ECOMORPHOLOGICAL PATTERNS OF SMALL SYMPATRIC FISH FROM A NEOTROPICAL RESERVOIR

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ABSTRACT - In this study, we sought to identify ecomorphological patterns of ten species of sympatric small fish (*Astyanax altiparanae, Astyanax fasciatus, Bryconamericus stramineus, B. iheringi, Cheirodon stenodon, Characidium fasciatum, Geophagus brasiliensis, Hyphessobrycon anisitsi, Piabina argentea* and *Steindachnerina insculpta*) in a stretch of the Veados River (23º16'80''S/48º38'67''W), under the influence of the Jurumirim reservoir (Paranapanema River, Brazil). Samples were collected monthly between August/96 and December/97 using seine nests. Biometric measurements were taken from fifteen individuals of each species following the criteria proposed by Lagler et al. (1977) for determination of the sixteen ecomorphological attributes used in ordination techniques (Principal Component Analysis - PCA). The first axis of the component explained 36.63% of the total variance and the second axis explained 25.96%. The ecological variables that influenced the disposition of the species in the morphological space were swimming ability, distribution in the water column and position of the mouth (where food is ingested). These variables separated nektonic species from benthic species. The attributes related to swimming ability and position of the species in the water column distinguished two groups of species. The nektonic species were continuous and active swimmers occupying the intermediate and upper region of the water column (*A. altiparanae, A. fasciatus, B. stramineus, B. iheringi, C. stenodon, H. anisitsi, P. argentea* and *S. insculpta*), and the nectobenthic species were identified as stationary (*C. fasciatum* and *G. brasiliensis*), obtaining food from the substrate. These analyses showed that species that share morphological similarities were also similar with regard to habitat occupation, which was to be expected. This reinforces the hypothesis that the period of feeding activity and food availability minimize the effects of competition by the species studied. The results demonstrate the importance of applying the Principal Component Analysis in ecomorphological studies, revealing its use as an excellent tool to estimate the ecological relationship between fish species and their distribution in the water column.

Key words: Ecomorphology, Freshwater Fishes, sympatric species, Jurumirim reservoir.

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PADRÕES ECOMORFOLÓGICOS DE CHARACIFORMES SIMPÁTRICOS DE PEQUENO PORTE DE REPRESA NEOTROPICAL

RESUMO - No presente trabalho procuramos identificar padrões ecomorfológicos de dez espécies de peixes simpátricos de pequeno porte (*Astyanax altiparanae*, *Astyanax fasciatus*, *Bryconamericus stramineus*, *B. iheringi*, *Cheirodon stenodon*, *Characidium fasciatum*, *Geophagus brasiliensis*, *Hyphessobrycon anisitsi*, *Piabina argentea* e *Steindachnerina insculpta*) de trecho do rio dos Veados (23º16’80’’S/48º38’67’’W) sob influência da represa de Jurumirim (rio Paranapanema, Brasil). As coletas foram realizadas mensalmente com redes de arrasto entre agosto/96 e dezembro/97. Para tanto, quinze exemplares de cada espécie foram submetidos a uma série de medidas biométricas seguindo os critérios propostos por Lagler et al. (1977) para determinação dos dezesseis atributos ecomorfológicos utilizados na técnica de ordenamento (Análise de Componentes Principais – ACP). O primeiro eixo da componente explicou 36,63% e o segundo eixo 25,96% da variância total dos dados. As variáveis ecológicas que influenciaram na disposição das espécies no espaço morfológico foram a habilidade natatória, a distribuição na coluna d’água e a posição da boca (local da tomada do alimento). Estas variáveis separaram as espécies nectônicas das espécies bentônicas. Os atributos relacionados com a habilidade natatória e com a posição das espécies na coluna d’água permitiram distinguir dois grupos de espécies, sendo as nectônicas nadadoras contínuas e ativas que ocupam a região intermediária e a coluna superior da água (*A. altiparanae*, *A. fasciatus*, *B. stramineus*, *B. iheringi*, *C. stenodon*, *H. anisitsi*, *P. argentea* e *S. insculpta*), e as nectobentônicas, identificadas como estacionárias (*C. fasciatum* e *G. brasiliensis*), que tomam o alimento junto ao substrato. Essas análises mostraram que as espécies que apresentam semelhanças na morfologia também apresentaram semelhança na ocupação do hábitat, o que era de se esperar, tudo isso só reforça a hipótese de que o período de atividade alimentar e a disponibilidade de alimento minimizam os efeitos da competição pelas espécies de peixes estudadas. Os resultados demonstraram a importância da aplicação da Análise de Componentes Principais em estudos de ecomorfologia, revelando, desta forma, sua utilização como um excelente instrumento para estimar o relacionamento ecológico entre as espécies de peixes e a sua distribuição na coluna d’água.

Palavras-chave: Ecomorfologia, peixes de água doce, simpatria, grandes represas.

INTRODUCTION

The understanding of the relationships between functional morphology and ecological performance was defined by Winemiller et al. (1995) as ecomorphology. According to Hespenheide (1973), ecomorphology derives from the premise that ecological relationships can be deduced from appropriate sets of morphological characteristics. The main objective of this type of study is to understand the relationship between the morphology of an organism and its ecology (Beaumord, 2000). This relationship between the shape and the ecology, based on a series of morphological attributes, was reported by Gosline (1971), Gatz (1979a e 1979b), Webb (1984), Wainwright & Richards (1995), Adite & Winemiller (1997), Freire & Agostinho (2001), Beaumord (2000), Casatti & Castro (2006) and Mazzoni et al. (2010).

The pioneers of this study were Keast & Webb (1966), who examined freshwater fish. They found that the structures of the mouth and body of the fish, combined with habitat specializations and preferences, were the cause of the substantial decrease in interspecific competition. Moyle & Senanayake (1984) verified the habitat preferences of the fish fauna of tropical streams, using ordination methods. In these methods, such as the principal components analysis, the identified multivariate axes reflect, by assumption, the environmental variables that affect the choice of habitat by each species of fish in the assemblage (Felley & Felley, 1987).

This ecomorphological approach has been used in several studies on fish assemblages (Gatz 1979a e 1979b; Mahon, 1984; Watson & Balon, 1984; Balon et al., 1986; Wikramanayake, 1990; Winemiller, 1991; Beaumord, 1991; Beaumord & Petrere, 1994, Uieda, 1995) always based on the assumption that the morphological differences between species may be linked to different environmental and biological pressures in evolutionary time. The morphometric and biometric indexes (ecomorphological attributes) are differential patterns that express the characteristics of individuals in relation to their environment and therefore can be interpreted as indicators of life habits or adaptations of species to occupy different habitats (Gatz, 1979b; Mahon, 1984; Watson & Balon, 1984).

The present study aimed to determine the ecomorphological pattern and the ecological relationship between ten species of small sympatric fish and their position in the morphospace, using as a model the presence of these species in a coastal stretch of a river under the strong influence of a large artificial reservoir.

MATERIAL AND METHODS

Fish Collection

Monthly collections of fish were made from December/1997 to August/1996, in a stretch where the Veados River mouth (23º16'80" S and 48º38'67" W) enters Jurumirim reservoir (Upper Paranapanema River, state of São Paulo) (Figure 1). The fish were caught by hauls with a 10m x 1.5m seine net and 5.0 mm mesh size along the coastal region of the area. The fish caught were identified using the relevant literature (Britski, 1972, Britski et al., 1988, Britski et al., 1999, Reis et al., 2003). The criteria for selection of dominant species are described in Castro (2003). Voucher specimens of these species are deposited in the Fish Collection of the Departamento de Morfologia under care of the curator Dr. Cláudio Oliveira and in the Museu of the Departamento de Zoologia of the Universidade Estadual Paulista, São José do Rio Preto, São Paulo. Voucher specimens of *A. altiparanae* (LBP 1168), *A. fasciatus* (LBP 97), *C. stenodon*

(LBP 71), *C. fasciatum* (LBP 065), *G. brasiliensis* (LBP 102), *H. anisitsi* (LBP 2743), *P. argentea* (LBP 2744), a n d *S. insculpta* (LBP 1302) are deposited in the Laboratório de Biologia e Genética de Peixes (LBP), Departamento de Morfologia, Universidade Estadual Paulista, Botucatu, São Paulo. The species *B. stramineus* (DZSJRP 2774) and *B. iheringi* (DZSJRP 3317) are deposited in the Museu do Departamento de Zoologia da Universidade Estadual Paulista, São José do Rio Preto, São Paulo.

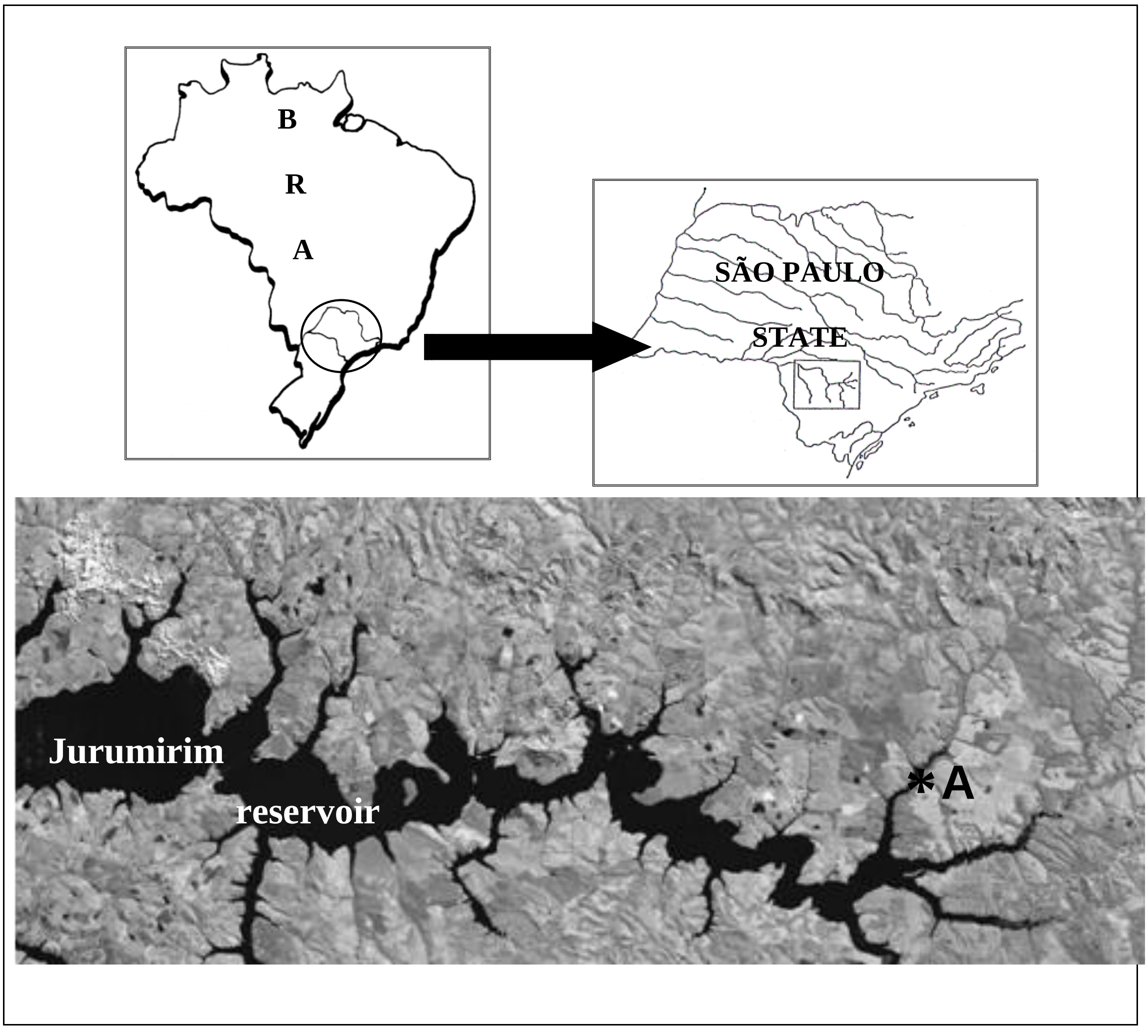

Fig. 1. Satellite image (Land Sat II) of the Jurumirim reservoir, Upper Paranapanema River, SP (source: www.cdbrasil.cnpm.embrapa.br). **A* -** sampling area (Recantos dos Cambarás - Itatinga, SP).

Morphometric measurements

After taxonomic identification, fifteen adult specimens were selected, when possible, of each species in order to determine their ecomorphological attributes. The use of adult individuals, the selection of which was based on the minimum size at first sexual maturation, aimed to minimize allometric differences in ontogenetic development (Gatz, 1979a, Gatz, 1979b, Wikramanayake, 1990) that could affect the results.

The species studied were: *Astyanax altiparanae* Garutti & Britski, 2000, *Astyanax fasciatus* (Cuvier, 1819), *Bryconamericus stramineus* Eigenmann, 1908, *Bryconamericus iheringi* (Boulenger, 1887), *Cheirodon stenodon* Eigenmann, 1915, *Characidium fasciatum* Reinhardt, 1866, *Geophagus brasiliensis* (Quoy & Gaimard, 1824), *Hyphessobrycon anisitsi* (Eigenmann, 1907), *Piabina argentea* Reinhardt, 1867, and *Steindachnerina insculpta* (Fernández-Yépez, 1948).

The fifteen specimens of each species were subjected to a series of biometric measurements using calipers (0.05 mm precision), following the criteria proposed by Lagler et al. (1977), except when estimating the area of some structures such as fins and body. The area of these structures was determined by outlining their perimeter (mm^2 = metric unit) on squared paper (Beaumord & Petrere, 1994).

The biometrics were used to determine 16 ecomorphological attributes (see Table 1) based on Gatz (1979a, 1979b), Mahon (1984), Watson & Balon (1984), Balon et al. (1986), Winemiller (1991), Beaumord & Petrere (1994), Uieda (1995), Casatti (1996), Beaumord (2000) and Freire & Agostinho (2001).

Table 1. Morphological attributes, their definitions and ecological meanings used for ecomorphological interpretation.

ACRONYM	ATTRIBUTE	DEFINITION		MEANING
CI	**Compression Index**	maximum body depth divided by maximum body width	➲	High values indicate laterally compressed fish inhabiting lentic waters;
RD	**Relative depth**	maximum body depth divided by standard length	➲	Attribute inversely related to fast water environments and directly related to their capacity for making vertical turns (Gatz, 1979b);
RCPL	**Relative caudal peduncle length**	Length of caudal peduncle divided by standard length	➲	Long peduncles indicate fish with good swimming ability inhabiting turbulent waters (Watson & Balon, 1984);
CPCI	**Caudal peduncle compression index**	caudal peduncle depth divided by the caudal peduncle width	➲	Long peduncles indicate slow swimmers that cannot maneuver easily which can affect their performance in bursts of speed as the depth of the body increases among the different species (Gatz, 1979b);
IVF	**Index of ventral flattening**	Maximum midline depth divided by maximum body depth	➲	Low values are associated with high hydrodynamic environments, enabling benthic fish to maintain their position even when stationary (Mahon, 1984);
RADF	**Relative area of dorsal fin**	Dorsal fin area divided by body area	➲	The dorsal fin has a stabilizing role, functioning also as a rudder; dorsal fins with relatively small areas are more efficient in fast flowing waters (Gosline, 1971);
RAPF	**Relative area of pectoral fin**	Pectoral fin area divided by body area	➲	High values indicate slow swimmers which use their pectoral fins to perform maneuvers and breakings, or fishes inhabiting fast waters which use them as airfoils to deflect the water current and maintain themselves in close contact with the substrate (Alexander, 1967);
PFAR	**Pectoral fin aspect ratio**	Maximum length of pectoral fin divided by its maximum width	➲	High values indicate long and narrow fins, present in highly migratory species (Keast & Webb, 1966);
RACF	**Relative area of caudal fin**	Caudal fin area divided by body area	➲	High values indicate caudal fins able to produce rapid bursts, typical of benthic fishes (Balon et al., 1986);
CFAR	**Caudal fin aspect ratio**	Square of caudal fin height divided by its area	➲	High values indicate active and continuous swimmers (Gatz, 1979b);
RHL	**Relative head length**	head length divided by the standard length	➲	High values may indicate species that are able to feed on relatively larger prey (Watson & Balon, 1984);
REP	**Relative eye position**	depth of the eye midline divided by the head depth	➲	High values indicate dorsally located eyes, typical of benthic fishes while in nektonic species, the eyes tend to be located laterally (Gatz, 1979b);
RMW	**Relative mouth width**	mouth width divided by standard length	➲	High values indicate fishes able to feed on relatively large prey (Gatz, 1979a).
RMH	**Relative mouth height**	mouth height divided by standard length	➲	Attribute related to the size of the food, also associated with the hydrodynamic morphology (Watson & Balon, 1984);
MR	**Mouth ratio**	Height of mouth divided by its width	➲	High values indicate fish with relatively narrow mouth, but with a large opening, suggesting piscivorous species (Beaumord, 1991);
MO	**Mouth orientation**	defined by the angle formed between the tangential plane to both lips and the perpendicular plane to the longitudinal axis of the body when the mouth is open according to Gatz (1979)	➲	The value obtained indicates at which height of the water column the fish feeds (Balon et al., 1986).

Data Analysis

To determine the existence of different morphological patterns between the studied species, a Principal Component Analysis (PCA) was performed on the log_{10}-transformed data matrix of the 16 ecomorphological attributes. PCA is a technique that consists in the reduction of data using linear combinations of the original variables and ordination of the correlated data (McCune & Mefforrd, 1997). In order to determine the correlation of these attributes, the eigenvectors of the PCA were plotted to verify the positions occupied by the individual fish within the ecomorphological space. The axes retained for interpretation of the results were those with eigenvalues greater than the broken-stick eigenvalues (McCune & Mefforrd, 1997), therefore, they were the only ones that could be interpreted ecologically. For this analysis we used the software PC-ORD, vol. 4.0 (McCune & Mefforrd, 1997).

RESULTS

Table 2 shows the mean values of 16 ecomorphological attributes for the ten species of fish, the matrix of which was applied to a PCA that originated the first two components with eigenvalues greater and significant according to the Broken-Stick test (table 3). The first two axes (PC1 and PC2) were used for interpretation of ecological attributes of these species. Mean scores (centroids) obtained for these two significant axes are shown in Figure 2, in which the first axis (PC1) explained 36.63% of the variance of the model. The attributes that contributed negatively to the formation of this axis were relative depth (RD), relative head length (RHL), relative mouth width (RMW) and relative mouth height (RMH), and the only attribute that contributed positively was the relative area of caudal fin (RACF).

Table 2. Arithmetic mean of the 16 ecomorphological attributes calculated for the ten species of sympatric Characiforms in the Veados River under the influence of the Jurumirim reservoir (Upper Paranapanema River, SP).

CI - Compression index, RD – Relative depth; RCPL - Relative caudal peduncle length; CPCI - Caudal peduncle compression index; IVF- Index of ventral flattening; RADF – Relative area of dorsal fin, RAPF – Relative area of pectoral fin; PFAR - Pectoral fin aspect ratio; RACF – Relative area of caudal fin; CFAR - Caudal fin aspect ratio; RHL - Relative head length; REP - Relative eye position; RMW – Relative mouth width; RMH – Relative mouth height; MR – Mouth ration; MO – Mouth orientation, N - number of specimens used.

Acronym	CI	RD	RCPL	CPCI	IVF	RADF	RAPF	PFAR	RACF	CFAR	RHL	REP	RMW	RMH	MR	MO	N
Aal	2.76	0.39	0.07	3.79	0.40	0.10	0.06	2.08	0.22	1.23	0.28	0.59	0.08	0.04	0.55	1.06	15
Afa	2.69	0.32	0.09	2.53	0.53	0.11	0.06	2.32	0.30	1.18	0.28	0.61	0.08	0.06	0.82	0.86	15
Bih	2.14	0.30	0.10	2.53	0.46	0.10	0.08	1.87	0.29	1.09	0.28	0.50	0.06	0.04	0.69	0.72	15
Bst	1.83	0.23	0.12	2.04	0.51	0.08	0.06	1.94	0.28	1.11	0.21	0.58	0.05	0.03	0.60	0.78	15
Cfa	1.44	0.23	0.15	2.33	0.46	0.13	0.13	2.07	0.23	0.93	0.25	0.61	0.04	0.03	0.89	1.06	15
Cst	2.53	0.32	0.11	2.79	0.51	0.10	0.06	2.33	0.29	1.29	0.26	0.57	0.05	0.04	0.79	0.83	15
Gbr	2.32	0.41	0.12	3.40	0.29	0.17	0.12	1.88	0.09	0.88	0.36	0.70	0.09	0.08	0.84	1.22	15
Han	2.75	0.38	0.09	3.05	0.51	0.10	0.07	1.89	0.25	1.31	0.29	0.50	0.08	0.05	0.66	1.11	15
Par	2.12	0.26	0.12	2.31	0.35	0.10	0.07	1.97	0.25	1.03	0.26	0.53	0.07	0.04	0.64	1.28	15
Sin	1.92	0.29	0.10	2.22	0.37	0.13	0.04	2.63	0.29	1.09	0.29	0.54	0.05	0.03	0.59	0.84	15

Species: Aal (*A. altiparanae*), Afa (*A. fasciatus*), Bih (*B. iheringi*), Bst (*B. stramineus*), Cfa (*C. fasciatum*), Cst (*C. stenodon*), Gbr (*G. brasiliensis*), Han (*H. anisitsi*), Par (*P. argentea*) e Sin (*S. insculpta*).

The positive scores for the first axis (PC1) were observed for *B. stramineus* (Bst), *B. iheringi* (Bih), *P. argentea* (Par), *S. insculpta* (Sin), *C. fasciatum* (Cfa) and *C. stenodon* (Cst). However, for the species *G. brasiliensis* (Gbr), *A. altiparanae* (Aal), *H. anisitsi* (Han) and A. *fasciatus* (Afa), the scores were negative.

Observing the positive coefficients of the first axis (PC1), it can be noted that these species (acronyms Bst, Bih, Par, Sin, Cfa and Cst) share, in common, the smallest relative depths and the smallest dimensions of the head and mouth as well as high values for the relative area of caudal fin. However, the second group (negative values of PC1 - acronyms Gbr, Aal, Han and Afa) is characterized by presenting distinct morphological attributes from the first group, which are fish with tall bodies, longer heads and larger mouths than those of the first group, mainly discriminating species of Characiformes with nektonic habits from those with relatively lower bodies and benthic habits.

Table 3. Results of the Principal Component Analysis extracted from the morphometric measurements of ten fish species. The values that contributed most to the axes formation are in bold.

Morphology	PC1	PC2
Compression Index (CI)	-0.186	**-0.404**
Relative depth (RD)	**-0.354**	-0.248
Relative caudal peduncle length (RCPL)	0.104	**0.442**
Caudal peduncle compression index (CPCI)	-0.290	-0.202
Index of ventral flattening (IVF)	0.223	-0.143
Relative area of dorsal fin (RADF)	-0.270	0.275
Relative area of pectoral fin (RAPF)	-0.167	**0.377**
Pectoral fin aspect ratio (PFAR)	0.086	-0.084
Relative area of caudal fin (RACF)	**0.327**	-0.151
Caudal fin aspect ratio (CFAR)	0.096	**-0.371**
Relative head length (RHL)	**-0.375**	-0.006
Relative eye position (REP)	-0.243	0.206
Relative mouth width (RMW)	**-0.353**	-0.185
Relative mouth height (RMH)	**-0.365**	-0.013
Mouth ratio (MR)	-0.117	0.238
Mouth orientation (MO)	-0.186	**-0.404**
% of variance	36.63	25.96
Eigenvalues	5.494	3.895
Broken-Stick	3.318	2.318

The projection of the mean scores of species for the first axis of the principal component (PC1), allows them to be separated, in morphological terms, into two distinct groups. The first group (positive scores) is formed by species with low bodies (fusiform) and with a large relative area of caudal fin, whereas the second group (negative scores) is formed by species with greater dimensions of the head and mouth, and relatively taller body than the species of the first group.

The second axis of the principal component (PC2) explained 25.96% of the data variance, adding to 62.59% of cumulative variance for the first two axes. Attributes that contributed positively to this axis of the component (PC2) were the relative caudal peduncle length (RCPL) and the relative area of pectoral fin (RAPF), whilst the compression index (CI), the caudal fin aspect ratio (CFAR) and the mouth orientation (MO) were the main negative contributors to the formation of PC2. In this component (PC2), the species *A. altiparanae* (Aal), *H. anisitsi* (Han), *A. fasciatus* (Afa) and *C. stenodon* (Cst) can be grouped together since they generated a negative coefficient, while the other species (acronyms Bst, Bih, Par, Sin and Cfa) showed a positive coefficient.

The ecomorphological attributes were also interpreted ecologically for the second axis of the principal component (PC2), demonstrating that the species (B. *stramineus, B. iheringi, P. argentes, S. insculpta* and *C. fasciatum*) that occupied the upper quadrant of Figure 2 generally show a long caudal peduncle, a large relative area of pectoral fin and a subterminal mouth.

Another relevant factor for the axis PC2 is the anterosuperior position of the mouth in species with negative scores (*A. altiparanae, A. fasciatus* and *H. anisitsi*), in contrast to species with positive scores and terminal or subterminal mouths.

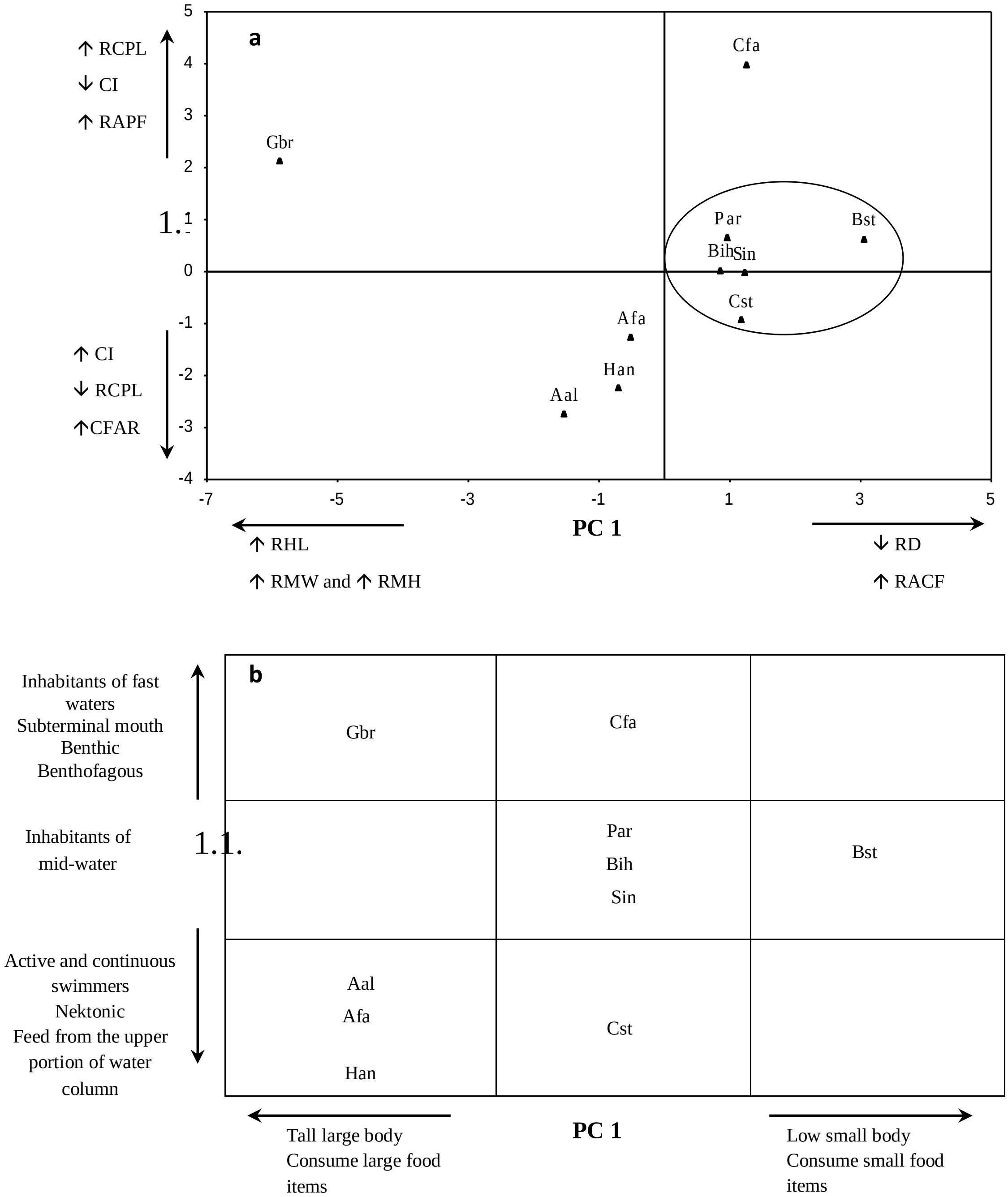

Figura 2. a: Projection of species in the morphological space derived from PC1 (size: relative depth and size of mouth) and PC2 (body shape: lateral compression index, relative caudal peduncle length, relative area of pectoral fin and caudal fin aspect ration; diet: mouth orientation). b: Schematic grid of the distribution of the groups obtained by Principal Component Analysis.

The results indicate that large relative area of pectoral fin was an important characteristic for the species *C. fasciatum* which can seen by the isolated position of this dot-species in Figure 2. However, the isolation of the dot-species *G. brasiliensis*, which also occupied a distinct position in Figure 2, revealed more negative scores for the first axis (PC1), demonstrating that this species, in relation to the others, had larger body proportions, confirming its position in the morphological space (see Fig. 2).

DISCUSSION

Studies of segregation and habitat sharing in fish assemblages have used multivariate techniques to detect the main variables related to habitat selection by fish species (Felley & Hill, 1983). The ecological study of the fauna of a tropical stream conducted by Moyle & Senanayake (1984) included an analysis of habitat preference. Felley & Felley (1987) argue hypothetically that this approach identifies the multivariate axes related to reality, and also, which environmental variables are associated with species habitat choice. Watson & Balon (1984) conceptualize that the total space of the niche can be defined by a multidimensional coordinate system, where the position of the space filled with a species is denominated the niche volume and the sum of the individual volumes occupied by a group of species characterizes the niche space of the community.

In the current study the results were used as indicatives for the interpretation of morphological characteristics as a means of predicting the niche occupation by morphologically similar fish species. The axes identified consistent ecomorphological patterns and segregated species according to the eigenvalues obtained in the PCA for each significant attribute. The two principal axes of the PCA defined the relative positions of the fish in the morphospace.

Gatz (1979a) evaluated 56 ecomorphological characteristics of freshwater fishes and showed that the axes were formed by variables related to predation, habitat use, ability to carry out maneuvers and vertical zonation of the fish species studied.

The ecomorphological pattern, determined by the grouping of the fish species studied, showed structural differences associated to ecological variables such as feeding mode, position in the water column, and swimming performance, as can be seen in Figure 2b. These variables make a clear distinction between the species of Characiformes studied, allocating the nektonic species (Aal, Afa, Han and Cst) in the lower portion and the benthic species (Gbr and Cfa) in the upper portion of the diagram.

Parallel studies on the natural diet of these species (Castro & Carvalho, 2014), also help to establish the distribution of these species in the ecomorphological space, since the species with acronyms Bih, Par, Sin, Bst and Cst, classified as omnivores and detritivores (generalists), and the specialist species Aal, Afa, Cfa and Gbra, that have diets sustained mainly by terrestrial and aquatic insects, occupy different spatial positions. It can be noted, therefore, that the distribution of species in the grid followed a pattern in which species of generalist feeding habits, determined by the terminal position of the mouth, occupied the central area of the graph and the other species with more specialized diets, i.e. with the mouth facing the upper or lower region, were displaced to the edge of the quadrants.

The distribution of specialist species in the PCA axes coincided with their morphological pattern. Thus, *A. altiparanae*, *A. fasciatus* and *H. anisitsi* were characterized as pelagic species, mainly inhabiting the surface and midwater near the coastal region. A similar pattern was found for *A. altiparanae* in another river of the Upper Paraná River basin (Orsi, 2001).

Castro & Carvalho (2014) report that the first two species consume mainly terrestrial insects from the land/water interface of the Veados River, reinforcing the hypothesis that *A. altiparanae* and *A. fasciatus* preferentially occupy the coastal stretch.

Uieda (1984) studied the occurrence and distribution of fish in headwater streams and observed that *A. altiparanae* and *H. anisitsi* inhabited the surface and mid-water regions of stagnant or fast waters. In studies related to the identification of the type of food ingested by *A. altiparanae*, Arcifa & Meschiatti (1993), Esteves & Galetti (1995), Bennemann et al. (2000) and Orsi (2001) obtained similar results. The body shape, with a high lateral compression index and anterosuperior position of the mouth in *A. altiparanae* are characteristics that lead this species to occupy the upper layers of the water column, a fact corroborated by its position in the morphospace.

On the other hand, the species *B. stramineus*, *B. iheringi*, *P. argentea*, *S insculpta* and *C. stenodon*, located in the central region of the grid, have dietary habits between omnivory and detrivory (Castro & Carvalho, 2014), suggesting that they should preferentially occupy the middle or the bottom of the water column. The morphological pattern observed in these species, based on their ecomorphological attributes, such as smaller relative depths of the body and smaller head and mouth dimensions as well as high values of the relative area of the caudal fin, indicates that these species of fish prefer to occupy the benthic region of the river, reinforcing the morphological proximity associated to the similarity in occupation of the spatial niche space. As a means to minimize interspecific competition, the species evolve to occupy different positions along a resource gradient (Watson & Balon, 1984).

The ecological interpretation of ecomorphological attributes by the second axis of the principal component (PC2) placed the species *B. stramineus*, *B. iheringi*, *P. argentes*, *S. insculpta* and *C. fasciatum* in the upper quadrant of Figure 2. The morphological characteristics of these species: long caudal peduncle, large relative area of pectoral fin and subterminal mouth, leads us to infer that this axis represents the vertical distribution of species in the water column and the velocity of the water current in which they live. The characteristics related to the pectoral fins reveal their use as current deflectors for species that live in fast flowing waters or as structures that help slow swimming individuals perform vertical maneuvers and breakings. Another relevant factor for axis PC2 is the anterosuperior position of the mouth in species with negative scores (*A. altiparanae*, *A. fasciatus* and *H. anisitsi*), which indicates that they ingest food in the most upper region of the water column as opposed to species (Bih, Bst, Par, Cfa and Sin) with positive scores that occupy the mid-column of the water, have terminal or subterminal mouths and live in the benthic zone feeding close to the sediment.

The species *C. fasciatum*, dorsal-ventrally flattened, was located in the upper part of the left quadrant of Figure 2. That is, its position in the morphospace reflected the large area of its pectoral fin, a characteristic that seems to help it remain near the bottom. According to Alexander (1967), the presence of pectoral fins with large areas indicates characteristics of inhabitants of rapid waters that use these structures as current deflectors, with the goal of maintaining close contact with the substrate. Casatti (1996) recorded the presence of this species in rapids environments and stated that the availability of food and protection from predators are advantages to explore these habitats.

The analysis of attributes related to morphology and diet, inferred by the size and position of the mouth of the fish species, characterized a few ecological variables that isolated the species in the morphospace. Thus, species such as *A. altiparanae, A. fasciatus, H. anisitsi* and *C. stenodon* were identified as those presenting anterosuperior mouth and a diet based on capturing food in the upper water column, with greater food niche breadth, considering the intake of food of allochthonous origin, as opposed to the species *C. fasciatum* and *G. brasiliensis*, with subterminal mouth and a diet based on capturing food (aquatic insects) on the bottom of the river, and the generalist species (*P.*

argentea, B. iheringi, S. insculpta and *B. stramineus*), with terminal and subterminal mouths and omnivorous/detritivorous habits.

Direct observation is another important instrument for identifying the distribution, behavior and feeding mode of species in loco. Nevertheless, there were many difficulties in the application of in loco observation techniques, mainly due to low water transparency, making it impossible to verify whether this ecomorphological model of the distribution of species in the morphospace resembles the distribution of species in nature. However, the results of several authors regarding this theme (Uieda, 1984; Arcifa & Meschiatti, 1993; Esteves & Galetti, 1995; Casatti, 1996; Bennemann et al., 2000 and Orsi, 2001) for the species of fish of the Upper Paraná River, suggest that our ecomorphological model is suitable for the ichthyofauna studied.

In short, it can be concluded that this ecomorphological approach functioned as an effective tool for establishing ecomorphological patterns and patterns in the relationships between form and ecology of these small sympatric Characiforms in an important tributary of the Jurumirim reservoir in the Upper Paranapanema River basin.

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