

# Diet and ecomorphology of *Leporinus reticulatus* (Characiformes: Anostomidae) from the upper Rio Juruena, MT, Brazil: ontogenetic shifts related to the feeding ecology

Mariana MACHADO-EVANGELISTA<sup>1\*</sup>, André Luiz Henríques ESGUÍCERO<sup>2</sup>, Marlene Sofia ARCIFA<sup>3</sup>, Thiago Nilton Alves PEREIRA<sup>2</sup>

- 1 Universidade Estadual Paulista Júlio de Mesquita Filho, Centro de Aquicultura da UNESP, Via de Acesso Prof. Paulo Donato Castellane, s/n, CEP 14884-900 Jaboticabal, SP, Brazil.
- <sup>2</sup> Universidade de São Paulo, Laboratório de Ictiologia de Ribeirão Preto, Departamento de Biologia, Avenida Bandeirantes, 3900, CEP 14040-901, Ribeirão Preto, SP, Brazil.
- 3 Universidade de São Paulo, Laboratório de Limnologia, Departamento de Biologia, Avenida Bandeirantes, 3900, CEP 14040-901, Ribeirão Preto, SP, Brazil.
- \* Corresponding author: mariana.mevangelista@gmail.com

#### **ABSTRACT**

The conservation of diverse and well-distributed fish taxa, as the genus *Leporinus*, relies intrinsically on the knowledge of the ecological attributes of its representatives. Aiming to increase this knowledge, studies on diet and ecomorphology are ideal to provide important information about species ecology. Thus, this study aimed to analyze aspects of feeding ecology of *L. reticulatus*, from the upper Rio Juruena, Mato Grosso State, Brazil. The diet of specimens in different ontogenetic stages was compared, as well as their teeth morphology and ecomorphological attributes. *Leporinus reticulatus* presented omnivorous diet, with higher consumption of invertebrates by smaller specimens (younger ones), and gradual introduction of plant items in larger specimens (older ones). The items consumed by the individuals and the ecomorphological attributes indicated that the species is generalist and opportunistic, besides its association with the river bottom, evidencing a benthic feeding behavior. This species presents a gradual ontogenetic modification in teeth shape and mouth positioning, ranging from a terminal mouth with tricuspid teeth, in smaller specimens, to an inferior mouth with spatula shaped teeth with no cusps, in larger specimens. The ecomorphological attributes indicate an increasing swimming efficiency, and ability for performing vertical displacements, along the ontogenetic development, which in addition to the morphological ontogenetic alterations in the buccal apparatus, contributes to a better ability to explore another niches.

KEYWORDS: Neotropical ichthyofauna, freshwater fish, trophic ecology, ontogenetic morphological variation.

# Dieta e ecomorfologia de *Leporinus reticulatus* (Characiformes: Anostomidae) do alto Rio Juruena, MT, Brasil: alterações ontogenéticas relacionadas à ecologia alimentar

#### RESUMO

A conservação de táxons de peixes de grande diversidade e amplamente distribuídos, como o gênero *Leporinus*, depende intrinsicamente do conhecimento de atributos ecológicos de seus representantes. Objetivando o aumento deste conhecimento, estudos que abordam a dieta e a ecomorfologia são ideais para prover informações importantes sobre a ecologia de espécies. Assim, este trabalho teve como objetivo analisar aspectos da ecologia alimentar de *L. reticulatus* originários do alto Rio Juruena, estado do Mato Grosso, Brasil. Foi comparada a dieta de espécimes em diferentes estágios ontogenéticos, assim como a morfologia dos dentes e atributos ecomorfológicos. *Leporinus reticulatus* apresentou dieta onívora, com maior consumo de invertebrados pelos espécimes de menor porte (mais jovens), e introdução gradual de itens vegetais por espécimes de maior porte (mais velhos). Os itens consumidos pelos indivíduos e os atributos ecomorfológicos indicaram que esta espécie é generalista e oportunista, além de sua associação com o fundo do rio, evidenciando um comportamento alimentar bentônico. Esta espécie apresenta modificação ontogenética gradual no formato dos dentes e posição da boca, variando de uma boca terminal e dentes tricúspides, em espécimes menores, a uma boca inferior e dentes em forma de espátula sem cúspides, em espécimes maiores. Os atributos ecomorfológicos indicaram um crescente aumento na eficiência natatória, e na habilidade de realizar deslocamentos verticais, ao longo do desenvolvimento ontogenético, o que, em conjunto às alterações morfológicas ontogenéticas no aparato bucal, contribuem para uma melhor habilidade em explorar outros nichos.

PALAVRAS-GHAVE: ictiofauna Neotropical, peixes dulcícolas, ecologia trófica, variação ontogenética morfológica.

#### INTRODUCTION

The genus Leporinus Agassiz 1829, popularly known as "aracus" or "piaus", is represented by 87 species (Eschmeyer 2015), being the most diverse genus of the family Anostomidae. The representatives of this genus are widely distributed from southern Central America to southern South America (Garavello and Britski 2003), with the Rio Amazonas basin holding the largest diversity and endemism of species. Some species of Leporinus reach approximately 40 cm of standard length (Garavello and Britski 2003), and are very important economically as food resource, other small-sized species has great economic importance in fish hobbyist industry (Santos et al. 1996). In general, this genus has been consistently threatened by deleterious anthropic impacts, as the recent construction of dams in Amazonian rivers for energetic purposes (Agostinho et al. 2007; ANEEL 2015). Thus, the conservation of this genus depends mainly on the knowledge of its diversity and ecological features of its representatives.

In order to contribute to the knowledge of some ecological attributes of *Leporinus* species and its conservation, we studied some ecomorphological and diet aspects of *Leporinus reticulatus* Britski & Garavello 1993. This is a small-sized species of *Leporinus*, up to approximately 14 cm standard length (Birindelli and Britski 2009), which has been found only in the Rio Tapajós basin. There are no previous studies on the diet of this species and, about its morphology, Birindelli and Britski (2009) observed an allometric change in its snout, which was greater in the larger specimens due to elongation and rearrangement of several skull bones during ontogeny, but no comments were made about the buccal apparatus. Additionally, there is no available information on its biology, especially about how it is influenced by these changes.

Studies involving the investigation of fish feeding habits provide important information about the biology of the species, allowing the analysis of the ecological role of a particular species in an ecosystem (Windell and Bowen 1978). Diet studies help to understand the interactions among fish and other organisms in the environment (Luz *et al.* 2001) and provide subsidies for the comprehension of how species use the available food items, besides their responses to environmental changes and availability of food resources (Goulding 1980).

Most studies on fish feeding ecology evaluate the temporal and spatial variations in the diet of these animals. Few studies aim to compare the diet of individuals of different ontogenetic stages from the same place, and caught in the same period (Vitule and Aranha 2002). This approach is crucial for the knowledge of the ontogenetic variations in the food spectrum, which leads to the understanding of changes in energy demand (Abelha *et al.* 2001), exploration of new habitats, and maturational and morphological changes, such as improvement in mobility and morphological shifts in structures related to the digestive system (Wootton 1998).

The exploitation of different food resources along the ontogenetic development can be reflected in morphological changes, which can improve the capacity of utilization of food resources. The analysis of ecomorphological attributes of different ontogenetic stages seeks to understand relationships between morphological and ecological aspects (Peres-Neto 1999). Regarding to fish, two kind of analysis are common in these studies. One is the detection of patterns based on trophic morphology directly related to the food intake, such as size and position of the mouth and intestine length (Fugi *et al.* 2001). The second analysis concerns to aspects involved in locomotion and occupation of habitat by these animals (Freire and Agostinho 2001). The combination of ecomorphological and dietary data leads to consistent information about species ecology (Balassa *et al.* 2004), especially in relation to habitat occupation.

Thus, this study aimed to analyze some aspects of feeding ecology of *Leporinus reticulatus*, from the upper Rio Juruena, Mato Grosso state, Brazil. The diet of specimens in different ontogenetic stages was compared, as well as their teeth morphology and ecomorphological attributes.

#### MATERIALS AND METHODS

#### Study area

The study area (13° 22' 38" S, 59° 01' 00" W and 13° 03' 53" S, 58° 58' 48" W) encompasses a stretch of approximately 45 km of the upper Rio Juruena (Figure 1), a third order river, located in the Mato Grosso State, Brazil. The confluence of Juruena and Teles Pires rivers, distant 550 km from the headwaters of the Rio Juruena, originates the Rio Tapajós, a tributary of the right margin of the Rio Amazonas.

The headwaters of Rio Juruena are located at the Parecis Plateau, in a savanna ecosystem ("cerrado"). In this area, characterized by rapids and riffles, the water is totally transparent and poor in nutrients (N, P, and Ca). Biochemical oxygen demand (BOD) and fecal coliform bacteria are low, indicating that anthropic contributions are negligible. Macrophytes are not abundant and are distributed in discrete and sparse stands, sometimes covering a sand plateau onshore. The surrounding area, cultivated with soybean, corn, and rice, is isolated from the river by riparian vegetation, which can act as a filter to the runoff of terrestrial nutrients to the river.

#### **Biological material**

The fish used on the study were donated to the Laboratório de Limnologia do Departamento de Biologia, Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Universidade de São Paulo, by the company JGP Consultoria e Participações LTDA. The samplings were obtained during a monitoring program of the Rio Juruena ichthyofauna. According to the data provided by the donating company, the biological material used in the present study was obtained in samplings

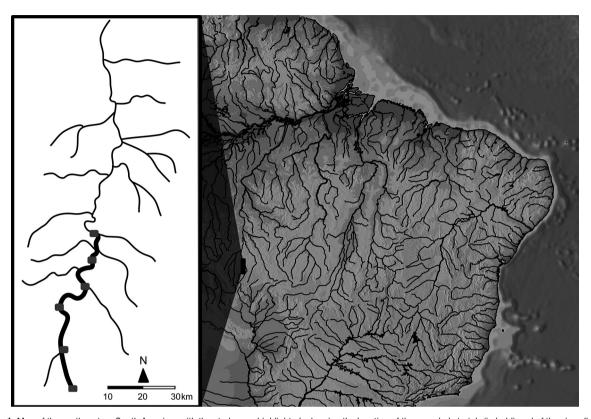


Figure 1. Map of the northeastern South America, with the study area highlighted, showing the location of the sampled stretch (in bold) and of the six collection sites (gray squares) in the upper Rio Juruena, Mato Grosso State, Brazil.

carried out during six days in November 2008, January and August 2009, and April and August 2010. The fish were caught by seine net, 5mm between knots, utilized in the marginal area, and two gill nets, 10m long each one, with 15 and 20mm between adjacent knots, exposed during 24 hours in marginal areas, and inspected every 12 hours. Each sampling methodology was applied at six sites, randomly distributed along a river stretch of 45km, with a minimum distance of 5km between them, covering backwater, rapid and riffle habitats. The specimens were donated in 10% formaldehyde solution, and after the transference to 70% ethanol solution, all individuals were deposited at the Laboratório de Ictiologia de Ribeirão Preto (LIRP) do Departamento de Biologia, Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Universidade de São Paulo, under the identification number LIRP 9659 to 9666 and 11350.

#### **Diet analysis**

The specimens were measured, weighed, and the stomach and gut were removed. The stomach contents of ninety-two individuals, with standard length (SL) from 16.9 to 131.4mm, were evaluated. The repletion index of the stomachs was identified as empty (no items), partially full (0% < to <75%

volume), and full (≥75% volume). To avoid the aggregation of highly digested items, only the content of the anterior half of the stomachs were transferred to a gridded Petri dish and analyzed under the stereomicroscope, where items were identified and quantified. The quantitative evaluation of the content was made according to the subjective method, thus the percentage contribution by volume of each food category to the total contents was estimated by eye (Hyslop 1980). Although arbitrary, the specimens were separated in size classes based on their diets, taking into account shifts in dietary items or their relative contribution. The validity of the diet similarity observed in the size classes established was tested by a detrended correspondence analysis (DCA), which was performed using the software Past 3.01 (Hammer et al. 2001). The establishment of size classes in this study aimed to provide a better understanding of the ontogenetic shifts of Leporinus reticulatus.

#### **Ecomorphological and dentition analysis**

In order to observe and better understand the ontogenetic morphological variations reported by Birindelli and Britski (2009), four specimens (24.0, 39.2, 81.1 and 124.9mm SL) of each size class, defined after the diet analysis, was cleared

and stained (CS), following the method proposed by Taylor and Van Dyke (1985). The specimens were dissected and the buccal apparatus was analyzed. Teeth nomenclature followed Guisande *et al.* (2012).

The ecomorphological evaluation was carried out in 40 specimens, representatives of the four size classes established (N=15; N=4; N=6; and N=15 for the classes 1, 2, 3, and 4, respectively). In order to ensure the accuracy of the measurements, the specimens chosen were those whose fins were not damaged. The measurements, which were taken with a caliper (0.1 mm precision), were used to calculate 11 selected ecomorphological attributes: compression index, relative depth of body, relative caudal peduncle length, caudal peduncle compression index, index of ventral flatness, relative pectoral fin area, aspect ratio of the caudal fin, aspect ratio of the pectoral fin, relative caudal fin area, relative eye position, and relative head length. The method and description of each ecomorphological attribute were minutely reviewed by Freire and Agostinho (2001), Casatti and Castro (2006), and Teixeira and Bennemann (2007).

To verify the possible ecomorphological variation in the ontogenetic development, a discriminant analysis with the analysis of the canonic components (reviewed in Miles *et al.* 1987), was performed using the software Past 3.01 (Hammer *et al.* 2001). Only canonical axes with eigenvalue higher than 1.0 were considered.

#### **RESULTS**

#### Diet analysis

Of the 92 individuals analyzed, 27 had empty stomachs and 65 had stomach with dietary items, of these, eight presented full stomach. The diet of the Leporinus reticulatus was characterized by the consumption mainly of invertebrates and vegetal, represented by ten dietary items (Table 1), besides sandy sediment and detritus. The diet variation along the ontogenetic development is gradual, difficulting the separation of the sample in well-established size classes. However, the observed dietary distribution pattern indicated the existence of four size classes (Figure 2), as follows: class 1 - 16.9 to 34.6mm SL (N = 59); class 2 - 35.8 to 40.8mm SL (N = 4); class 3 - 45.7 to 102.5mm SL (N = 6); class 4 -102.9 to 131.4 mm SL (N = 23). The establishment of these four size classes was reinforced by the DCA analyses (Figure 3). However, the real number of size classes, and their exact limits, are highly dependent of the sampling size, and will not be discussed in this study.

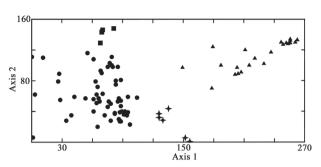
In general, there was a change in the representativeness of invertebrate and vegetal items along the ontogenetic development (Table 1). The abundance of items of vegetal origin, such as filamentous algae, pieces of macrophyte

**Table 1.** Average relative abundance of the food items for each size class of the species *Leporinus reticulatus*.

Food Items		Size Classes			
		2	3	4	
Chironomidae	16.3	18.5	2.7	8.2	
Trichoptera	4.0	5.5	32.5	3.6	
Ephemeroptera	0.0	0.0	1.8	8.0	
Cladocera	4.5	2.3	0.0	0.0	
Nematoda	4.2	3.8	8.0	1.1	
Invertebrate remains	53.8	49.3	30.3	17.3	
Rhizopodea - shelled ameba	4.0	0.0	0.0	0.0	
Filamentous algae	8.0	0.0	12.3	7.3	
Plant fragments, macrophyte roots and seeds	1.9	0.5	7.8	5.5	
Soybean seeds	0.0	0.0	0.0	44.5	
Sandy sediment and detritus	10.5	20.1	11.8	11.7	



**Figure 2.** Representatives of the size classes of *Leporinus reticulatus*: A - class 1; B - class 2; C - class 3; D - class 4. White bars are scales of 10mm. This figure is color in the electronic version.



**Figure 3.** Detrended component analysis of the dietary items of *Leporinus reticulatus*. Dots - size class 1; squares - size class 2; stars - size class 3; and triangles - size class 4.

roots and plant fragments, increased in the diet along the ontogenetic development, while the abundance of items of invertebrate origin, such as chironomid, cladocerans, nematodes and shelled amebas decreased.

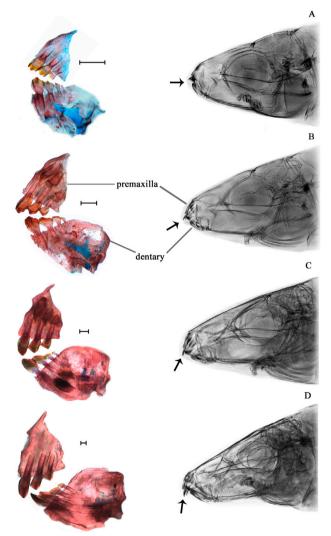
The diet differentiation between size classes 1 and 2 and size classes 3 and 4 was highlighted mainly by the high consumption of chironomid, cladocerans and nematodes by the first two size classes, besides the insignificant consumption of vegetal items (Table 1). The diet of size class 1 was characterized by the higher consumption of cladocerans, nematodes and shelled ameba; this last item was absent in the other three size classes, and the main difference in the diet between the size classes 1 and 2. In the size class 3, although the higher contribution of Trichoptera, it was observed the significant inclusion of vegetal items in the diet, but only in the size class 4 there was a significant decrease of invertebrate consumption and the inclusion of soybean seeds in the diet.

#### **Dentition analysis**

All specimens presented the following combination of teeth: a single row of four teeth in each dentary bone, and a single row with three teeth in each premaxillary bone, both teeth rows decreasing gradually in size to the posterior direction. The dentary teeth are very close to each other, with low overlap some times, forming a continuous cutting edge. The maxilla are toothless.

This *Leporinus* species presented a gradual ontogenetic modification in tooth shape and mouth positioning. In specimens of size class 1 (Figure 4a), teeth are tricuspid, with prominent cusps and the central cusp larger than the lateral ones; the mouth is terminal; the premaxillary teeth are positioned diagonally in an antero-ventral direction, at an angle of approximately 45° in relation to a dorsi-ventral body axis; the dentary teeth are parallel to this same axis, positioned in a dorsal direction. In specimens of the class 2 (Figure 4b), a partial fusion of the two-anteriormost dentary teeth cusps and of the two-posteriormost premaxillary teeth cusps are observed; the mouth is subterminal; the premaxillary teeth

are positioned diagonally in an antero-ventral direction, at an angle of approximately 30° in relation to a dorsi-ventral body axis; the dentary teeth are positioned diagonally in an anterodorsal direction, at an angle of approximately 45° in relation to a dorsi-ventral body axis. In specimens of the class 3 (Figure 4c), the teeth cusps are almost totally fused, with a residual lateral cusp present in premaxillary teeth; the mouth is almost inferior; the premaxillary teeth are positioned diagonally in an antero-ventral direction, at an angle of approximately 15° in relation to a dorsi-ventral body axis; the dentary teeth are positioned diagonally in an antero-dorsal direction, at an angle of approximately 60° in relation to a dorsi-ventral body



**Figure 4.** Radiography of the cranial region (right figures) and images of the CS dentary and premaxillary bones (left figures) of a representative of each *Leporinus reticulatus* size class: A - class 1, B - class 2, C - class 3 and D - class 4. Black bars are scales of 0.4mm. Arrows indicate the mouth orientation in relation to an antero-posterior axis of the body. This figure is color in the electronic version .

axis. In the specimens from class 4 (Figure 4d), teeth cusps are totally fused, the teeth are in spatula shape with a single cutting edge; the mouth is inferior; the premaxillary teeth are positioned parallel, in ventral direction, in relation to a dorsiventral body axis; the dentary teeth are positioned diagonally in an antero-dorsal direction, at an angle of approximately 70° in relation to a dorsi-ventral body axis. The modifications reported to the teeth morphology were also observed in the replacement teeth, corroborating the idea of an ontogenetic modification and discarding the possibility of modification due only to the wear over the life of the specimen.

#### **Ecomorphology**

The discriminant analysis performed with the ecomorphological attributes obtained revealed a significant differentiation between the four size classes (Wilks' lambda = 0.054, p<0.01). The analysis of canonic components produced three axes (Table 2), and the first two, that together represent 93.7 % of all variation, were used to create a dispersion graph of the individual scores (Figure 5), in which can be observed the ecomorphological differentiation among the size classes. The most evident differentiation is of the size class 4 in relation to the first two size classes, performed by the first axis (Figure 5). The variables with higher participation in the first axis were compression index, relative depth, and aspect ratio of caudal fin. Another differentiation observed is between the first two size classes, performed by the second axis (Figure 5), with the relative area of the pectoral fin and the aspect ratio of the pectoral fin having a higher participation (Table 2). The class 3 occupied an intermediate position in relation to the other groups, indicating that the ecomorphological alterations are gradual and continuous along the ontogeny. This ontogenetic variation, observed in the ecomorphological attributes of *L*. reticulatus, corroborates the size class determination based on the diet analysis.

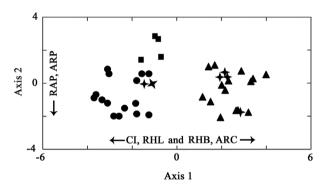
#### DISCUSSION

The presence of animal and vegetal sources in the diet of *Leporinus reticulatus* indicates its omnivory, as suggested by Goulding (1980) for the genus, agreeing with studies on other *Leporinus* species (Hahn *et al.* 1998; Albrechet and Pellegrini-Caramaschi 2003; Montenegro *et al.* 2010). However, trends to herbivory and invertivory are also reported (Balassa *et al.* 2004; Melo and Röpke 2004; Mendonça *et al.* 2004). Representatives of Anostomidae are generalists (Goulding 1980); their dietary plasticity and opportunism are evidenced by the consumption of soybean seeds by *L. reticulatus* in the Juruena River, an item that was introduced in the aquatic environment by anthropic actions.

The feeding habits of *Leporinus* are generally related to the bottom (Albrecht and Pellegrini-Caramaschi 2003; Mendonça

**Table 2.** Standardized coefficients for canonical variables analyzed. In bold, scores with greater contribution to the formation of the axes.

Variables	Canonical Variables			
Valiables	Axis 1	Axis 2	Axis 3	
Compression index	-1.10	-0.31	0.03	
Relative height of the body	1.01	0.12	0.05	
Relative length of the caudal peduncle	0.04	0.27	-0.64	
Compression index of the caudal peduncle	-0.23	-0.37	-0.25	
Index of ventral flattening	0.30	0.08	0.44	
Relative area of the pectoral fin	0.05	-1.11	-0.61	
Aspect ratio of the caudal fin	0.52	0.12	-0.17	
Aspect ratio of the pectoral fin	0.02	-0.69	-0.52	
Relative area of the caudal fin	-0.05	0.09	-0.10	
Eye position	0.34	-0.41	0.37	
Relative head length	-0.51	0.12	0.53	
Percent of the total Variation	79.658	14.006	2.471	
Eigenvalue	12.753	2.241	1.001	



**Figure 5.** Score graphic of the first two axes produced by the analysis of canonic components of the ecomorphological attributes calculated to the specimens representatives of the four size classes of *Leporinus reticulatus*. CI (Compression index), RHB (Relative height of the body), RAP (Relative area of the pectoral fin), ARC (Aspect ratio of the caudal fin), ARP (Aspect ratio of the pectoral fin), and RHL (Relative head length), are the variables with higher participation in the variation explained by the respective axis (Table 2). Dots - size class 1; squares - size class 2; stars - size class 3; and triangles - size class 4.

et al. 2004; Montenegro et al. 2010), and L. reticulatus is no exception to this observation. Dietary items, such as chironomids and caddisflies, nematodes, shelled amebas, benthic cladocerans, filamentous algae, and the presence of sediment in the stomachs point to its behavior of catching food at the bottom. According to in situ observations by Sazima (1986), L. lacustris is a nibbler that explores the substrate for picking up small items, or for biting larger ones. The presence of sediment in the stomach contents of L. reticulatus

indicates that there is no food selection in the oral cavity and a mechanism for eliminating inorganic particles by the gill rakers, known for other benthivores (Fugi *et al.* 2007).

Despite the fact that contributions from allochthonous sources are essential for sustaining the trophic levels in rivers, particularly in the upper reaches (Allan and Castillo 2007), there is a higher contribution of autochthonous resources in the diet of *L. reticulatus*. Autochthonous resources for fish species of lower trophic levels can encompass autotrophs, such as macrophytes and benthic algae, and benthic heterotrophs, mostly dominated by immature insects, associated to the sediment, as observed for this species. The ingestion of animal items can be related to their higher abundance in the environment, pointing to the predominance of a generalist feeding habit (Lowe-McConnell 1999).

The lower contribution of vegetal items, in relation to the animal items, observed in smaller specimens of *L. reticulatus* (mainly size classes 1 and 2; presumably composed by young specimens), could be related to the higher protein requirement by young fish specimens (Vitule *et al.* 2008). Older specimens are able to use more indigestible and low proteic items, as observed by the higher contribution of vegetal items in the diet of the larger *L. reticulatus* specimens (mainly size class 4; presumably composed by adult specimens). The increased exploitation of vegetal resources by the adults has been reported as frequent in other tropical freshwater fish species (Silva *et al.* 2007; Vitule *et al.* 2008; Mazzoni *et al.* 2010), including *L. taeniatus* (Alvim 1999), the only species of *Leporinus* where the ontogenetic variation of the diet has been already studied.

In addition to the ontogenetic variation of the diet of *L. reticulatus*, ontogenetic alterations of teeth morphology were noticed, which have been also reported in other fish species (Castro *et al.* 2004). The teeth morphology characterized by evident cusps is related to a predominant predation on invertebrates (Mohsin 1962), as observed in the size classes 1 and 2 of *L. reticulatus*. The less developed cusps are typical of omnivores and herbivores (Mohsin 1962), in accordance with the teeth morphology and the feeding habits of larger specimens of *L. reticulatus*.

The ingestion of smaller items, such as caddisflies, chironomids, and nematodes, by the larger specimens of *L. reticulatus* indicates that they do not select items by size, evidencing their opportunistic feeding behavior. The adaptive response of riverine fish to an environment subjected to disturbances and fluctuating resources, as the upper reaches of rivers, can be to enhance their food spectrum, reducing specializations and increasing the opportunistic feeding behavior (Lowe-McConnell 1999).

Low values of the relative body height and lower body compression, observed in all size classes of *L. reticulatus*,

would indicate the ability to occupy high hydrodynamic environments (Gatz 1979, Watson and Balon 1984), probably a requirement for their survival in the riffled stretch of the Rio Juruena. A higher height compression of the body reduces the ability for performing vertical displacements, and a high relative position of the eye indicates a benthic occupation (Gatz 1979), attributes more evident in smaller specimens of L. reticulatus, which presented a high composition of benthic resources (as Chironomidae larvae) in the diet. Therefore, smaller individuals are more efficient for exploring the substrate, whereas the larger ones, with lower body compression, have the additional skill of moving in the water column, exploring different habitats, which reflected in the greater diversity of dietary items, observed in larger specimens of L. reticulatus. Low values for the aspect ratio of the caudal fin point to less active and efficient swimmers (Gatz 1979). Regarding this attribute, larger specimens of L. reticulatus are more active and efficient than smaller ones. The increase of the ability for swimming and vertical displacements along the ontogenetic development, allows searching for resources in other microhabitats (Barreto 2005). The ability of larger L. reticulatus in widening the environmental exploration may end in a partial habitat segregation and lower food overlap between early and late stages.

In conclusion, *L. reticulatus* is an omnivorous species that explores mainly benthic habitats. Along its ontogenetic development, this species undergoes a series of morphological alterations, culminating in the ability to explore a wider range of niches in the Rio Juruena. Besides, there is a gradual variation in the diet along its ontogenetic development, in which smaller specimens (presumably younger ones) explores mainly invertebrates, with significant addition of vegetal items by larger specimens (older ones). These aspects seem to be important in the Rio Juruena, an oligotrophic river, since they decrease food and habitat overlap between different ontogenetic stages, lowering the population impact of a potential intraspecific competition.

#### **ACKNOWLEDGEMENTS**

We are grateful to JGP Consultoria e Participações LTDA for the donation of the biological material. We thank the Fundação de Amparo à Pesquisa do Estado de São Paulo for financial support (processes nº 4/09219-6, and 09/54931-0). MME was supported by the Conselho Nacional Desenvolvimento Científico e Tecnológico (CNPq). ALHE was financed by the National Program of Post Doctoral from Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (PNPD/CAPES; process nº 23038.008118/2010-34). TNAP was supported by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES)

#### REFERENCES

- Abelha, M.C.F.; Agostinho, A.A.; Goulart, E. 2001. Plasticidade trófica em peixes de água doce. *Acta Scientiarum*, 23:425-434.
- Agostinho, A.A.; Gomes, L.C.; Pelicice, F.M. 2007. Ecologia e Manejo de Recursos Pesqueiros em Reservatórios do Brasil. EDUEM, Maringá, 501p.
- Albrechet, M.P.; Pellegrini-Caramaschi, E. 2003. Feeding ecology of *Leporinus taeniofasciatus* (Characiformes: Anostomidae) before and after installation of a hydroelectric plant in the upper Rio Tocantins, Brazil. *Neotropical Ichthyology*. 1:53-60.
- Allan, J.D.; Castillo, M.M. 2007. Stream Ecology: structure and function of running waters. 2nd ed. Springer, Dordrecht, 444p.
- Alvim, M.C.C. 1999. Composição e alimentação da ictiofauna em um trecho do alto rio São Francisco, Município de Três Marias – MG. Dissertação de Mestrado, Centro de Ciências Biológicas e da Saúde/ Universidade Federal de São Carlos, São Carlos, São Paulo. 98p.
- ANEEL, 2015. Informações Técnicas, (http://www.aneel.gov.br/). Accessed on 7/02/2015.
- Balassa, G.C.; Fugi, R.; Hahn, N.S.; Galina, A.B. 2004. Dieta de espécies de Anostomidae (Teleostei, Characiformes) na área de influência do reservatório de Manso, Mato Grosso, Brasil. *Iheringia Serie Zoologia*, 94:77-82.
- Barreto, A.P. 2005. Características ecomorfológicas relacionadas à alimentação e ao uso do micro-hábitat em quatro espécies de Characiformes no Rio Morato Guaraqueçaba, PR. Tese de Doutorado, Centro de Ciências Biológicas e da Saúde/ Universidade Federal de São Carlos, São Carlos, São Paulo. 109p.
- Birindelli, J.L.O.; Britski, H.A. 2009. New species of the genus Leporinus Agassiz (Characiformes: Anostomidae) from the Rio Curuá, rio Xingu basin, Serra do Cachimbo, Brazil, with comments on Leporinus reticulatus. Neotropical Ichthyology, 7: 1-10.
- Britski, H.A.; Garavello, J.C. 1993. Descrição de duas espécies novas de *Leporinus* da bacia do Tapajós (Pisces, Characiformes). *Comunicações do Museu* de *Ciências e Tecnologia da PUCRS*, *Serie Zoologia*, 6: 29-40.
- Casatti, L.; Castro, R. 2006. Testing the ecomorphological hypothesis in a headwater riffles fish assemblage of the Rio S\u00e1o Francisco, southeastern Brazil. Neotropical Ichthyology, 4: 203-214.
- Castro, R.M.C.; Vari, R.P.; Oliveira, C. 2004. Phylogenetic analysis and redescription of the genus *Henochilus* (Characiformes: Characidae). *Copeia* 3: 496-506.
- Eschmeyer, W. N. Catalog of Fishes: Genera, Species, References, (http://research. calacademy.org/research/ichthyology/catalog/fishcatmain.asp). Accessed on 7/02/2015.
- Freire, A.G.; Agostinho, A.A. 2001. Ecomorfologia de oito espécies dominantes da ictiofauna do Reservatório de Itaipu (Paraná, Brasil). *Acta Limnologica Brasiliensia*, 13: 1-9.
- Fugi, R.; Agostinho, A.A.; Hahn, N.S. 2001. Trophic morphology of five benthic-feeding fish species of a tropical floodplain. *Brazilian Journal of Biology*, 61: 27-33.
- Fugi, R.; Hahn, N.S.; Novakowski, G.C.; Balassa, G.C. 2007. Ecologia alimentar da corvina, *Pachyurus bonariensis* (Perciformes, Sciaenidae) em duas baías do Pantanal, Mato Grosso, Brasil. *Iheringia Série Zoologia*, 97: 343-347.

- Garavello, J.C.; Britski, H.A. 2003. Family Anostomidae. In: Reis, R.E.; Kullander, S.O.; Ferraris Jr, C.F. (Ed.). Check List of the Freshwater Fishes of South and Central America. EDPUCRS, Porto Alegre, Rio Grande do Sul, p.71-86.
- Gatz J.R., A.J. 1979. Ecological morphology of freshwater stream fishes. *Tulane Studies in Zoology and Botany*, 21: 90-124.
- Goulding, M. 1980. The fishes and the forest: explorations in Amazonian natural history. University of California Press, Berkeley, 280p.
- Guisande, C.; Pelayo-Villamil, P.; Vera, M.; Manjarrés-Hernández, A.; Carvalho, M.R.; et al. 2012. Ecological factors and diversification among Neotropical characiforms. *International Journal of Ecology*, 2012: 1-20.
- Hahn, N.S.; Agostinho, A.A.; Gomes, L.C.; Bini, L.M. 1998. Estrutura trófica da ictiofauna do reservatório de Itaipu (Paraná-Brasil) nos primeiros anos de sua formação. *Interciencia*, 23: 299-305.
- Hammer, O.; Harper, D.A.T.; Ryan, P.D. 2001. PAST: Paleontological statistics software package for education and data analysis. *Palaeontologia Electronica*, 4: http://palaeo-electronica.org/2001\_1/past/issue1\_01.htm
- Hyslop, E.J. 1980. Stomach contents analysis a review of methods and their application. *Journal of Fish Biology*, 17: 411-429.
- Lowe-Mcconnell, R.H. 1999. Estudos Ecológicos de Comunidades de Peixes Tropicais. EDUSP, São Paulo, 584p.
- Luz, K.D.G.; Abujamra, F.; Agostinho, A.A.; Gomes, L.C. 2001.
  Caracterização trófica da ictiofauna de três lagoas da planície aluvial do alto rio Paraná, Brasil. *Acta Scientiarum*, 23: 401-407.
- Mazzoni, R.; Nery, L.L.; Iglesias-Rios, R. 2010. Ecologia e ontogenia da alimentação de *Astyanax janeiroensis* (Osteichthyes, Characidae) de um riacho costeiro do Sudeste do Brasil. *Biota Neotropica*, 10: 53-60.
- Melo, E.C.; Röpke, C.P. 2004. Alimentação e distribuição de piaus (Pisces, Anostomidae) na Planície do Bananal, Mato Grosso, Brasil. *Revista Brasileira de Zoologia*, 21: 51-56.
- Mendonça, F.P.; Hahn, N.S.; Loureiro-Crippa, V.E. 2004. Feeding aspects of *Leporinus amblyrhynchus* (Characiformes: Anostomidae) in the first stages of formation of a Neotropical reservoir, Brazil. *Neotropical Ichthyology*, 2: 145-150.
- Miles, D.B.; Ricklefs, R.E.; Travis, J. 1987. Concordance of ecomorphological relationships in three assemblages of passerine birds. *American Naturalist*, 129: 347-364.
- Mohsin, S.M. 1962. Comparative morphology and histology of the alimentary canals in certain groups of Indian teleosts. *Acta Zoologica*, 43: 79-133.
- Montenegro, A.K.A.; Torelli, J.E.R.; Marinho, R.S.A.; Crispim, M.C.; Hernandez, M.I.M. 2010. Aspects of the feeding and population structure of *Leporinus piau* Fowler, 1941 (Actinopterygii, Characiformes, Anostomidae) of Taperoá II Dam, semi-arid region of Paraíba, Brazil. *Biotemas*, 23: 101-110.
- Peres-Neto, P.R. 1999. Alguns métodos e estudos em ecomorfologia de peixes de riachos. *Oecologia Brasiliensis*, 6: 209-236.
- Santos, G.; Jégu, M.; Lima, A.C. 1996. Novas ocorrências de Leporinus pachycheilus Britski, 1976 e descrição de uma espécie

Diet and ecomorphology of *Leporinus reticulatus* (Characiformes: Anostomidae) from the upper Rio Juruena, MT, Brazil: ontogenetic shifts related to the feeding ecology

- nova do mesmo grupo na Amazônia Brasileira (Osteichthyes, Anostomidae). *Acta Amazonica*, 26, 265-280.
- Sazima, I. 1986. Similarities in feeding behaviour between some marine and freshwater fishes in two tropical communities. *Journal of Fish Biology*, 29: 53-65.
- Silva, E.L.; Fugi, R.; Hahn, N.S. 2007. Variações temporais e ontogenéticas na dieta de um peixe onívoro em ambiente impactado (reservatório) e em ambiente natural (baía) da bacia do rio Cuiabá. *Acta Scientiarum*, 29: 387-394.
- Taylor, W.R.; Van Dyke, G.C. 1985. Revised procedures for staining and clearing small fishes and other vertebrates for bone and cartilage study. *Cybium*, 9: 107-119.
- Teixeira, I.; Bennemann, S.T. 2007. Ecomorfologia refletindo a dieta dos peixes em um reservatório no sul do Brasil. *Biota Neotropica*, 7: 67-76.

- Vitule, J.R.S.; Aranha, M.R. 2002. Ecologia alimentar do lambari, Deuterodon langei Travassos, 1957 (Characidae, Tetragonopterinae), de diferentes tamanhos em um riacho da Floresta Atlântica, Paraná (Brasil). Acta Biológica Paranaense, 31: 137-150.
- Vitule, J.R.S.; Braga, M.R.; Aranha, J.M.R. 2008. Ontogenetic, spatial and temporal variations in the feeding ecology of *Deuterodon langei* Travassos, 1957 (Teleostei: Characidae) in a Neotropical stream from the Atlantic rainforest, southern Brazil. *Neotropical Ichthyology*. 6: 211-222.
- Watson, D.J.; Balon, E.K. 1984. Ecomorphological analysis of fish taxocenes in rainforest streams of northern Borneo. *Journal of Fish Biology*, 25: 371-384.
- Wootton, R. 1998. *Ecology of teleost fishes*. 2nd ed. Kluwer Academic Publishers, London, 386p.

Recebido em 20/02/2015 Aceito em 22/04/2015