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Ecomorphology and diet reflect the spatial segregation between two Siluriformes species inhabiting a stream of the Bodoquena Plateau, in Central Brazil

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ABSTRACT. *Pimelodella taenioptera* Miranda Ribeiro, 1914 and *Imparfinis schubarti* (Gomes, 1956) are two of the most common fish species in Bodoquena Plateau streams, Paraguay basin. These species have benthic habits and subaquatical observations suggested that they present differentiation in their preference for mesohabitat types. *Pimelodella taenioptera* shows preference for slow waters, such as pools, while *I. schubarti* is associated to riffles. In this study we investigated if the known patterns of mesohabitat use of *P. taenioptera* and *I. schubarti* can be predict by their ecomorphological and trophic traits. We described the dietary habits and ecomorphological attributes of *P. taenioptera* and *I. schubarti* individuals, captured in the Parque Nacional da Serra da Bodoquena (PNSB), Mato Grosso do Sul state, central Brazil. *Pimelodella taenioptera* presented a more generalist diet, consuming a total of 23 different food items. *Imparfinis schubarti* have a diet based exclusively on aquatic insects. The ecomorphological analysis revealed that the species differed in relation to five morphological traits associated to habitat use ($p < 0.01$). The results of this study reveal a clear functional dissimilarity between *P. taenioptera* and *I. shubarti*. The observed trophic and ecomorphological patterns are congruent with the known habitat use for these species and probably reflect the spatial and temporal variability on conditions and resources present in riffles and pools. Therefore, as expected, the morphological and feeding attributes represent predictive information related to mesohabitat use.

KEYWORDS. *Pimelodella*, *Imparfinis*, ecomorphogical traits, mesohabitats, trophic ecology.

RESUMO. Ecomorfologia e dieta refletem a segregação entre duas espécies de Siluriformes que habitam um córrego do Planalto da Bodoquena, no Brasil Central. *Pimelodella taenioptera* Miranda Ribeiro, 1914 e *Imparfinis schubarti* (Gomes, 1956) estão entre as espécies de peixe mais comuns nos riachos do Planalto da Bodoquena, bacia do rio Paraguai. Estas espécies compartilham hábito bentônico, entretanto observações subaquáticas sugerem que estas espécies apresentam diferenças na preferência por tipos de mesohábitats. *Pimelodella taenioptera* apresenta preferência por habitats lênticos, tais como poços, enquanto *I. schubarti* é associado a corredeiras. Neste estudo, investigamos se os padrões conhecidos de uso de mesohábitats de *P. taenioptera* e *I. schubarti* predizem suas características ecomorfológicas e tróficas. Descrevemos os hábitos alimentares e os atributos ecomorfológicos de indivíduos de *P. taenioptera* e *I. schubarti*, capturados no Parque Nacional da Serra da Bodoquena (PNSB), Estado do Mato Grosso do Sul, Brasil Central. *Pimelodella taenioptera* apresentou dieta mais generalista, consumindo um total de 23 itens alimentares. *Imparfinis schubarti* apresentou dieta exclusivamente composta por insetos aquáticos. A dieta de *P. taenioptera* foi mais variável na estação chuvosa do que na estação seca ($p=0,05$) e foi significativamente mais variável do que a dieta de *I. schubarti* ($p<0,01$). A variabilidade na composição da dieta entre indivíduos de *I. schubarti* não diferiu entre as estações ($p=0,48$). As análises ecomorfológicas revelaram que as espécies diferiram em relação a cinco traços morfológicos associados ao uso do hábitat ($p < 0,01$). Os resultados obtidos neste estudo revelam uma clara diferenciação funcional entre *P. taenioptera* e *I. shubarti*. Os padrões tróficos ecomorfológicos observados são compatíveis com o uso de habitat conhecido para essas espécies e, provavelmente, reflete a variabilidade espacial e temporal nas condições e recursos presentes em corredeiras e poços. Dessa forma, conforme esperado, os atributos morfológicos e tróficos representam informações com poder preditivo relacionadas ao uso de meso-hábitat.

PALAVRAS-CHAVE. *Pimelodella*, *Imparfinis*, traços ecomorfológicos, meso-hábitats, ecologia trófica.

Streams are complex environments represented by a mosaic of physical, chemical and biological conditions (Frissel *et al.*, 1986). Geomorphological and hydrological characteristics of streams are important to determine environmental heterogeneity and habitat availability for aquatic biota (Gorman & Karr, 1978). Accumulated evidence indicates that fish distribution across habitats is not random; instead, the fish-habitat relationship is mediated by functional traits (Poff, 1997; Teresa & Casatti, 2012; Pease *et al.*, 2012). This biological determinism takes its roots in evidence of ecological and evolutionary processes that explain contemporary patterns of species distribution.

A number of studies have shown that morphological traits of fish correlate with ecological aspects of the species (Casatti & Castro, 2006; Oliveira *et al.*, 2010). This relationship is the basis of ecomorphology (Peres-Neto, 1999), and it provides support for the use of morphology as a surrogate of functional traits (Pease *et al.*, 2012). For example, morphology has been associated with swimming performance, habitat use, reproductive behavior and foraging (Watson & Balon, 1984; Wootton, 1998).

According to the habitat filtering hypothesis, species occurring locally are those that present the traits needed to deal to environmental restrictions, or filters (Poff, 1997). Therefore, morphologically different species would be expected to occur in environmentally distinct habitats that are subject to the effects of different filters. In addition, ecomorphological differences between sympatric and phylogenetically related species would favor coexistence through differential use of resources (Wootton, 1998).

An alternative way to analyze the use of habitat by different species is through details of their feeding habits. Species that feed on detritus would be more related to benthic habitats, as well as those that feed primarily on items that fall into the water, such as allochthonous insects and fruits which would be more related to the surface. In addition, the variation in feeding habits of fish can be partially attributed to changes in the volume of water and turbidity, as well as the input of allochthonous material within streams across seasons (Payne, 1986). Besides the predictive value of feeding habits on habitat use at microhabitat scale, some patterns may also be identified across broader scales. For example, some studies have suggested that riffles are usually associated with low spatial and temporal variability in food availability (Angermeier & Schlosser, 1989; Teresa & Casatti, 2012), while pools have more variable alimentary items available (Angermeier & Karr, 1984; Berkman & Rabeni, 1987). These aspects could be reflected in the trophic structure of the assemblages, as we could expect that pool-dwelling fish species would have a higher spatial and temporal variation in the diet than riffle-dwelling species.

This study was conducted in Bodoquena Plateau, Mato Grosso do Sul, an important area where the headwaters of the most important rivers draining into the Pantanal are located (Behr, 2001). The fish fauna of this region is considered very particular, with several endemic forms and a high diversity when compared with other areas of the headwaters (Willink *et al.*, 2000). Subaquatical observations in the region suggested that two morphologically similar catfish species, *Pimelodella taenioptera* Miranda Ribeiro, 1914 and *Imparfinis schubarti* (Gomes, 1956), have spatial segregation, with *P. taenioptera* occurring mainly in pools and *I. schubarti* being most commonly found in riffles. In view of this, our aim was to investigate if the ecomorphological and trophic patterns of *P. taenioptera* and *I. schubarti* corroborate the known patterns of mesohabitat use for these species, considering the influences of seasonality. More specifically, we asked 1) if the ecomorphology of *P. taenioptera and I. schubarti* is predictive of their spatial segregation and, if so, which ecomorphological attributes would best explain the differences between these species; 2) if the diet of *P. taenioptera* and *I. schubarti* is predictive of their spatial segregation, and 3) if the diet variability differs within and between species, reflecting the patterns of resources availability expected for the mesohabitats where the species are found. We expect to found differences in the ecomorphology, diet composition and diet variability between *P. taenioptera* and *I. schubarti*, with higher variation in the diet among individuals of the pool-dwelling species, *P. taenioptera*. In relation to seasonality, we expect differences in the diet composition and diet variability between dry and rainy seasons for *P. taenioptera*, but not for *I schubarti*, as the former lives in a more spatially and temporally variable mesohabitat.

MATERIAL AND METHODS

Study area. The study was carried out in the Salobrinha stream located in the Parque Nacional da Serra da Bodoquena (PNSB), state of Mato Grosso do Sul, Central Brazil (Fig. 1). The park is located in the municipalities of Bonito, Bodoquena, Jardim and Porto Murtinho, in the south central part of Mato Grosso do Sul (21°08’02” to 20°38’26”S and 56°48’31” to 56°44’28”W), at the edge of the Pantanal of Nabileque, which is one of the priority areas for conservation of the biodiversity (MMA, 2002). The study site is located in the final stretch of Salobrinha stream, which flows through the PNSB area, where the vegetation is composed mostly of preserved semi-deciduous forest (Damasceno Jr. *et al.*, 2000).

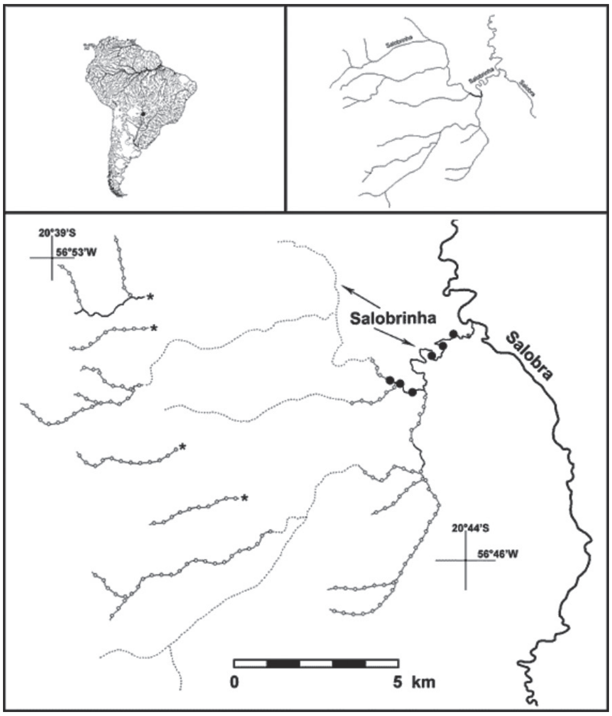

Fig. 1. Maps of the study area (Bodoquena, state of Mato Grosso do Sul, Brazil). On the main map, bottom lines with white circles represent intermittent stretches, dotted lines represent stretches with very ephemeral flow (only flowing during rain), and solid lines show the perennial stretches. Asterisks are sinks. Black circles are sampled sites.

Data sampling. Fish were collected at six sites in the Salobrinha stream, using electrofishing during daytime in the dry (July 2006) and rainy (March 2007) seasons. Specimens were fixed in formalin 10%, and in the laboratory, they were washed, identified and transferred to alcohol 70%.

Feeding. Feeding habits of the species were examined according to analysis of stomach contents from *P. taenioptera* individuals (n = 200) and *I. schubarti* individuals (n = 60). Fragments of leaves, fruits or other parts of higher plants were classified as plant matter, while insects or other invertebrates were identified to the lowest taxonomic level possible with the help of specialized literature (Borror & DeLong, 1988; Costa *et al.*, 2006). Once identified, the items were described as being allochthonous or autochthonous. The volume of items was calculated by the volumetric method (Hyslop, 1980), compressing the material with glass slides to a height of 1 mm on a plate in millimeters (Hellawell & Abel, 1971) and then converting the value to volume (1 mm³ = 0.001 ml).

Food items were grouped into broad food categories and then grouped according to their origin. Allochthonous resources included terrestrial insects (TIN), terrestrial invertebrates (TIV) (invertebrates other than insects) and terrestrial plants (TPL). Autochthonous resources included aquatic insects (AIN), aquatic invertebrates (AIV), fish (FIS) and algae (ALG). Detritus and sediment (DET) were considered of mixed origin.

Ecomorphology. For the analysis of ecomorphology, 15 morphological measures were taken from 38 individuals of *I. schubarti* and 50 individuals of *P. taenioptera*. Only adults were used to avoid allometric changes during ontogeny (Gatz, 1979a). The measures were obtained from Gatz (1979a), Watson & Balon (1984), Winemiller (1991) and Pouilly *et al.* (2003), and they were taken with the aid of a digital caliper with 0.01mm accuracy. Fins areas were taken in mm² from contour drawn on graph paper. Measurements were then applied to 12 ecomorphological traits (Tab. I) that represent aspects of habitat use and trophic ecology (Casatti & Castro, 2006; Oliveira *et al.*, 2010). Voucher specimens of *P. taenioptera* and *I. schubarti* were deposited in the Zoological Collection of the Universidade Federal de Mato Grosso do Sul (ZUFMS-PIS 2100, ZUFMS-PIS 2101).

Data analysis. To identify multivariate patterns in the feeding of the species, an exploratory ordination technique (NMDS - nonmetric multidimensional scaling analysis) was employed using the volume data for each food item. This analysis was followed by ANOSIM using the Bray-Curtis dissimilarity coefficient to test the null hypothesis that no differences exist in the diet between and within species across seasons (Clarke & Gorley, 2006).

In order to evaluate the between- and within-species diet variability, we calculated the multivariate dispersion in the diet of individuals by using the ‘betadisper’ function in the Vegan library in R. We compared the variability of the diet between species by pooling data from different seasons and between seasons within each species using the permutation test (‘permutest’ function).

Tab. I. Attributes used in the ecomorphological analysis with the corresponding measures taken and resulting ecological explanation.

Ecomorphological attribute	Measures taken	Ecological explanation
Compression Index (CI)	Body height divided by width	Higher values indicate laterally compressed fish that are inhabitants of slower waters (Gatz, 1979a)
Index of ventral flattening (IVA)	Height of the body below the imaginary midline divided by height	Lower values represent inhabitants of fast waters, allowing benthic individuals to maintain their position at the bottom without swimming (Hora, 1930)
Relative height of the body (RHB)	Body height divided by standard length	Inversely related to the speed of the animal and directly related to its ability to make vertical spins (Gatz, 1979a)
Relative length of caudal peduncle (RLCP)	Length of caudal peduncle divided by the standard length	Long peduncles indicate good swimmers with good resistance to sites with higher turbulence (Watson & Balon, 1984)
Compression index of caudal peduncle (CICP)	Height of caudal peduncle divided by its width	More compressed peduncles indicate fish with lower speed (Gatz, 1979b)
Relative area of pectoral fin (RaPF)	Area of pectoral fin divided by body surface area	High values are found in slower individuals who use fins for breaking and maneuvers, or in individuals who inhabit waters with greater flow, using the fins as current deflectors in order to remain close to the bottom (Watson & Balon, 1984)
Configuration of pectoral fin (CPF)	Ratio between length and width of pectoral fin	High values are common to fish that travel long distances (Mahon, 1984)
Relative area of caudal fin (RaCF)	Caudal fin area divided by body area	Caudal fins with larger relative areas are important for acceleration (Webb, 1977)
Configuration of the caudal fin (CCF)	Ratio of the square of the height of the caudal fin by its area	High values indicate active and continuous swimmers (Gatz, 1979a)
Relative length of the head (RLH)	Head length divided by standard length	Relative to the size of prey consumed. High values may indicate fish that feed on relatively larger prey (Gatz, 1979a).
Relative width of the mouth (RWM)	Mouth width divided by standard length	Relative to the size of prey consumed. High values may indicate fish that feed on relatively larger prey (Gatz, 1979a).
Relative height of the mouth (RHM)	Height of the mouth divided by standard length	Relative to the size of prey consumed. High values may indicate fish that feed on relatively larger prey (Gatz, 1979a)

We described ecomorphological variation within and between species through the principal component analysis (PCA) on a correlation matrix of ecomorphological traits. Significant PCA axes were identified by the broken-stick model (Jackson, 1993). Complementarily, ecomorphological differences between species were tested by multivariate analysis of variance (MANOVA) and the Pillai-Trace statistic.

RESULTS

Feeding. From the total of individuals analyzed, 43% and 45% of *P. taenioptera* and *I. schubarti* individuals contained some alimentary item in the stomach, respectively. A total of 23 different food items were found in the stomachs of *P. taenioptera* (Tab. II). Autochthonous items had volume corresponding to 89% of the diet. The allochthonous material consisted of adult insects (Curculionidae, Eumastacidae, Blattodea), immature insects (Lepidoptera), and plant matter. During the rainy season, a decrease was noted in the frequency of insects and an increased consumption of fish scales and plant matter (Tab. II). *Imparfinis schubarti* have a diet based on nine food items, all represented by aquatic insects (Tab. II; Fig. 2), with a predominance of Trichoptera (Tab. I).

Ordination analysis with NMDS revealed no tendency toward segregation between species or seasons (ANOSIM, p>0.43) (Fig. 2). The evaluation of the multivariate dispersion of diet between species revealed that the diet of *P. taenioptera* was significantly more variable than that of *I. schubarti* (p<0.01). The evaluation of within-species diet variability showed that *P. taenioptera* individuals exhibited a higher variation in the diet in the rainy season than the dry season (p=0.05). However, the variability in diet composition among individuals of *I. schubarti* did not differ between dry and rainy seasons (p=0.48).

Ecomorphology. The first two axes of the PCA explained 54% of the variance in the ecomorphological data (Fig. 3), with axis 1 accounting for 39.8% of the variation. The first axis segregated the two species, and it was influenced by compression index (CI), relative height of the body (RHB), compression index of the caudal peduncle (CIPC), relative area of pectoral fin (RaPF) and relative area of caudal fin (RaCF) (eigenvectors = 0.80, 0.81, 0.73, -0.91, -0.83 respectively; Fig. 3). The second axis represented intraspecific variation in both species, and it was influenced by index of ventral flattening and relative length of the head. Only axis 1 had broken-stick eigenvalues significantly larger than random. The statistical test showed significant difference between the ecomorphological attributes of both species (Gl = 1, F = 157, p <0.01).

Tab. II. Volume (%) of consumed items by *P. taenioptera* Miranda Ribeiro, 2014 and *I. schubarti* (Gomes, 1956) in the Salobrinha stream, Mato Grosso do Sul, Brazil, in dry and rainy seasons.

Feeding item	*Pimelodella taenioptera*		*Imparfinis schubarti*	
	Dry	Rainy	Dry	Rainy
Autochthonous items				
Coleoptera, Elmidae	19	10	13	16
Coleoptera, Psephenidae	7.7	2.5	7.4	-
Diptera, Simuliidae	-	-	26	-
Diptera, Chironomidae	1.65	-	-	0.7
Ephemeroptera	-	-	2.5	-
Ephemeroptera, Leptophlebiidae	20	32	2.5	18
Hemiptera, Gerridae	-	1	-	-
Hemiptera, Naucoridae	-	2	-	-
Megaloptera, Corydalidae	-	4	-	-
Odonata	2.4	0.8	-	-
Odonata, Lestidae	0.8	-	-	-
Plecoptera, Perlidae	-	-	4.3	-
Trichoptera	9	3	1.2	-
Trichoptera, Calamoceratidae	0.8	-	-	11
Trichoptera, Hydropsychidae	18	10	43	38
Allochthonous items				
Blattodea	0.8	-	-	-
Coleoptera	2	-	-	-
Coleoptera, Curculionidae	0.5	6	-	-
Hymenoptera,Formicidae	0.8	-	-	-
Lepidoptera	-	0.5	-	16
Orthoptera, Eumastacidae	12	-	-	-
Scales	28	6	-	-
Plant matter	4	18	-	-
Mixed origin				
Debris	-	-	-	10

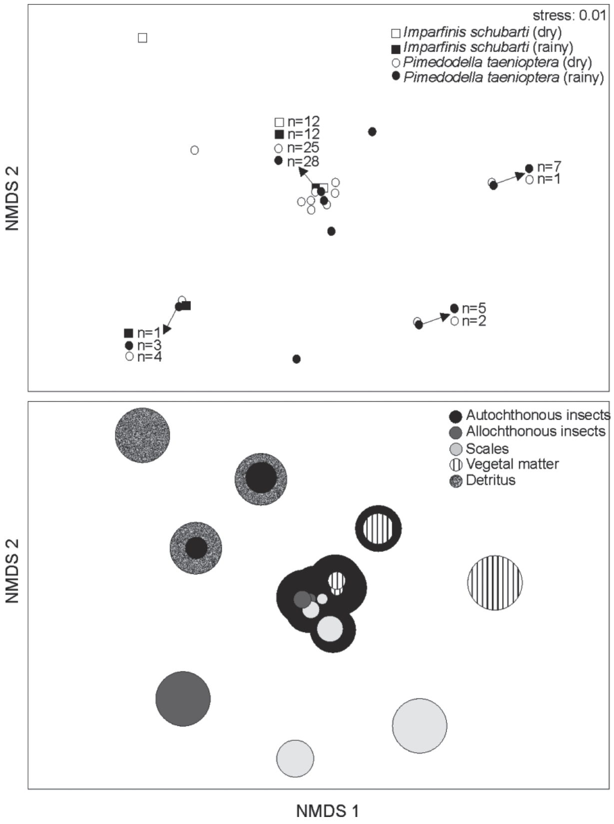

Fig. 2. Bi-dimensional projection of the axes resulting from Non-Metric Multidimensional Scaling analysis (NMDS), showing the ordination of individuals based on the grouped food items consumed (above). The importance of each food item category is expressed by the size of the bubble.

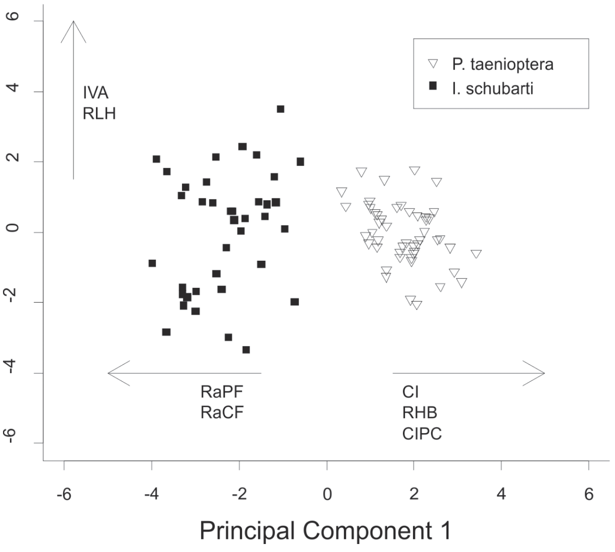

Fig. 3. Dispersion of the scores of the first two PCA axes, calculated with the correlation matrix of 12 ecomorphological attributes. The attributes that most influenced this distribution are shown: IVA, Index of ventral flattening; RLH, Relative length of the head; RaPF, Relative area of pectoral fin; RaCF, Relative area of caudal fin; CI, Compression index; RHB, Relative height of the body; CIPC, Compression index of caudal fin.

DISCUSSION

Knowledge about functional traits exhibited by species in relation to environmental gradients is a basic premise for prediction of species distributions across environmental gradients. In the present study, we described two important groups of functional traits, specifically, diet and ecomorphology, for two representative stream species in the Paraguay basin system. Previously subaquatic observations suggested that the studied species presents spatial segregation, with *Pimelodella taenioptera* occurring preferentially in pools, while *I. schubarti* is associated with riffles. The results of the present study provided support for this pattern and confirm the predictive value of diet and ecomorphology to infer habitat use.

Pimelodella taenioptera had a generalist diet, with the highest frequencies reported for aquatic insects. Terrestrial insects, fish scales and plant material supplemented the diet of this species. It is speculated that scales were captured through substrate since no remnants of fish intake in the analyzed stomach were observed, differing from *Pimelodella pappenheimi* Ahl, 1925 of Atlantic forest which, in addition to insects, also eats fish (ARANHA *et al.*, 1998). A diet generalist, as exhibited by *P. taenioptera*, is compatible with pool-dwelling species which face low current velocity and often rich food resources (ANGERMEIER & KARR, 1983; BÜRHNHEIM, 2002).

The consumption of plant matter registered in this study has already been reported for *Pimelodella* species (VIANA *et al.*, 2006; RONDINELI *et al.*, 2011). However, it is important to note that the largest amount of plant material was consumed in the rainy season. The increased frequency of this item in the feeding of *P. taenioptera* during rainy season is probably a response to a reduction in density of aquatic insects, which are eventually washed away by floods, as ascertained by RIGHI-CAVALLARO *et al.* (2010). Alternatively, plant material increases during the rainy season by the input of plant debris washed into the stream, increasing the availability of this resource and, at the same time, contributing to the increase of variability in the diet of this species during that season. These results are congruent with the temporally variable resources availability reported for pools (ANGERMEIER & KARR, 1983). The opposite patterns have been suggested for riffles, whose environmental conditions and resource availability would be less variable than found in pools (TERESA & CASATTI, 2012).

The diet of *Imparfinis schubarti* consisted exclusively of autochthonous items, differing from the findings of MAZZONI *et al.* (2010) who studied a stream from the upper Tocantins basin (west central Brazil) and especially identified insects of allochthonous origin in the diet of *Imparfinis borodini* Mees & Cala, 1989 and *Imparfinis* **cf.** *schubarti*. However, other studies focusing on other species of *Imparfinis*, as well as *I. schubarti*, have confirmed the results reported here (FERREIRA & CASATTI, 2006; SILVA *et al.*, 2012). In contrast to the patterns observed for *P. taenioptera*, the less variable and strictly insectivorous diet exhibited by the studied riffle-dwelling species corroborates previous findings that have highlighted the dominance of insectivorous species with more specialized habitats in riffles (Casatti & Castro, 1998; Teresa & Casatti, 2012). The fast water velocity and the limited availability of food items present in riffles (Angermeier & Schlosser, 1989) are restrictive conditions which, according to Teresa & Casatti (2012), are successfully explored by two dominant functional groups: benthic-grazers-periphytivorous species, as represented mainly by loricariid species, and benthic-speculators-insectivorous fish, as represented by heptapterid species. Our results are congruent with this generalization, as *I. schubarti* may be considered a typical species of the latter group.

No marked differences were seen in the diet between species. This is evident when food items are grouped into broader food categories. In this case, the diet of *Imparfinis schubarti* is a subset of the *Pimelodella taenioptera* diet, with both showing a diet composed mainly of insects. However, the diet of *P. taenioptera* includes items not represented in the diet of *I. schubarti*, such as plant matter, allochthonous insects and scales. In a more detailed view, the main differences between the species were related to the frequency of consumption of certain insect orders. *Imparfinis schubarti* had a diet with fewer orders of insects and with greater participation, both in frequency and volume, of immature stages of Hydropsychidae (Trichoptera). Furthermore, the occurrence of Simuliidae, but only in the diet of *I. schubarti*, is also an indication of the use of riffles because these insects are immature forms of flies typical of fast waters (Ward, 1992). The highest consumption frequencies in the diet of *P. taenioptera* were, in decreasing order, the insect families Leptophlebiidae (Ephemeroptera), Elmidae (Coleoptera), Chironomidae (Diptera) and Hydropsychidae (Trichoptera). According to Righi-Cavallaro *et al.* (2010), these four families of insects are the most abundant in the community of insects found in the Salobrinha stream, even though chironomids suffer a drastic numerical drop during the rainy season. This reinforces *P. taenioptera* as an opportunist species, possibly feeding on the most common items available.

Based on the ecomorphological aspects, it was possible to differentiate the two species with respect to attributes related to swimming speed and acceleration. The three attributes related to *Pimelodella taenioptera* are compatible with living in pools (Oliveira *et al.*, 2010) and indicate lower swimming speed when compared to other species of catfish. *Imparfinis schubarti* had larger pectoral and caudal fins, traits which are typical configurations of the morphology of species associated with fast-flowing habitats (Watson & Balon, 1984), contributing to the success of this species in riffles.

The present study revealed that, despite their close phylogenetic relationship, there is a clear functional dissimilarity between *Pimelodella taenioptera* and *Imparfinis schubarti*. These patterns are congruent with the habitat use known for these species and, probably reflect the spatial and temporal variability on conditions and resources present in riffles and pools. Therefore, as expected, the morphological and feeding attributes represent predictive information related to mesohabitat use.

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