raising. Consequently, the original forest cover, denominated by Maack (2002) as Campos Gerais (physionomic structure corresponding to native grassy vegetation and woods of *Araucaria*), was greatly replaced by agriculture cultivation and exotic forage pasture. The riparian vegetation along the reservoir's margin is composed predominantly by grass associated to scattered arboreal vegetation, including small groupings of *Araucaria* and of the exotic *Pinus*.

Sampling. Fishes were quarterly collected from April 1996 to January 1997 and from April 1998 to January 1999 with gill nets (2.4; to 16.0 cm diagonally stretched) and trammel nets (6.0; 7.0; 8.0 cm stretched mesh) left for 24 hours in the riverine and lacustrine zones of the reservoir (*sensu* Thornton, 1990a). Fishes were removed in the morning (8:00h), afternoon (16:00h) and night (22:00h). Captured specimens were fixed in the field in 10% formalin solution and brought to laboratories of the Núcleo de Pesquisas em Limnologia, Ictiologia e Aqüicultura (Nupélia), Universidade Estadual de Maringá (PR). All specimens were identified, enumerated, weighed (g), measured (total and standard length; cm) and dissected. The gonadal maturity stages were obtained and the stomachs were isolated and placed in 70% alcohol until analysis. Voucher specimens were deposited in the Ichthyological Collection of the Núcleo de Pesquisas em Limnologia, Ictiologia e Aqüicultura (Nupélia), Universidade Estadual de Maringá: NUP 657.

Data analysis. Stomach contents were analyzed according to volumetric method (percentage of volume of each item in relation to the total volume of the stomach contents) (Hyslop, 1980). Volume of each food item was determined using graduate test tubes and a counting chamber for items whose volume was lower than 0.1ml (*sensu* Hellawell & Abel, 1971). In cases that the small size of food items (algae, testate amoebae and others) made impracticable their separation, the volume was estimated through attribution of percentage values in relation to the total volume of the stomach content. The contribution of food items in the diet was expressed in percentage of volume (%V).

The matrix data of stomachs contents volume was summarized by detrended correspondence analysis (DCA) (Hill & Gauch Jr., 1980; Gauch Jr., 1982) using the program PC-ORD (McCune & Mefford, 1997). Considering the sampling years (1996/1997 and 1998/1999), sampling months (April, July, October and January), sampling sites (riverine and lacustrine zones) and specimens sex (female and male) as factors, time-space and sex differences in diet composition were tested by one-way ANOVA of null models, computed by the program EcoSim (Gotelli & Entsminger, 2001) using the axes scores from DCA as variables. Only axes with eigenvalues > 0.20 were tested (Matthews, 1998). Significance level implicated

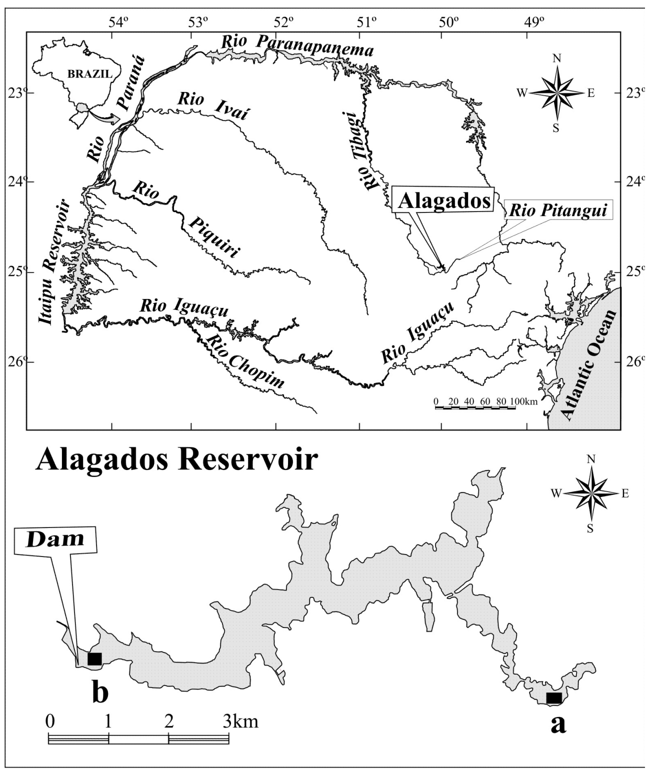

Fig. 1. Localization and morphometry of Alagados Reservoir, Paraná, Brazil, depicting sample sites: a=riverine zone; b=lacustrine zone.

α<0.05 after 5000 randomization. In these analyses, all food items consumed were grouped into seven categories of food resources of wide composition, denominated as "detritus/ sediment", "plant matter", "algae", "aquatic insects", "other aquatic invertebrates", "terrestrial insects" and "rests of insects" (Tab. 1).

Results

In total 4227 specimens of *A. paranae* were captured and 711 stomach contents were analyzed to include, at least, 40 stomachs contends *per* sample period. The results comprised adults feeding, since the smallest examined individual (standard length=5.0 cm) presented resting gonads. It was not possible to identify the sex of 7 specimens, therefore, only 704 specimens were considered in the analysis between females and males.

Food spectrum. The species presented a diversified food spectrum, including detritus/sediment and several taxa of animal and plant origin (Tab. 1). The ones more intensively consumed were detritus/sediment (%V=63.02), plant matter (%V=24.24) and algae (%V=6.11). Detritus/sediment was frequently composed by particles of plant origin, associated to variable portions of sediment (mineral fraction) and, sometimes, to remains of invertebrates and fishes. The consumption of plant matter included mainly fruits and seeds, which were found in the form of fragments, and smaller amounts of leaves, stems and roots. The absence of whole fruits and seeds prevented their taxonomic identification, but, it was possible to identify a lot of starch. Among the algae, the most expressive members (obviously due to their largest size) were filamentous forms of Chlorophyceae and Cyanophyceae, represented, respectively, by species of *Spirogyra* and *Oscillatoria*. In spite of low contribution in volume, periphytics Bacillariophyceae were constantly observed (mainly *Surirella*, *Pinularia* and *Cymbella*) and they were frequently associated to detritus/sediment. Other items, corresponding to the portion of animal origin food resources (aquatic insects, other aquatic invertebrates, terrestrial insects and rests of insects) accounted only for 6.63% of the total volume of consumed resources. Among those, the predominant ones were immature forms of Diptera, mainly Chironomidae; Odonata larvae; Hemiptera, mainly Notonectidae and Gerridae; Oligochaeta; Amphipoda; Bryozoa; Hymenoptera and Coleoptera.

Diet variation. The number of specimens considered in the analysis below are specified in the legend of Fig. 2a, 2b, 2c and 2d. Detritus/sediment and plant matter were the predominant consumed items among the analyzed factors (sampling years, sampling months, sampling sites and specimens sex; Fig. 2a; 2b; 2c; 2d, respectively). However, variations of food items proportions were observed and they were more expressive among sampling months and sampling sites. Plant matter showed peaks of consumption in April and October (%V=40.90 and 38.02, respectively) and detritus/sediment in July and January (%V=75.40 and 63.50, respectively). Between sampling sites, an increased consumption of algae was verified in the riverine zone (%V=16.87) in relation to the lacustrine zone (%V=0.96). These differences were linked to the foraging on *Spirogyra*, almost limited to the riverine zone. Additionally, a slight rise in the volume percentage of other aquatic invertebrates occurred in April and October of 1996

Table 1. Percentage of volume of identified food items consumed by *Astyanax paranae* in the Alagados Reservoir, Paraná State, Brazil.

Food items	Percentage of volume (% V)
Detritus/sediment	63.020
Plant Matter	
Fruits/ seeds Angyospermae	16.078
Root/leaf/stem Angyospermae	7.817
Pteridophyta	0.001
Bryophyta	0.342
Total	24.238
Algae	
Bacillariophyceae	
Penales	0.577
Centrales	0.054
Chlorophyceae	0.158
Spirogyra	3.748
Closterium	0.304
Cyanophyceae	
Oscillatoria	1.272
Total	6.113
Aquatic insects	
Diptera (larvae and pupae)	0.527
Ceratopogonidae (larvae)	0.004
Chaoboridae (larvae)	0.001
Chironomidae (larvae and pupae)	0.577
Culicidae (larvae)	0.003
Simulidae (larvae)	0.002
Coleoptera (larvae)	0.007
Ephemeroptera (nymph)	0.050
Hemiptera	0.081
Neuroptera	0.003
Odonata (nymph)	0.094
Plecoptera (larvae)	0.002
Trichoptera (larvae)	0.004
Total	1.355
Other aquatic invertebrates	
Arachnida	0.012
Hydracarina	<0.001
Amphipoda	0.117
Cladocera	0.013
Copepoda	0.008
Ostracoda	<0.001
Bryozoa	0.783
Oligochaeta	1.483
Testacea	0.043
Nematoda	0.001
Total	2.461
terrestrial insects	
Coleoptera	0.195
Diptera	0.019
Hemiptera	0.077
Homoptera	0.231
Hymenoptera	0.664
Isoptera	0.310
Lepidoptera	0.114
Orthoptera	0.141
Thysanoptera	0.001
Total	1.752
Rests of insects	1.061

(Fig. 2a e 2b). That occurred due to the ingestion of Oligochaeta by few specimens, intensively enough to lead Oligochaeta reach, approximately, 65% of the total volume of other aquatic invertebrates.

The first two axes from DCA were retained for analysis (axis 1 eigenvalue=0.85; axis 2 eigenvalue=0.57). The food items plant matter and detritus/sediment were the main ones responsible for the ordination of the specimens along the axis 1, while, along the axis 2, they were discriminated mainly by algae and terrestrial insects. ANOVA applied to DCA axes scores identified significant differences among the sampling months [IO=76.20; $p(o \geq e)=0.00$] related to the axis 1 (Fig. 3b) and between the sampling sites [IO=82.14; $p(o \geq e)=0.00$] related to the axis 2 (Fig. 3c). On the other hand, significant differences were not verified between the years [axis 1: IO=0.82, $p(o \geq e)=0.36$; axis 2: IO=1.82, $p(o \geq e)=0.18$] (Fig. 3a) and between specimens' sex [axis 1: IO=1.31, $p(o=e)=0.25$; axis 2: IO=3.79, $p(o \geq e)=0.51$] (Fig. 3d).

Discussion

Food spectrum. The wide food spectrum presented by *A. paranae* in Alagados Reservoir was consistent with the range of resources foraged by the species in streams, where it feeds predominantly on terrestrial and aquatic insects, leaves, fruits, seeds, algae and oligochaetes (Godoy, 1975; Ferreira, 2004). However, the expressive consumption of detritus/sediment in Alagados Reservoir was particularly intriguing, because of the unusual presence of this food resource as the main item in the diet of *Astyanax* species. In spite of their trophic opportunism, these characids have been related in literature as omnivorous, herbivorous, insectivorous and zooplanktivorous (Arcifa *et al*., 1991; Meschiatti, 1995; Esteves, 1996; Agostinho *et al.,* 1997; Castro & Casatti, 1997; Bennemann *et al*., 2000; Cassemiro *et al*., 2002; Vilella *et al*., 2002).

Distinct from its congeners, *Astyanax* sp.C, an endemic species (still not described) from the rio Iguaçu basin, presented detritivorous feeding habit and population dominance in the Segredo Reservoir (Fugi, 1998). The author argued that the change in the feeding habit, originally omnivorous (consumption of insects and plant matter) in riverine environment, would have been induced by environmental alterations originated from the recent formation of the reservoir. Additionally, Fugi (1998) attributed the exploration success of this kind of resource to the largest intestine length of *Astyanax* sp.C in relation to other *Astyanax* species appraised in the study. This attribute was not evaluated for *A. paranae* in Alagados Reservoir and it opens perspectives to further in-

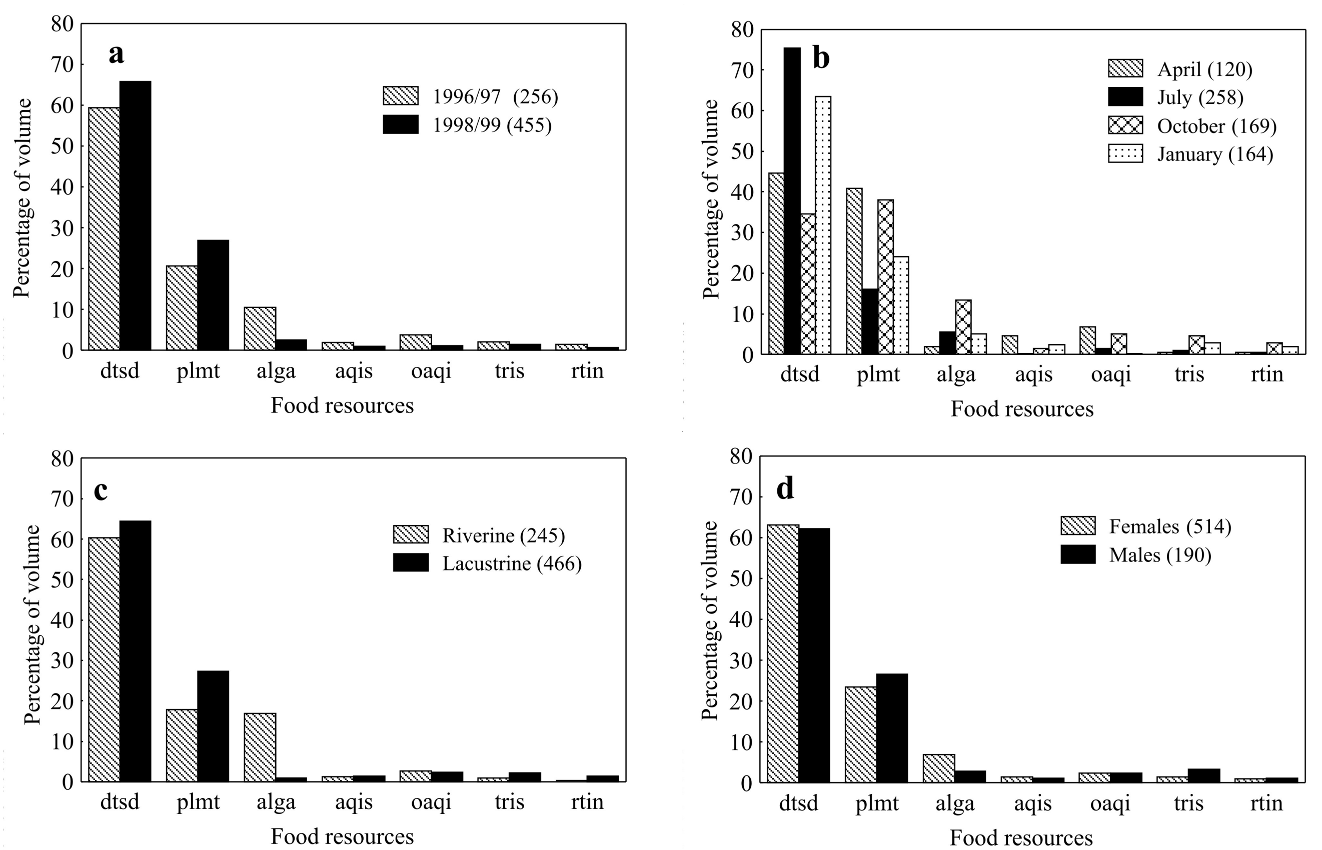

Fig. 2. Volumetric proportion of food resources consumed by *Astyanax paranae* in Alagados Reservoir, Paraná, Brazil, among sampling years (a), sampling months (b), sampling sites (c) and specimens sex (d). dtsd=detritus/sediment; plmt=plant matter; alga=algae; aqis= aquatic insects; oaqi=other aquatic invertebrates; tris=terrestrial insects; rtin=rests of insects. The number of specimens considered in each analysis are indicated in parenthesis in the legends.

vestigations. However, a parameter to that is the medium value of the intestinal ratio (ratio between the intestine length and fish total length) obtained by Barbieri (1992b) for *A. paranae* in stream population [Ribeirão do Fazzari, São Paulo], qualifying the species as characteristically omnivorous.

It is appropriate to highlight that detritus/sediment is commonly found in gastric contents of *Astyanax* species, however, it appears in small volumes, being predominantly associated to aquatic invertebrates or plant structure accumulated in the bottom, indicating the accidental ingestion during food taken (personal observation). The efficiency in the nutritional use of this kind of food has been attributed to trophic specialists (Loricariidae, Prochilodontidae, Curimatidae and Cichlidae) with morphologic adaptations of the digestive tract for this task, which include (not simultaneously) long intestine, mechanical stomach and low gastric pH (Bowen, 1983; Gerking, 1994; Delariva & Agostinho, 2001). In spite of the absence of those structures in *A. paranae*, the spatial and temporal constancy of detritus/sediment as the main item of the diet, allied to the species population abundance in Alagados Reservoir, suggested nutritional use of this food. Besides, detritus/sediment is a resource thoroughly available in reservoirs (Thornton, 1990b), then, the adopted diet would be energetically advantageous considering that detritus/sediment is an abundant and passive food. In other words, without the energetic costs present in activities of detection and capture of preys, since they frequently manifest escape mechanisms (Keenleyside, 1979) and seasonal oscillations in population abundance, as in the case of insects (Borror & DeLong, 1969).

Another point to consider is the variable composition and nutritional value of detritus. This is a food originated from different sources of carbon (cellulose, lignin, chitin and other) and presents particles of variable size, colonized in different degrees by fungi and bacteria, its main source of protein (Bowen, 1979; Yossa & Araujo-Lima, 1998; Crossman *et al.*, 2001; Moore *et al.*, 2004). In this context, it is possible to cogitate the occurrence in Alagados Reservoir of detritus qualitatively improved. Moore *et al.* (2004) argued that the quality of detritus could be fomented when it is nutritionally enriched and submitted to different degrees of previous decomposition. These conditions are possibly being reached through the intensive use of fertilizers and application of no tillage planting technique in agricultural activities developed in the reservoir drainage basin. This fact, added to features such as low periphytics biomass (Rodrigues *et al.*, 2005), inexpressive macrophytes colonization and scarce riparian vegetation, suggested that in Alagados Reservoir detritus is

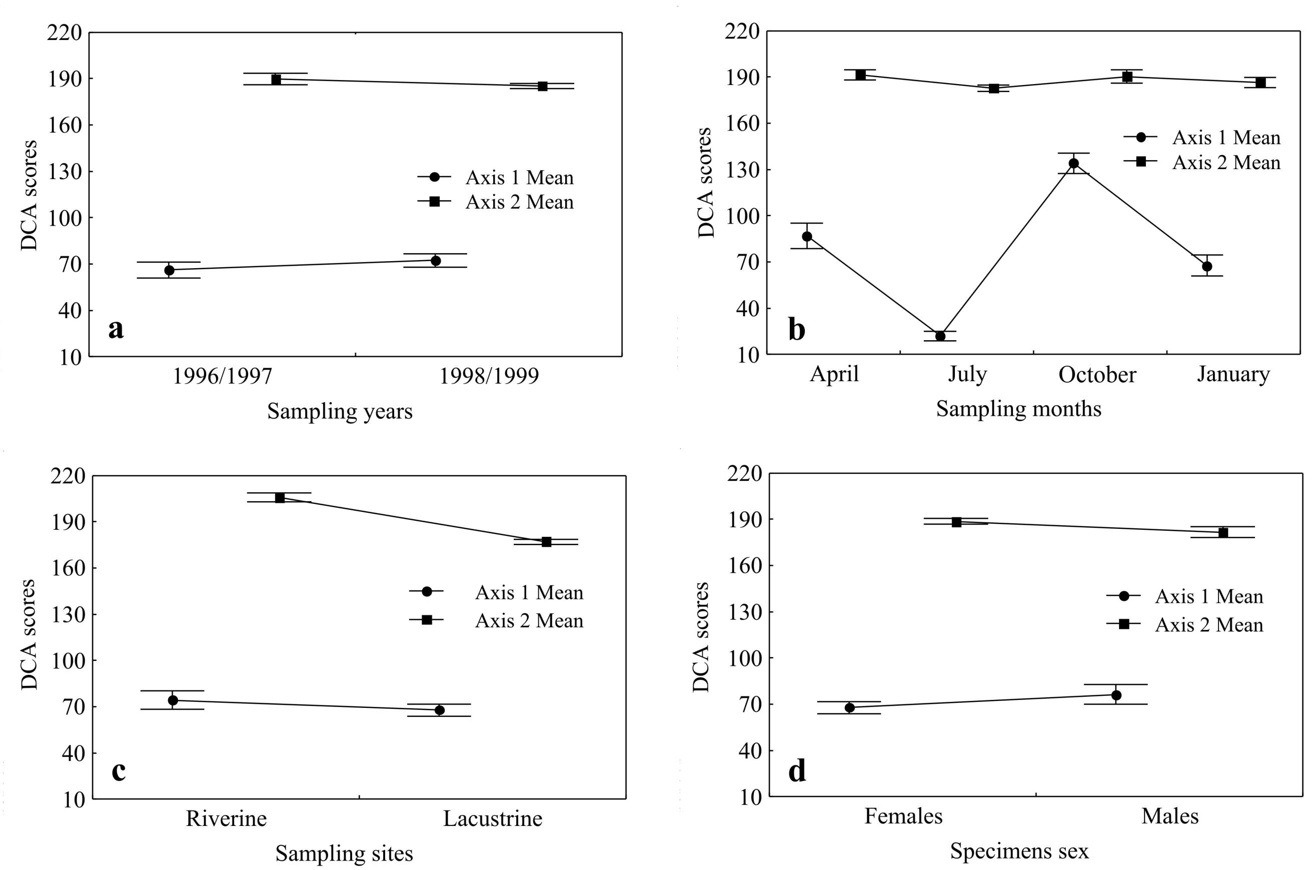

Fig. 3. Average values (± standart error) of the axes scores from DCA ordination of *Astyanax paranae*'s stomach contents volume among sampling years (a), sampling months (b), sampling sites (c) and specimens sex (d) in Alagados Reservoir, Paraná, Brazil.

predominantly allochthonous and mainly composed by remains from agricultural activities. Obviously, future analyses will be necessary to confirm this hypothesis, particularly those related to stable isotopes.

It is well known that fish's diet reflects the environment's food supply (Lawlor, 1980; Wallace Jr., 1981; Winemiller, 1989; Gerking, 1994; Lowe-McConnell, 1999; Wootton, 1999; Abelha *et al*, 2001), so, the low participation of other resources in the feeding of *A. paranae* in this study may be attributed to their low availability in the reservoir. The species feeding behavior reinforces this idea, since this characin presents intense exploratory activity, preferentially occupying the middle of the water column, which allows it to capture foods from the surface and the bottom, besides picking up items transported by the flow (Ferreira, 2004).

The constancy of plant structures such as leaves, fruits and seeds in the diet of *A. paranae* in other environments (Ferreira, 2004), indicated the species predisposition in the use of this resource and is consistent with the high consumption of plant matter in Alagados Reservoir. The high intake of starch rich seeds and fruits suggested that they proceed mainly from Gramineae species and that they represented an important energetic source for *A. paranae*. This food possibly proceeded from grassy vegetation on the margin compounding the riparian vegetation and from cultivated pastures in the area of reservoir drainage basin.

Considering the consumption of algae, their high occurrence associated to portions of detritus/sediment indicated that they were predominantly taken during ingestion of detritus/sediment and not pulled off from substratum colonized by periphyton. This fact could be justified by the low biomass of periphytics algae in Alagados Reservoir (Rodrigues *et al*., 2005) and the intrinsic link of benthic algae to non live detritus/sediment extract (Bowen, 1983; Gerking, 1994; Yossa & Araujo-Lima, 1998; Crossman *et al*., 2001; Moore *et al*., 2004). Occurrences of algae in the diet of *A. paranae* were also reported for stream populations (Ferreira, 2004), however, the absence or inexpressive consumption of detritus/sediment indicated, in these cases, the intentional ingestion of this food.

The low consumption of insects in this study was discordant with Ferreira (2004) findings for *A. paranae* diet in streams, where aquatic and terrestrial insects were intensively preyed. Two possibilities can be discussed. First, in the context of the optimal foraging theory (Gerking, 1994), indicating that, in spite of insects being a nutritionally advantageous food, they might have occurred in population densities that constrained their consumers' energy profit. Data are not available regarding the reservoir colonization by aquatic insects, however, in the case of the terrestrial ones, their low occurrence would be related to impoverished riparian vegetation with consequent reduction in shelter, food and reproduction sites for these organisms. Second, the irrelevance of insects also suggested the hypothesis that *A. paranae* has obtained satisfactory levels of protein originating from bacteria and fungi associated to detritus/sediment.

Diet variation. Fish trophic flexibility, understood as the species capacity to shift the diet when oscillations in food abundance arises (Gerking, 1994), has been thoroughly related to in literature (Goulding, 1980; Hahn *et al*., 1992; Poff & Allan, 1995; Lolis & Andrian, 1996; Bennemann *et al*., 2000; Abelha *et al*., 2001; Cassemiro *et al*., 2002; Abelha & Goulart, 2004) and characterizes fishes as efficient environmental samplers (Winemiller, 1989). Thus, the spatial and temporal constancy of detritus/sediment and plant matter as the main resources used by *A. paranae* in Alagados Reservoir suggested that they were widely available to the species during the study period.

The lentic character of reservoirs favors the deposition processes of diversified materials transported from the drainage basin, resulting in abundance of detritus/sediment in these environments (Thornton, 1990b). This fact indicated that the observed variations in the consumption proportions of detritus/sediment and plant matter would be resulted, actually, from changes in the readiness of the last. It is possible to consider that abundance of vegetation in the reservoir basin area would be both modulated. First, by the action of seasonality on species life cycle, since most of them reduces vegetative growth and interrupts the fructification process in winter (Glenn-Lewin *et al*., 1992). Second, by the intensity of rains in the area, phenomenon attributed by Thornton (1990b) of larger importance in the transport and introduction of allochthonous material in reservoirs. In the studied region, the dry period corresponds to the winter (Maack, 2002), therefore, the smaller ingestion of plant matter in July could be attributed as much to the effect of seasonality, as to reduction in the transport of materials due to the station low pluviometry. On the other hand, the expressive participation of plant matter in the diet of *A. paranae* in October could be credited to the availability of litter material (including fruits and seeds) accumulated in the soil during the winter and brought into the reservoir by spring rainfalls (the rainy station). The existence of wide stretches in the drainage basin area cultivated with oats and wheat during winter (personal observation) may additionally contribute to litter composition. The seasonal input of allochthonous material into aquatic environment was quantified by Uieda & Kikuchi (1995) in a tributary of Paranapanema River basin (SP). The authors verified that the sampled amount was always larger in the rainy period (October to March) and the samples were predominantly from plant origin due to the falling of leaves during the winter (dry season). Still in this context, the intensive foraging of *A. paranae* on plant matter in April was coincident with the end of the reproductive cycle of Gramineae species, when great amount of fruits and seeds are spread in the environment (Glenn-Lewin *et al*., 1992; Lara *et al*., 2003).

The increment in the consumption of algae in the riverine zone in relation to lacustrine one was in coherence with the higher availability of nutrients found in the former (Moschini-Carlos *et al*., 1999; Thornton, 1999b), considering that nutrients are one of the main limiting factors to algae communities development (Lampert & Sommer, 1997). The consumption of

Spirogyra, practically restricted to riverine zone influenced the observed differences due to the largest size of this alga in relation to other preyed taxa. In spite of the minor importance of invertebrates in *A. paranae* diet, the relevance of Oligochaeta in the stomach contents of few specimens in April and October of 1996 enhanced the species opportunistic feeding habit.

Finally, in agreement with the objectives proposed in this study for *A. paranae*, it could be concluded that: (i) the diet predominantly composed by detritus/sediment, with seasonal occurrence of larger participation of plant matter, indicated detritivorous feeding habit tending to herbivory; (ii) spatial and temporal significant differences on diet highlighted the species feeding flexibility; (iii) the expressive consumption of detritus/sediment, a food resource unusual in the species diet but abundant in reservoirs, characterized its trophic opportunism.

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