

Ecomorphology and diet of two species of *Acestrorhynchus* from Brazilian Northeast

by

Elaine C. dos S. DOURADO (1), Jorge L.S. NUNES (2) & Nivaldo M. PIORSKI* (3)



© SFI
Received: 22 Mar. 2013
Accepted: 8 Jan. 2015
Editor: K. Rousseau

Key words

Acestrorhynchidae
Acestrorhynchus falcatus
Acestrorhynchus heterolepis
Geometric morphometry
Trophic morphology
Habitat use
Neotropical fish

Abstract. – *Acestrorhynchus falcatus* (Bloch, 1794) and *A. heterolepis* (Cope, 1878) are two species frequently found in rivers from Baixada Maranhense, Maranhão State, northeastern of Brazil. The ecomorphological adaptations of these species were studied based on a collection of 445 specimens using morphometric tools. Seventeen landmarks were defined on the lateral side of the individuals and digitalized by the TPS Dig program. The data matrix was submitted to a Relative Warps Analysis (RWA) and a Canonical Variables Analysis (CVA) in order to identify the morphological patterns of each species. In addition, observations about the digestive tract of each species and diet comparison through the feeding ecology are provided. The main differences between *A. falcatus* and *A. heterolepis*, as indicated by the analysis, were associated with swimming agility and prey size. *A. heterolepis* has a shallow body, close to a fusiform profile, deep caudal fin and low caudal peduncle. In contrast, *A. falcatus* possesses a shorter head and a lower caudal fin, better adapted to capture small preys and to live in mid-lower region of the water column. According to these traits, the two species probably avoid competition by catching prey of different sizes and using distinct strategies for this procedure.

Résumé. – Écomorphologie et régime alimentaire de deux *Acestrorhynchus* du Nord-Est du Brésil.

Acestrorhynchus falcatus (Bloch, 1794) et *A. heterolepis* (Cope, 1878) sont deux espèces distinctes fréquentes dans le Nord-Est du Brésil, État de Maranhão. Les adaptations écomorphologiques ont été étudiées au moyen d'une technique de morphométrie géométrique appliquée sur 445 spécimens. Dix-sept points remarquables anatomiques ont été définis sur les côtés de chaque individu et établis par le programme TPS Dig. Une matrice de données a été soumise à l'Analyse de Déformation Relative et à l'Analyse de Variables Canoniques afin d'identifier les modèles morphologiques de chaque espèce. De plus, des informations sur l'écologie trophique ont été obtenues par le biais d'observations relatives du tractus digestif et d'une comparaison du régime alimentaire de chaque espèce. Les différences les plus importantes entre *A. falcatus* et *A. heterolepis* sont associées à l'habileté à nager et à la taille des proies ingérées. *A. heterolepis* possède un corps légèrement moins élevé, proche d'un profil fusiforme, une nageoire caudale large et un pédoncule caudal étroit. Au contraire, *A. falcatus* possède une tête plus courte et une nageoire caudale plus basse, mieux adaptées à la capture des petites proies et à la vie dans la région moyenne-basse de la colonne d'eau. Selon ces attributs, les deux espèces présentent une tendance à la ségrégation en fonction de la capture de proies de différentes tailles et, probablement, de l'emploi de stratégies distinctes pour ce procédé.

Ecomorphological studies generally focus on relationships between functional morphology of individuals, species or communities and their ecology (Gatz, 1979a; Ponton and Méricoux, 2000). Many behavioural patterns and morphological adaptations of fish species have evolved in relation to swimming ability (Webb, 1984), avoidance of predation (Keast, 1985) and exploitation of resources (Gatz, 1979b). Such adaptations have been inferred by analysis of body and fin shapes, colour patterns and features of the digestive tract (Piet, 1998; Breda *et al.*, 2005; Piorski *et al.*, 2005, 2007; Teixeira and Bennemann, 2007).

Usually, ecomorphological analyses use ratios between variables that have some functional interpretation. For example, relative head length is a ratio between head length and standard length interpreted as indicative of the size of

prey ingested by a predator (Gatz, 1979a; Casatti and Castro, 2006; Ferrito *et al.*, 2007). Winemiller (1991) arguments, in a certain way, have contributed to spread the use of ratios in such analysis. According to this the author, ratios are desirable for asking ecological questions of morphological data in contrast to the anatomical landmark method, because this restricts the ability of the analysis to detect general features of form related to ecological function.

In the last two decades, the analysis of morphological shape has been improved by advances of geometric morphometrics (Bookstein, 1991; Zelditch *et al.*, 2004). This new approach captures the geometry of morphological structures of interest, and preserves this information throughout the analysis (Rohlf and Marcus, 1993; Adams *et al.*, 2004).

The mechanisms employed by fish for feeding repre-

(1) Instituto Federal do Maranhão, Povoado Poraquê, s/n, Zona Rural, 65400-000, Cod6, Maranhão, Brazil. [ecsdourado@yahoo.com.br]

(2) Universidade Federal do Maranhão, Laboratório de Organismos Aquáticos, BR 222, Km 04, s/n, Boa Vista, 65500000, Chapadinha, Maranhão, Brazil. [silvanunes@yahoo.com]

(3) Universidade Federal do Maranhão, Departamento de Biologia, Avenida dos Portugueses s/n, 65080040, São Luís, Maranhão, Brazil.

* Corresponding author [nivaldopiorski@yahoo.com.br]

sent adaptations which enable them to obtain advantages over particular types of prey (Alexander, 1967; Wootton, 1990). Such adaptations appear as differences in body and fin shapes which are frequently greater among individuals of the same species than among closely related species of the same assemblage (Greenwood, 1975). Among fish, the principal differences can be viewed in the mouth form, teeth, gill rakers and intestine length and form. Carnivorous fish have large mouth gapes with large, well-developed teeth, short and coarsely spaced gill rakers and short intestines, and fish which feed on small prey items usually have relatively small mouths and teeth, longer and numerous gill rakers and long intestines (Keast and Webb, 1966; Hugueny and Pouilly, 1999; Fugi *et al.*, 2001). Then, the morphological differences between fish species and, as a result, differences in feeding mechanisms and the corresponding foraging modes allow sympatric species to coexist by minimizing or avoiding interspecific competition (Labropoulou and Eleftheriou, 1997; Piorski *et al.*, 2005).

The genera *Acestrorhynchus* Eigenmann & Kennedy 1903 has a wide distribution in the South American drainages. It includes about 15 species, such as *Acestrorhynchus falcatus* (Bloch, 1794) and *Acestrorhynchus heterolepis* (Cope, 1878) known as “urubarana” and “urubarana mucura”, respectively. *Acestrorhynchus falcatus* is cited for the Amazon basin, rivers of Guyana, Surinam, French Guyana and Orinoco basins while *A. heterolepis* occurs in the Amazon and Orinoco rivers (Menezes, 1969). Both species were confirmed by Dr. Naécio A. Menezes – MZUSP, this being the first record of *A. heterolepis* for river drainages of Maranhão State. This species is easily identified by the presence of the laterosensory canal of each lateral line scale with an upper and lower small branch (versus, only one branch in other *Acestrorhynchus* species). Both species have little commercial value and studies on their biology are scarce.

In this paper we aimed to describe the ecomorphological adaptations of the species, and argue whether the variables generated by geometric morphometric analysis can estimate the ecomorphological adaptations.

MATERIAL AND METHODS

The samples of *Acestrorhynchus falcatus* and *Acestrorhynchus heterolepis* were collected trimonthly from November 1997 through March 2001 using gill nets of different mesh sizes (10, 20, 30 and 40 mm mesh). In the Turiçu River (02°13'31.72"S, 45°17'59.76"W) the specimens were caught in four sites located at the middle course of the river, next to the city of Santa Helena in the Environmental Protected Area of Baixada Maranhense. In each sampling site, gill nets were fished for approximately six hours. The material obtained was fixed in 10% formalin and taken to the laboratory. After the fixation period, the specimens were transferred to alcohol (70%) and deposited in the Fish Collection of the Universidade Federal do Maranhão. A total of 299 specimens of *A. falcatus* (129-195 mm standard length, SL) and 146 specimens of *A. heterolepis* (166-247 mm SL) were studied.

Morphometric analysis

Individual pictures of the species were digitalized and seventeen landmarks (Bookstein, 1991) were defined on the left side of each individual (Fig. 1): (1) snout tip; (2) anterior margin of eye orbit; (3) posterior margin of eye orbit; (4) posterior margin of maxilla; (5) point at the edge of body vertically aligned with landmark 6; (6) inferior limit of opercle; (7) posterior margin of opercle; (8) origin of pectoral fin base; (9) origin of dorsal fin base; (10) end of dorsal fin base; (11) origin of adipose fin base; (12) end of adipose fin base; (13) superior lobe of caudal fin; (14) inferior lobe of caudal fin; (15) end of anal fin base; (16) origin of anal fin base; (17) origin of pelvic fin base.

Landmarks were transformed into shape Cartesian coordinates by the TPS Digit program (Rohlf, 2010). After obtaining the data, the next step in a geometric morphometric analysis is to remove non-shape variation. This was done by a Generalized Procrustes Analysis (GPA) that superimposes landmark configuration using least-square estimates for translation and rotation parameters. Then, the shape changes were described by the method of the thin-plate splines decomposed by their partial warps (PW) (see Bookstein, 1991; Rohlf *et al.*, 1996). This method allows modelling

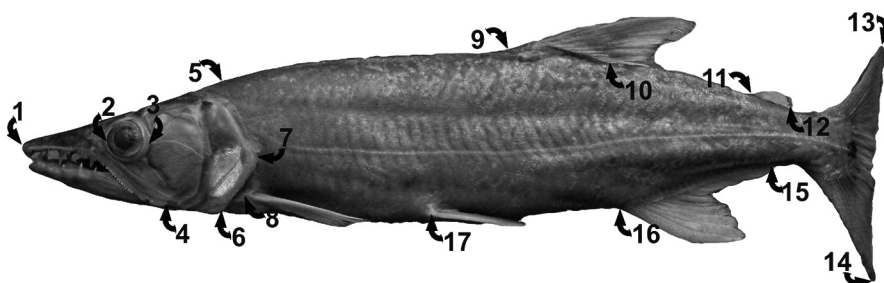


Figure 1. - Landmarks on the lateral region of *Acestrorhynchus heterolepis*. See text for definition of each landmark.

shape change as a deformation between landmarks, splitting the deformation into uniform and non-uniform components. The changes which are the same at all regions on the organism and show neither spatial gradients nor spatial localization are described by the uniform component, whereas the non-uniform component describes local differences over regions of the body (Rohlf *et al.*, 1996). After, the non-uniform component can be decomposed into a series of components ordered by their spatial scales (Monteiro and Reis, 1999). The X-axis on the uniform component corresponds to the anteroposterior axis, and the Y-axis corresponds to the dorsoventral axis of the fish bodies (Cavalcanti *et al.*, 1999).

The shape coordinates of the aligned specimens were projected on the principal warps, creating the W matrix, which was submitted to Discriminant Analysis (DA).

The coordinates and the scores of the partial warps of each specimen were projected and regressed, in that same order, on the discriminant axis, using the TPSRegr (Rohlf, 2007) software.

Feeding habit analysis

Characterization of the digestive tract

The digestive tract was characterized by the number and form of the gill rakers, number and disposition of teeth, mouth shape and intestine shape. The snout length (the distance between snout tip and anterior margin of the eye orbit) and the mouth height (taken as the maximum gap of the mouth) were measured and the proportion in relation to head length (the distance between snout tip and the most posterior margin of opercle) were recorded. The intestinal quotient (IQ) was used as a relative measure of the intestine length. This index was obtained by the ratio between intestinal and standard lengths (SL) of the fish (Zavala-Camin, 1996). The *t*-test was used to test for differences between the mean values of IQ of both species. All measurements were made to the nearest 0.1 mm using vernier callipers.

Diet analysis

Diet was studied by analysis of stomach contents of specimens caught from April 2000 to January 2001. The analysis was restricted to this period because of the low number of animals with empty stomachs, in contrast to years 1998 and 1999. For each specimen, the stomach contents were described according to occurrence and volumetric methods (Hyslop, 1980), combined in the Alimentary Index (IA_i), proposed by Kawakami and Vazzoler (1980), where:

$$IA_i = \frac{F_i \times V_i}{\sum_{n=1}^n (F_i \times V_i)}$$

IA_i = feeding index of item *i*;

i = 1, 2,... *n* food item;

F_i = frequency of occurrence of food item *i*;

V_i = volume of food item *i*;

Items were identified to the lowest possible taxonomic level. For some items, this was not possible due to high degree of digestion or because only bits of the item were found in the stomach. When whole items were found in the stomach contents, the total length of each was measured to test the hypothesis of no difference in prey size between species of *Acestrorhynchus*, using the Mann-Whitney test (Zar, 1999).

The Proportional Overlap Index (POI) (Schoener, 1968) was obtained to evaluate the degree of overlapping in diets of the two species of *Acestrorhynchus*. The index was calculated by the equation $R_0 = 1 - 0.5(\sum |P_{ij} - P_{ik}|)$, where: R₀ is the overlap value; P_{ij} and P_{ik} are the proportional compositions of food item *i* for species *j* and *k*, respectively. If the overlap value equals 0, then the diet of the species are fully distinct. In contrast, the species show total overlapping of the food item when R₀ equals 1.

RESULTS

Morphometric analysis

Differences between the species *A. falcatus* and *A. heterolepis* were shown by Discriminant Analysis (DA; Wilks's $\lambda = 0.90$, $p < 0.05$; $F_{(2,4)} = 22.15$), which was applied on individual scores of the uniform component (Fig. 2A). By this analysis, *A. falcatus* has a higher body than *A. heterolepis* (Fig. 2B). Morphometric differences were also indicated by this same analysis when it was applied on the non-uniform components (Wilks's $\lambda = 0.16$, $p < 0.05$; $F_{(28,374)} = 72.79$). The species were discriminated on the axis produced by DA, where positive scores were associated with *A. falcatus* and negative ones with *A. heterolepis* (Fig. 3A).

The shape changes linked to the discriminant axis pointed out that the highest variations towards the positive deviation were exhibited by *A. falcatus*. In this species, the snout moved to the right side on the horizontal axis of the grid deformations. On the other hand, the anal fin base, which is defined by landmarks 15 and 16, moved in the opposite direction, going away from the caudal fin (Fig. 3B). On the vertical axis, *A. falcatus* was characterized by the nearest position of landmarks 13 and 14, which evaluated the caudal fin height. In smaller intensity, upward displacements of landmarks 9, 10, 11 and 12 and downward displacements of landmarks 6, 8 and 17 can be observed (Fig. 3B).

In contrast to *A. falcatus*, the snout of *A. heterolepis* moves to the left, elongating the head, and the anal fin base (vectors 15 and 16) is closer to the caudal fin, reducing the length of caudal peduncle (Fig. 3B). In the vertical axis, the nearness of landmarks 12 and 15 results in reduction of the caudal peduncle height. The opposite displacements occur with points 13 and 14, on which the caudal fin height is built. In this same axis, the vectors associated with landmarks 9

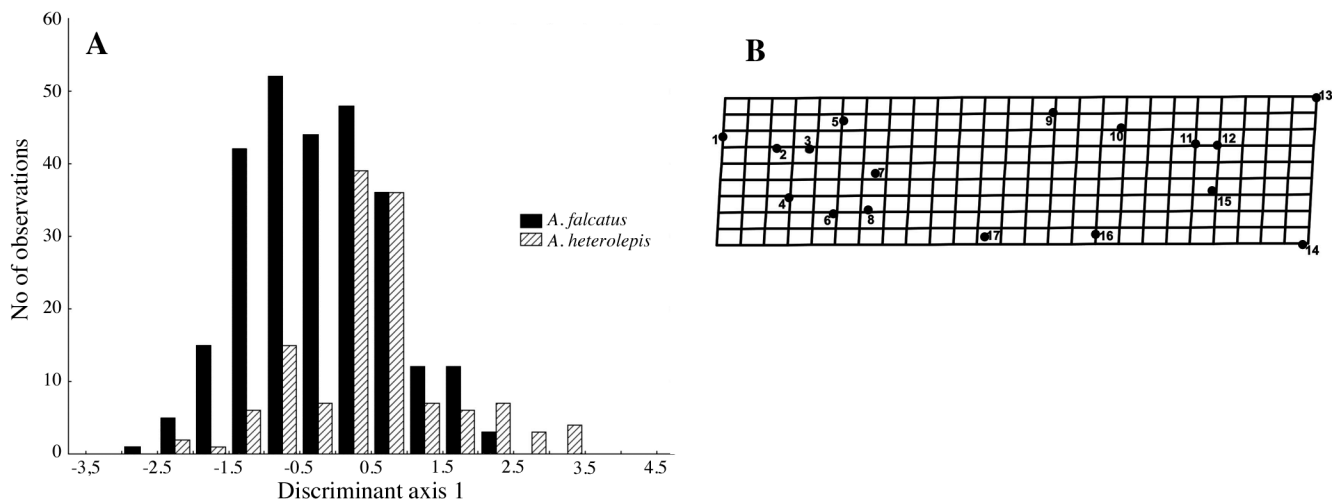


Figure 2. - **A:** Discriminant analysis on the uniform component. **B:** Deformations grid showing the global variation of all landmarks in the uniform component. The grid was configured to represent the variations associated with the positive side of the discriminant axis.

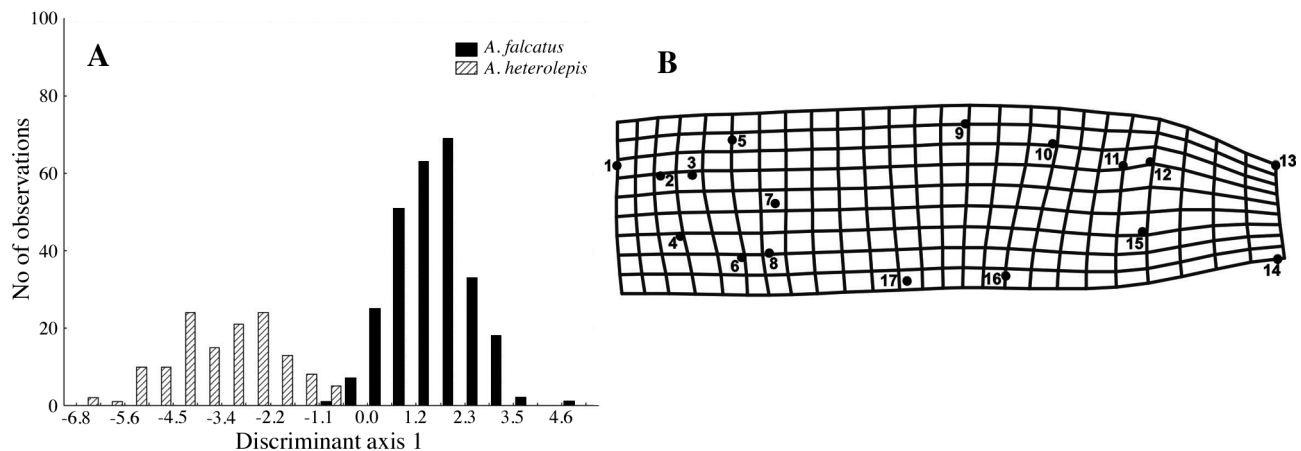


Figure 3. - **A:** Discriminant analysis on the non-uniform component. **B:** Deformations grid showing the local variations of all landmarks describing the differences between the species. The grid was configured to represent the variations associated with the positive side of the discriminant axis.

and 10 (the dorsal fins base) move downward and close to ventral region of body (Fig. 3B).

Characterization of the digestive tract

Acestrorhynchus falcatus bears a short snout (length 37% of head length – HL) and the height of the terminal mouth is about half (0.52) of HL. In *A. heterolepis*, the snout is long (length 51% of HL) and the height of the terminal mouth is about three times (0.71) HL.

Both species show well-developed conical teeth, which are slightly curved backward. When the mouth is closed, the inferior jaw has an angle of about 45° with the horizontal plane. The upper jaw of *A. heterolepis* is characterized by the presence of two premaxilla foraminae to shelter the first two pairs of conical teeth of the lower jaw. The premaxilla has three canine teeth. Between the first and the sec-

ond canine teeth, there is a row with 9 to 11 small, thin and conical teeth. Maxilla has two well-developed canine teeth, with two or three smaller conical teeth between them. After the canine teeth, there is a row with 29 to 32 tiny teeth. On the anterior border of the dentary, there are well-developed canine teeth associated with two or three smaller teeth; in the median portion of the dentary, three smaller canine teeth are present, followed by a row with 13 to 21 smaller conical teeth. Some individuals of *A. falcatus* (N = 14) present two premaxilla foraminae, although only one foramine is more common (N = 285). The premaxilla of this species has two canine teeth and a row with six to ten small teeth between them. In the maxilla, two canine teeth are inserted among small conical teeth, followed by 27 to 30 smaller conical teeth. The arrangement and teeth shape on the anterior edge of the dentary in *A. falcatus* is like that of *A. heterolepis*, but

the canine tooth is slightly smaller. In *A. falcatus*, the median region of dentary bone has three canine and 11 to 20 small and thin conical teeth.

In both species, the gill rakers on the first branchial arch are short and decrease in size towards the lower portion. In *A. heterolepis*, the gill rakers are thin and vary from 38 to 42 in number, while *A. falcatus* presents 22 to 29 gill rakers, surrounded by spines.

In both species, the digestive tract is characterized by a lengthened stomach, numerous filiform pyloric caeca, and a short tubular intestine.

The mean IQ of *A. falcatus* (0.94 ± 0.04) was significantly different from that of *A. heterolepis* (0.89 ± 0.02) ($t = 8.47$, $g.l. = 133$, $p < 0.0001$).

Diet composition

A total of 10 food items were identified in the stomach contents of *A. heterolepis* ($N = 96$). *Sternopygus macrurus* was the predominant item in stomachs (84.3%) of this species as showed by the values of the alimentary index (IAi). Fish remains (13.26%), Erythrinidae (1.02%) and *Charax* sp. (0.76%) were found in smaller proportions, along with other species of fish with low IAi values (Tab. I).

The diet of *A. falcatus* ($n = 189$) consisted of 17 food items. In this species the most important item was *S. macru-*

rus (47.6%), followed by fish remains (26.64%), *Poptella compressa* (7.72%), *Cheirodon* sp. (4.72%), Characiformes (4.39%), larva of *Anchovia* sp. (3.88%) and *Hemiodopsis* sp. (1.4%) (Tab. I).

The temporal analysis indicated that *S. macrurus* and fish remains were the food item found in stomachs of *A. heterolepis* in all sampling months (Fig. 4A). The food item *S. macrurus* was always the most frequent, except in June 2000 when fish remains were higher. The others food items only occurred once or twice in low frequencies from April 2000 to January 2001. August 2001 was the month with the highest number (7) of items in the stomachs of *A. heterolepis*.

Cheirodon sp. was found in the stomachs of *A. falcatus* in all months (Fig. 4B). However, this item usually occurred in low frequencies, being surpassed by fish remains and *S. macrurus* that were absent only once. *Hemiodus* sp. occurred from April to August 2000 at frequencies below 15%, like the remaining food items. The highest number of food items in stomachs of *A. falcatus* was recorded in June 2000 (8) and August 2000 (9 items).

The POI had a value of 0.81, indicating a high overlap between the diets of the two species of *Acestrorhynchus*.

In *A. falcatus*, the size of the ingested prey varied from 12 mm to 81 mm ($\bar{x} = 45.53 \pm 15.94$; $n = 36$), while in *A. heterolepis* it varied from 58 mm to 126 mm ($\bar{x} = 88.68 \pm 16.42$; $n = 22$). Significant differences between the means were found according to the Mann-Whitney test, indicating that *A. heterolepis* consumes larger preys than *A. falcatus* ($U = 12.5$; $p < 0.05$).

Table I. - Percentual values of IAi for the prey items of *Acestrorhynchus falcatus* and *A. heterolepis* caught from November 1997 to March 2001 in the Turiaçu River.

Prey items	IAi (%) <i>A. falcatus</i>	IAi (%) <i>A. heterolepis</i>
<i>Sternopygus macrurus</i>	47.56	84.37
Fish remains	26.64	13.26
<i>Poptella compressa</i>	7.72	—
<i>Cheirodon</i> sp.	4.72	0.17
Characiformes	4.39	0.07
<i>Anchovia</i> sp. larvae	3.88	—
<i>Hemiodopsis</i> sp.	1.42	—
<i>Leporinus friderici</i>	0.89	—
Plant material	0.81	—
<i>Roeboides</i> sp.	0.68	—
<i>Crenicichla</i> sp.	0.37	—
<i>Loricaria</i> sp. larvae	0.26	—
Crustacea	0.18	—
<i>Acestrorhynchus</i> sp.	0.16	0.10
<i>Pygocentrus nattereri</i>	0.16	—
<i>Astyanax</i> sp.	0.11	—
Erythrinidae	0.05	1.02
<i>Bryconops</i> sp.	—	0.17
<i>Charax</i> sp.	—	0.76
Gymnotiformes	—	0.03
<i>Metynnis</i> sp.	—	0.03

DISCUSSION

In the present work, differences between the two species of *Acestrorhynchus* were shown by both the morphometric and diet analyses.

Ecomorphology

In general, global variations of all landmarks showed that the body of *A. heterolepis* is lower and more elongated than that of *A. falcatus*. Although a lower and elongated body does not necessarily characterize a fusiform body, in this paper the *A. heterolepis* body is considered close to a streamlined profile. Other morphometric measures support this, such as the combination of high caudal fin and low caudal peduncle in *A. heterolepis*. In fact, streamlined profiles are characterized by a slowly tapering tail and a ratio (Finess Ratio – FR) of maximum length to maximum diameter of between 2 and 6 (Blake, 1983). FR values higher than 4.5 in streamlined bodies is not critical to increase resistance to motion (see Blake, 1983), and this obviously is the case in *Acestrorhynchus* species.

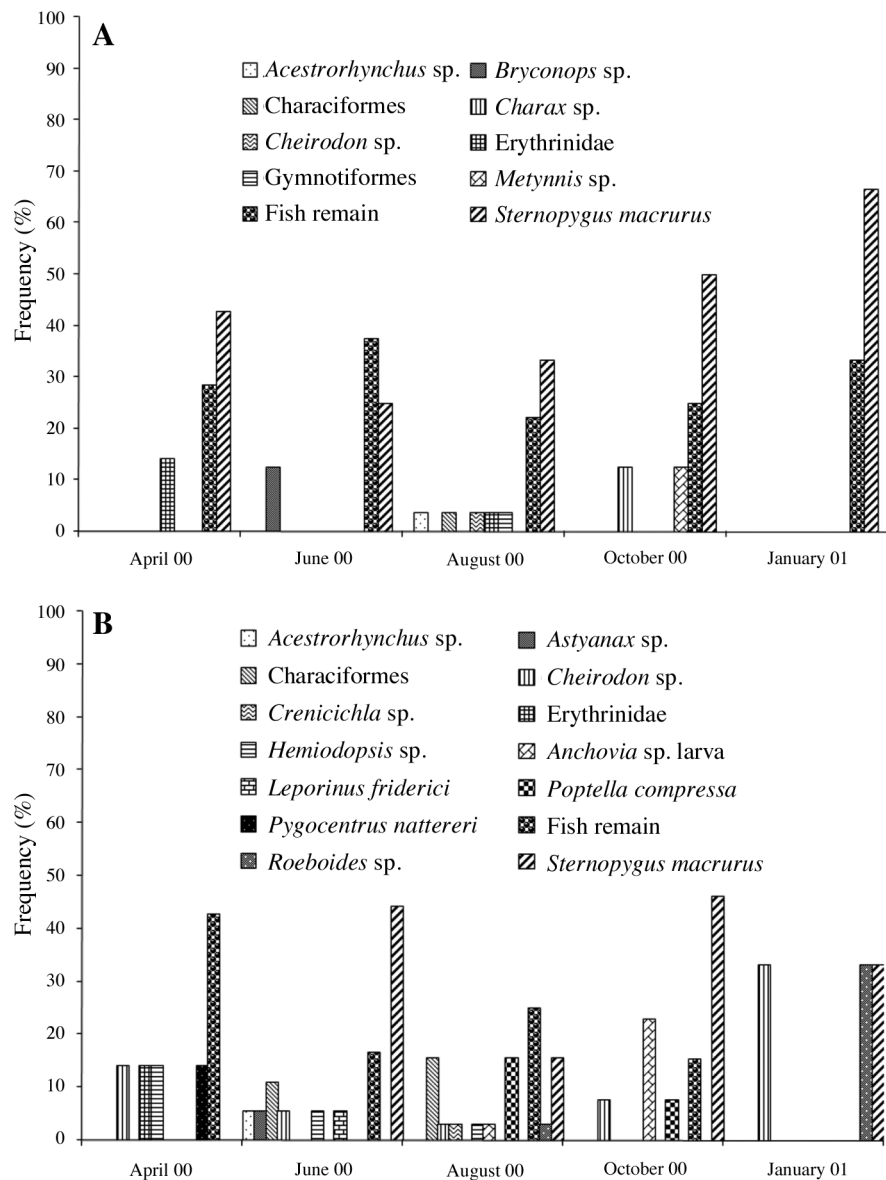


Figure 4. - Temporal variation in the frequency of occurrence of food items in stomachs from April 2000 to January 2001. **A:** *A. heterolepis*; **B:** *A. falcatus*.

The fusiform shape is typical of fast swimming fish, because it reduces the forces generated both by the friction between bodies and water and by the pressure differences resulting from the displacement of water as the fish is in motion (Helfman *et al.*, 1997; Breda *et al.*, 2005; Fish and Lauder, 2006). Thus, in spite of the differences, both species present typical characteristics of active swimming fish. The features of *A. heterolepis* cited above allow it to develop higher speeds than *A. falcatus*. In addition, the most posterior position of the caudal fin in *A. heterolepis* suggests that fast lunges on the prey are a part of the feeding strategy.

The non-uniform component of RWA showed that general differences between *A. falcatus* and *A. heterolepis* are due to variations in caudal fin, caudal peduncle and body

depths, and snout and maxilla lengths. In *A. heterolepis*, the snout and maxilla lengths and the caudal fin depth are larger, while in *A. falcatus*, the caudal peduncle and body depths are higher.

Differences in snout length are intimately related with head size and therefore with prey size (Gatz, 1979b; Pior-ski *et al.*, 2005), indicating that *A. heterolepis* tends to capture larger prey than *A. falcatus*. A traditional way to evaluate this is by indexes such as mouth ratio and snout ratio. Although these indexes are convenient to obtain functional information about structures, the correlation resulting from ratios among independent variables results in the problem of spurious correlation (Peres-Neto, 1995). Analyses based on geometric morphology, on the other hand, do not use pro-

portions, thereby removing the above. Nevertheless, one can argue that there is a great loss of functional information using morphometric geometry. Although this should be true for some extensions, information of body shape or a more constrained body area is improved with analysis using this approach, which is the goal of an ecomorphological study.

Assuming that an individual phenotype shows the relationship between its owner and the environment, integrated analysis of various parts of the body, from a functional point of view, is more advantageous than static analysis of the structure functionality based on ratios. In the current paper, areas of snout and head were assessed by landmarks 1 to 7 (see Fig. 1), and enabled us to make inferences on functionality of the structures. In traditional morphometrics, the head length is usually taken as the distance between snout tip and the most posterior margin of the opercle. However, this measurement does not capture the shape of the head and no structure associated to it. In our data, landmarks 4 and 7 do not move, indicating that displacements of landmark 1 correspond to real differences between the species and should be independent of head size.

Diet

The functional inferences above were supported by diet analysis, which indicated that *A. heterolepis* consumes whole prey with more frequency. In addition, fish such as *A. falcatus* and *A. heterolepis* that swallow large prey, or consume a large amount of food at the same time, usually have a large stomach (Nikolsky, 1963; Zavala-Camin, 1996).

Several authors have demonstrated the relationship between feeding habits and intestine length in Teleostei fish (Nikolsky, 1963; Fugi and Hahn 1991; Moraes *et al.*, 1997; Delariva and Agostinho, 2001). According to these studies, carnivorous fish usually present short intestines, as observed in the two species of *Acestrorhynchus*.

The analysis of the diet revealed that both species feed on fish. Occasionally, shrimp and plant material are found in stomachs of *A. falcatus*. Hahn *et al.* (2000) verified that specimens of *A. lacustris* above 10 cm of length consume only fish, supporting the studies of Benneman *et al.* (1996) for specimens of Tibagi River, in Paraná. Other authors found insects and plants in the stomachs of this species, although just as occasional items (Almeida *et al.*, 1997; Benneman *et al.*, 1996). In this light, the finding of other items, besides fish, in the diet of *Acestrorhynchus* can be attributed to consumption along with ingested fish prey.

Among the preys identified, *Sternopygus macrurus* was the most important for both species of *Acestrorhynchus*, although this item was more representative in the diet of *A. heterolepis* (80% of the total). Nevertheless, other prey items were important in the diet of *A. falcatus*, indicating that the species presents a wider food spectrum than *A. heterolepis*. In view of the POI value, which showed that the spe-

cies have a similar feeding habit, the potential competition between them should be reduced by feeding diversification and differential habitat. Although this hypothesis has not been tested, it is common in fish with similar morphological adaptations, as noted by Piorski *et al.* (2005) in a study with two species of piranhas. The authors noted that one of the piranhas consumed a greater variety of food items than the other species, as found for the *Acestrorhynchus* species in the present study.

According to Barthem (1987), *Acestrorhynchus* sp. is more active at dusk, in spite of not showing preference for illuminated or darkness periods. This may explain the greater predation on *S. macrurus* that, like other gymnotiformes, hides among the marginal vegetation, in the sandy or muddy bottom during the time when daylight is bright, leaving the hiding places for the open water in the evening twilight (Bullock *et al.*, 1979; Crampton, 1998).

Fish fragments were the next most important item in diet of both species, occurring in smaller percentage in the stomachs of *A. heterolepis*. This indicates that *A. heterolepis* has greater capacity to ingest whole prey than *A. falcatus*.

In general, morphological features associated to prey size represent one of the most important adaptations developed by predators in sympatry in response to overlap in diet and competition (Huskey and Turingan, 1998; Piet, 1998; Cussac *et al.*, 1998). Labropoulou and Eleftheriou (1997), for example, found differences in morphology of the feeding apparatus among pairs of sympatric species, suggesting segregation of trophic niche between them. Hugueny and Pouilly (1999) identified positive correlation between mouth height and standard length in piscivorous fish, sustaining the Wainwright and Richard (1995) hypothesis that the mouth height has an important role in the interspecific variation of the diet in fish communities.

Although *A. falcatus* and *A. heterolepis* are similar species, the principal difference between them is related with swimming agility and prey size. Thus, the presence in *A. heterolepis* of a shallow body, close to a fusiforme profile, deep caudal fin and low caudal peduncle should enable it to occupy the mid-upper region of the water column. Moreover, the body shape features of this species allow it to swim faster and sporadically jump in order to capture prey. In contrast, *A. falcatus* possesses a shorter head and lower caudal fin, better adapted to capture small preys and to live in the mid-lower region of the water column.

Acknowledgments. – We thank Dr. Naércio A. Menezes – MZUSP for helping with the identification of *Acestrorhynchus* species in this study. We are grateful to Dr. Guillaume Rousseau (UEMA) for the translation of the Résumé, and to David Palmer who reviewed the text in English.

REFERENCES

- ADAMS D.C., ROHLF F.J. & SLICE D.E., 2004. - Geometric morphometrics: ten years of progress following the 'revolution'. *Ital. J. Zool.*, 71: 5-16.
- ALEXANDER R.M., 1967. - Functional Design in Fishes. 160 p. London: Hutchinson Univ. Library.
- ALMEIDA V.L.L.d., HAHN N.S. & VAZZOLER A.E.A.d.M., 1997. - Feeding patterns in five predatory fishes of the high Paraná River floodplain (PR, Brazil). *Ecol. Freshw. Fish*, 6: 123-133.
- BARTHEM R.B., 1987. - Uso de redes de espera no estudo de ritmos circadianos de algumas espécies de peixes nos lagos de várzea do Rio Solimões. *Rev. Bras. Zool.*, 3: 409-422.
- BENNEMANN S.T., ORSI M.L. & SHIBATTA O.A., 1996. - Atividade alimentar de espécies de peixe do Rio Tibagi relacionada com o desenvolvimento de gordura e das gônadas. *Rev. Bras. Zool.*, 13: 501-512.
- BLAKE R.W., 1983. - Fish Locomotion. 208 p. Cambridge: Cambridge Univ. Press.
- BOOKSTEIN F.L., 1991. - Morphometrics Tools for Landmark Data: Geometry and Biology. 433 p. New York: Cambridge Univ. Press.
- BREDA L., OLIVEIRA E.F. & GOULART E., 2005. - Ecomorfologia de locomoção de peixes com enfoque para espécies neotropicais. *Acta Sci.*, 27: 371-381.
- BULLOCK T.H., FERNANDES-SOUZA N., GRAF W., HELLI-GENBERG W., LANGNER G., MEYER D.L., PIMENTEL-SOUZA, F., SCHEICH H. & VIANCOUR T.A., 1979. - Aspectos do uso da descarga do órgão elétrico e eletrorrecepção nos Gymnotoidei e outros peixes amazônicos. *Acta Amazon.*, 9: 549-572.
- CASATTI L. & CASTRO R.M.C., 2006. - Testing the ecomorphological hypothesis in a headwater riffles fish assemblage of the rio São Francisco, southeastern Brazil. *Neotrop. Ichthyol.*, 4: 203-214.
- CAVALCANTI M.J., MONTEIRO L.R. & LOPES P.R.D., 1999. - Landmark-based morphometric analysis in selected species of serranid fishes (Perciformes: Teleostei). *Zool. Stud.*, 38: 287-294.
- CRAMPTON W.G.R., 1998. - Electric signal design and habitat preferences in a species rich assemblage of gymnotiform fishes from the Upper Amazon basin. *Ann. Acad. Bras. Ciênc.*, 70: 805-847.
- CUSSAC V.E., RUZZANTE D., WALDE S., MACCHI P.J., OJEDA V., ALONSO M.F. & DENEGRÍ M.A., 1998. - Body shape variation of three species of *Percichthys* in relation to their coexistence in the Limay River basin, in the northern Patagonia. *Environ. Biol. Fish.*, 53: 143-153.
- DELARIVA R.L. & AGOSTINHO A.A., 2001. - Relationship between morphology and diets of six neotropical loriciids. *J. Fish Biol.*, 58: 832-847.
- FERRITO V., MANNINO M.C., PAPPALARDO A.M. & TIGANO C., 2007. - Morphological variation among populations *Aphanius fasciatus* Nardo, 1827 (Teleostei, Cyprinodontidae) from the Mediterranean. *J. Fish Biol.*, 70: 1-20.
- FISH F.E. & LAUDER G.V., 2006. - Passive and active flow control by swimming fishes and mammals. *Annu. Rev. Fluid Mech.*, 38: 193-224.
- FUGIR. & HAHN N.S., 1991. - Espectro alimentar e relações morfológicas com o aparelho digestivo de três espécies de peixes comedores de fundo do Rio Paraná, Brasil. *Rev. Bras. Biol.*, 51: 873-879.
- FUGIR R., AGOSTINHO A.A. & HAHN N.S., 2001. - Thopfic morphology of five benthic-feeding fish species of a tropical floodplain. *Rev. Bras. Biol.*, 61: 27-33.
- GATZ A.J.J., 1979a. - Community organization in fishes as indicated by morphological features. *Ecology*, 60: 711-718.
- GATZ A.J.J., 1979b. - Ecological morphology of freshwater stream fishes. *Tulane Stud. Zool. Bot.*, 21: 91-124.
- GREENWOOD P.H., 1975. - A History of Fishes. 3rd edit., 467 p. New York: John Wiley & Sons.
- HAHN N.S., DELARIVA R.L. & LOUREIRO V.E., 2000. - Feeding of *Acestrorhynchus lacustris* (Characidae): a post impoundment studies on Itaipu Reservoir, Upper Paraná River, PR. *Braz. Arch. Biol. Technol.*, 43: 207-213.
- HELFMAN G.S., COLLETTE B.B. & FACEY D.E., 1997. - The Diversity of Fishes. 544 p. Oxford: Blackwell Science.
- HUGUENY B. & POUILLY M., 1999. - Morphological correlates of diet in an assemblage of West African freshwater fishes. *J. Fish Biol.*, 54: 1310-1325.
- HUSKEY S.H. & TURIGAN R.G., 1998. - Variation in prey-resource utilization and oral jaw gape between two populations of largemouth bass, *Micropterus salmoides*. *J. Fish Biol.*, 51: 67-86.
- HYSLOP E.J., 1980. - Stomach contents analysis – a review of methods and their applications. *J. Fish Biol.*, 17: 411-429.
- KAWAKAMI E. & VAZZOLER G., 1980. - Método gráfico e estimativa de índice alimentar aplicado no estudo de alimentação de peixes. *Bol. Inst. Oceanogr.*, 29: 205-207.
- KEAST A., 1985. - The piscivore feeding guild of fishes in small freshwater ecosystems. *Environ. Biol. Fish.*, 12: 119-129.
- KEAST A. & WEBB D., 1966. - Mouth and body form relative to feeding ecology in the fish fauna of a small lake, Lake Opinicon, Ontario. *J. Fish. Res. Board Can.*, 23: 1845-1874.
- LABROPOULOU M. & ELEFThERIOU A., 1997. - The foraging ecology of two pairs of congeneric demersal fish species: important of morphological characteristics in prey selection. *J. Fish Biol.*, 50: 324-340.
- MENEZES N.A., 1969. - Systematic and evolution of the tribe Acestrorhynchini (Pisces, Characidae). *Arg. Zool.*, 18: 1-150.
- MONTEIRO L.R. & REIS S.F., 1999. - Princípios de Morfometria geométrica. 198 p. Ribeirão Preto: Holos.
- MORAES M.F.P.G., BARBOLA I.F. & GUEDES E.A.C., 1997. - Alimentação e relações morfológicas com o aparelho digestivo de "Curimbatá", *Prochilodus lineatus* (Valenciennes) (Osteichthyes, Prochilodontidae) de uma lagoa do Sul do Brasil. *Rev. Bras. Biol.*, 14: 169-180.
- NIKOLSKY G.V., 1963. - The Ecology of Fishes. 352 p. London: Academic Press.
- PERES-NETO P.R., 1995. - Introdução a análises morfométricas, In: Tópicos em tratamento de dados biológicos (Peres-Neto P.R., Valentin J.L. & Fernandez, F.A.S. eds), pp. 57-89. Rio de Janeiro: Univ. Federal do Rio de Janeiro.
- PIET G.J., 1998. - Ecomorphology of a size-structured tropical freshwater fish community. *Environ. Biol. Fish.*, 51: 67-86.
- PIORSKI N.M., ALVES J.R.L., MACHADO M.R.B. & CORREIA M.M.F., 2005. - Alimentação e ecomorfologia de duas espécies de piranhas (Characiformes: Characidae) do Lago de Viana, estado do Maranhão, Brasil. *Acta Amazon.*, 35: 63-70.
- PIORSKI N.M., DOURADO E.C.S. & NUNES J.L.S., 2007. - Análise ecomorfológica de três espécies de peixes do Parque Estadual Marinho do Parcel de Manuel Luiz, Maranhão, Brasil. *Bol. Lab. Hidrobiol.*, 20: 70-76.

- PONTON D. & MÉRIGOUX S., 2000. - Comparative morphology and diet of young cichlids in the dammed Sinnamary river, French Guiana, South America. *J. Fish Biol.*, 56: 87-102.
- ROHLF F.J., 2007. - tpsRegr, shape regression, version 1.34. . Department of Ecology and Evolution, State Univ. of New York at Stony Brook.
- ROHLF F.J., 2010. - tpsDig, Version 2.15. Department of Ecology and Evolution, State Univ. of New York, New York: Stony Brook.
- ROHLF F.J. & MARCUS L.F., 1993. - A revolution in morphometrics. *Trends Ecol. Evol.*, 8: 129-132.
- ROHLF F.J., LO A. & CORTI M., 1996. - Morphometric analysis of old world Talpidae (Mammalia, Insectivora) using partial – warps scores. *Syst. Biol.*, 45: 344-362.
- SCHOENER T.W., 1968. - The anolis lizards of Bimini: resource partitioning in a complex fauna. *Ecology*, 49: 704-726.
- TEIXEIRA I. & BENNEMANN S.T., 2007. - Ecomorfologia refletindo a dieta dos peixes em um reservatório no sul do Brasil. *Biota Neotrop.*, 7: 67-76.
- WAINWRIGHT P.C. & RICHARD B.A., 1995. - Predicting patterns of prey use from morphology of fishes. *Environ. Biol. Fish.*, 44: 97-113.
- WEBB P.W., 1984. - Body form, locomotion and foraging in aquatic vertebrates. *Am. Zool.*, 24: 107-120.
- WINEMILLER K.O., 1991. - Ecomorphological diversification in lowland freshwater fish assemblages from biotic regions. *Ecol. Monograph.*, 61: 343-365.
- WOOTTON R.J., 1990. - Ecology of Teleost Fishes. 392 p. New York: Chapman & Hall.
- ZAR J.H., 1999. - Biostatistical Analysis. 4th edit., 938p. New Jersey: Prentice-Hall.
- ZAVALA-CAMIN L.A., 1996. - Introdução aos Estudos sobre Alimentação natural de Peixes. 129 p. Maringá: EDUEM.
- ZELDITCH M.L., SWIDERSKI D.L., SHEETS H.D. & FINK W.L., 2004. - Geometric Morphometrics for Biologists: a Primer. 416 p. New York: Elsevier Academic Press.