Article

Feeding strategy and morphology as indicators of habitat use and coexistence of two loricariid fishes from a Brazilian coastal stream

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Abstract: We aimed to evaluate the relationship between form and function of two Loricariidae species (*Hypostomus punctatus and Parotocinclus maculicauda*) from a Neotropical coastal stream. We performed morphological-dietary analysis and discussed their coexistence strategies, as well. We hypothesized that both species use similar food resources according to their morphology but differences in habitat use facilitate their coexistence. In order to test this hypothesis, morphology, diet and habitat use were analyzed for both species. Trophic variance and the Pianka Niche Overlap index were calculated to explore the differences in trophic niche. Correlations between species abundance and water flow were applied to test habitat use. Principal Component Analysis and one Permutational Multivariate Analysis of Variance were applied to test differences between morphology and diet of both species. Morphological-dietary relationships were tested with Mantel test correlations. Total abundance of *H. punctatus* was higher in the stream channel with higher water flow. The dominant food items were sediment and organic matter for both species, and high trophic niche overlap was revealed. Additionally, morphology did not explain feeding habits for both species. Morphological characteristics were significantly different, especially for intestine length, relative area of the dorsal fin, ventral flattening and mouth attributes. The study site was rich in sand sediment, mud, and clay that are not considered good substrates to the establishment and growing of periphyton, which is an important trophic resource to Loricariidae species. Here, low consumption of periphyton can provide a possible explanation for the feeding similarity and the weak morphological-dietary relationships for both species. Thus, the environmental conditions can be more important for diet composition when compared to the similar and specialized morphology of loricariids.
Keywords: ecomorphology, trophic niche overlap, stream-dwelling fish, Atlantic rainforest.

Estratégia alimentar e morfologia como indicativos do uso do habitat e da coexistência de dois loricarídeos em um riacho costeiro do Brasil

Resumo: Nós tivemos como objetivo avaliar a relação entre forma e função em duas espécies de Loricariidae (*Hypostomus punctatus e Parotocinclus maculicauda*) de um riacho costeiro neotropical. Nós testamos as relações entre morfologia e dieta e também discutimos suas estratégias de coexistência. Nossa hipótese é de que as duas espécies utilizam os mesmos recursos alimentares de acordo com sua morfologia, porém diferenças no uso do habitat facilitam sua coexistência. Para testar essa hipótese, a morfologia, a dieta e o uso do habitat foram analisados em ambas as espécies. A variância trófica e o Índice de Sobreposição de Nicho de Pianka foram calculados para explorar as diferenças no nicho trófico. Correlações entre a abundância das espécies e velocidade da água foram aplicadas para testar o uso do habitat. Análises de Componentes Principais e Análises de Variância Multivariada Permutacional foram aplicadas para testar as diferenças entre morfologia e dieta para ambas as espécies. As correlações entre morfologia e dieta foram testadas a partir de correlações com teste de Mantel. A abundância total de *H. punctatus* foi maior no canal do riacho com maior velocidade no fluxo da água. Os itens alimentares dominantes foram detrito/sedimento e matéria orgânica em ambas as espécies e uma alta sobreposição de nicho alimentar foi encontrada. Adicionalmente, a morfologia não explicou os hábitos alimentares para ambas as espécies.

As características morfológicas foram significativamente diferentes, em especial o comprimento do intestino, área relativa da nadadeira dorsal, achatamento dorsoventral e atributos da boca. A localidade de estudo é rica em substrato de areia, lodo e argila, que não são consideradas superfícies propícias para o estabelecimento e crescimento do perifíton, um recurso alimentar importante para as espécies de Loricariidae. Neste estudo, o baixo consumo de perifíton pode explicar a similaridade trófica e a baixa correlação entre morfologia e dieta em ambas as espécies. Dessa forma, as condições ambientais podem ser mais importantes para definir a composição da dieta quando comparadas a morfologia similar e especializada desses loricarídeos..

Palavras-chave: *ecomorfologia, ecologia trófica, sobreposição de nicho, peixes de riacho, Mata Atlântica.*

Introduction

Fish coexistence, in special the one involving close related species, is an important point in the understanding of natural community organization (Wooton 1990). Information about diet and feeding strategies can reveal fundamental aspects of fish life history traits that enable species to coexist (Schoener 1974, Silva et al. 2019) and maintain viable populations in the community. Feeding strategies reflect morphology and individual foraging performance (Douglas & Matthews 1992, do Carmo et al. 2015) and are frequently described by those corporal characters related to fish movement (Celestino et al. 2017, Conde-Saldaña et al. 2017) as well as feeding tactics (Ramírez et al. 2015). The synergy of those aspects, of fish form and function, can be well described by the ecomorphological approach (Oliveira et al. 2010, Feilich & López-Fernández 2019) and explain habitat occupation (Sabino & Castro 1990, Wood & Bain 1995, Tulli 2012) and coexistence of some close related species (Villares-Junior et al. 2016).

Coexistence of close related species is normally mediated by spatial, feeding and/or morphological segregation (Wikramanayake 1990, Jackson et al. 2001, Abilhoa et al. 2016). In this context, studies on feeding habit and resource partitioning contribute to the understanding of species interactions in aquatic systems (e.g. Ross 1986, Lowe-McConnell 1987, Esteves & Aranha 1999, Mazzoni et al. 2012, Leitão et al. 2015). In scenarios of high abundance and diversity of resources, coexistence can occur without negative interaction between species (Pianka 1973, Hurlbert 1978) and feeding overlap does not necessarily imply the existence of direct competition (Lawlor 1980, Frehse et al. 2015). It is expected that when close related species coexist, niche breadth is narrowed and feeding specialization reduce competition chance (MacArthur 1972, Young et al. 2010).

Siluriformes is one of the most abundant order of fish from South America, especially in waters with high turbidity and large amounts of suspended sediment (Barbarino Duke & Winemiller 2003). Loricariidae is the largest and most specialized family of the order and is distributed throughout South America (Burgess 1989). Loricariidae species are highly specialized and have adaptations related to morphology, feeding habits, and digestive processes, including processing of debris, sediment, algae, and periphyton (Gerking 1994, Mazzoni et al. 2010, Lujan et al. 2011). For example, the suctorial oral disc, larger fins and the shape of caudal fins are structures that help these species to attach to stream bottom, to hold position in faster waters and as indicators of swimming and propulsion ability (Buck & Sazima 1995, Casatti et al. 2005).

The relationship between morphology and ecological functions have been described for loricariids (e.g. Delariva & Agostinho 2001, Lujan et al. 2011, Leitão et al. 2015), revealing the importance of feeding and habitat use specialization in the segregation of ecological niches between co-existing species. For stream fish species, analyses involving ecomorphology are considered as a valid assay within-family species comparisons (Douglas & Matthews 1992) and morphology can explain feeding habits for some species (Maldonado et al. 2009, Ramírez et al. 2015). However, dietary-morphological relationships are not well defined for all fish assemblages and morphology was not considered as a good descriptor of diet in other species (Manna et al. 2019). Stream-dwelling fish have high plasticity and versatility in their diet on Neotropical environments (Lowe-McConnell 1987, Svanbäck & Persson 2004) which can improve this weak correlation between morphology and diet (Labropoulou & Eleftheriou 1997, Boyle & Horn 2006). Thus, it seems important to test this relationship, especially between co-existing species with similar ecological requirements.

Parotocinclus and *Hypostomus* species are normally classified as grazers or herbivores with benthonic behavior, inhabiting the bottoms of streams and/or submerged vegetation (Costa 1987, Casatti 2002, Mazzoni et al. 2010, Villares-Junior et al. 2016). We present here a comparative analysis of morphology, diet and habitat use of two of these Loricariidae species, namely *Parotocinclus maculicauda* (Steindachner, 1877) and *Hypostomus punctatus* Valenciennes, 1840. These species were the only loricariids inhabiting the studied stream and coexisting in all collected sites (Miranda & Mazzoni 2015). Knowing that these closely related Loricariidae species have specialized similar morphology (Lujan et al. 2011, Borzone Mas et al. 2019), we predicted that morphology will explain dietary habits, but differences in habitat exploration should be the strategy to facilitate their coexistence.

Material and Methods

1. Data collection

Fishes were sampled at Mato Grosso stream that drains the northwest of Saquarema municipality in the State of Rio de Janeiro, southeastern Brazil (22°52'S, 42°40'W and 22°53'S, 42°34'W). This stream is a third order stream with its headwaters 500 m above sea level. The stream is 11 km long and discharges into the Saquarema Lagoon. It is a typical coastal stream with water levels regulated only by rainfall (~1.500 mm yr^{-1}) and run-off. Sampling sites from which data of total abundance and habitat use were sampled are located along Mato Grosso stream and in Roncador stream, one tributary of Mato Grosso stream (Figure 1). The sampling site which diet and morphology were analyzed (22°52'24,7''S and 42°39'06,4''W) is located in the lowlands of the Mato Grosso stream in a grassland area with gravel and sand substrata, an absence of canopy and scarce riparian vegetation. Total abundance and data of habitat use were also sampled in this site.
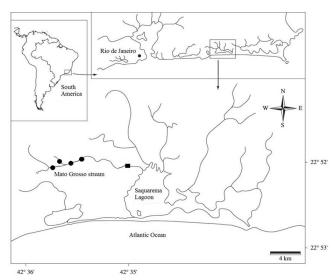
Figure 1. Map of the study area with all sampled sites. Black circles represent the sites that habitat use and morphology were sampled and black square represents the site that morphology and diet were sampled.

Physical characteristics were quantified in the two types of habitats that both species occur, classified as "stream channel" and "stream bank" along a 100 m stretch. Total depth, water flow and substrate were measured on both habitats. We marked 50 transverse transects along the 100 m stream stretch with five meters apart. Along each transect we measured the depth (cm), water flow (m/s) and substrate type at five equidistant points (spaced according to the transect width). The two points closer to stream bank represented the measurements of the habitat "stream bank". Depth measurements were taken with metric rulers and water flow with a digital flow meter (Global Water FP101). Substrate types were classified as mud, sand, gravel, boulder and bedrock following Manna et al (2014). Proportion of each substrate type were calculated using quadrats of 20 cm^2 in the same five points along each transect.

For habitat use, fish were sampled by electrofishing (Mazzoni et al. 2000) through successive removals, following the Zippin method (Zippin 1958). We achieved the premises of constant electrofishing effort and capturability expected by the Zippin method in all sites. Sampling was conducted bimonthly from March 2006 to February 2007 in daytime. Fish for diet analysis were sampled in the same period of the year with seines (mesh size 0.5 mm) in both habitats along 100 m stretch of downstream site (Figure 1). Each sampled fish was anesthetized with a dilute solution of MS222, in accordance with the applicable Brazilian environmental legislation (collecting permit IBAMA/MMA 02022.002475/2006-10, authorization number 118/2006 – DIFAP/IBAMA). Voucher specimens were placed in the ichthyological collection of the National Museum of Rio de Janeiro (*Hypostomus punctatus* - MNRJ 29993, 30008, 30013; *Parotocinclus maculicauda* - MNRJ 29957, 29981, 30023). For morphology, 20 preserved specimens of each studied species were randomly selected from all sampled months and all other specimens were used for dietary analysis. Specimens for diet and morphology analyses were not the same individuals.

2. Laboratory procedures

Sampled fish were conditioned in ice for transportation; total weight (WT, g) and standard length (SL, cm) were determined in the laboratory. Morphological data (Table 1) were taken by a caliper (0.01 mm), whereas fin areas were calculated on a graph paper. Sample size were determined following Gatz (1979). Based on these data, 16 ecomorphological traits, listed on Table 2, were calculated (Gatz 1979, Watson & Balon 1984, Casatti & Castro 2006). These traits are calculated with ecomorphological indices that are able to remove allometric effects in posterior analyses (Gatz 1979). Additionally, all analyzed specimens were adults. Specimens with more than 4.6 cm of standard length for *Hypostomus punctatus* and 2.5 cm for *Parotocinclus maculicauda* were considered adults (Lima 2012, *unpublished data*).

The intestine of each specimen was removed through a longitudinal abdominal incision, distended, and measured (gut length = GL, cm). The first third of the intestine was fixed in formalin (5%) and kept in alcohol (70%) for subsequent analysis. Intestine contents were diluted and analyzed in a Sedgewick-Rafter counting camera, under an optical microscope, according to procedures described by Mazzoni et al. (2010). Diet items were identified to the lowest feasible taxonomic level (Bicudo & Bicudo 1970, Mugnai et al. 2010). Food items were grouped into eight broad categories: diatoms, filamentous algae, cyanobacteria, plant debris, insects, scale, organic matter and sediment (the classification of food items was adapted from Teresa et al. 2015 and Manna et al. 2019). Plant debris were identified as any fragment of allocthonous plants, such as leaves, seeds or litter. Organic matter was identified as autochthonous animal or vegetal fragments with unknown taxonomic classification. Sediment was identified as sand particles. A total of 62 specimens of *H. punctatus* and 117 specimens of *P. maculicauda* were used for diet analysis.

3. Data analysis

An analysis of similarity (ANOSIM) was applied to test the physical differences between the two sampled habitats (stream channel vs. stream bank). ANOSIM was performed using data from stream depth, water flow and substrate type. The units from stream depth and water flow were transformed to the same unit (i.e. meters), and the unit from substrate type was transformed using arcsine square root transformation. After that, we scaled each variable to a null mean and a standard deviation of 1, to give them the same weight, and we then computed Euclidean distance between sampled points using the scaled values. ANOSIM was applied using this distance matrix.

To test the relationship between species and habitat use (i.e. water flow) we ran Pearson correlation test between number of individuals (total abundance) and water flow values. These correlations were applied using data from sites along the stream, including the site that diet and morphology were analyzed (details on sampling sites in Figure 1). The two habitats that fish occurred were classified as stream bank with lower values of water flow (<0.1 m/s) and as stream channel with higher values of water flow (>0.1 m/s). We tested the existence of correlation between water flow and stream depth using Pearson correlation and these variables were highly correlated. Thus, we decided to use water flow as the only habitat variable on this relationship. Furthermore, the morphology of loricariids is adapted to explore habitats with a higher range of water flow when compared to other habitat variables, providing high stability in riffles (Webb et al. 1996, Oliveira et al. 2010, Pagotto et al. 2011), justifying the higher influence

of this variable in habitat exploitation by loricariids. The other habitat variables were used to test the differences between stream bank and stream channel as mentioned above.

Diet items were quantified through Volumetric (*Vo*) and Frequency of Occurrence (*Fo*) methods (Hyslop 1980). Alimentary index for each food item, *AI* (*i*), designed to express the relative importance of different food items, was obtained by combining the volumetric occurrence with the frequency of occurrence (Kawakami & Vazzoler 1980, Hahn et al. 1997).

A principal component analysis (PCA) was applied based on the correlation matrix of morphology and diet data to illustrate the differences between species. One PCA was performed for morphological data and another PCA for diet data. Before performing the PCA, we transformed each morphological and diet trait to the same unit (millimeters in morphology and relative abundance of food items in diet). To test differences in diet composition between sampled months we performed an analysis of variance (ANOVA) using relative abundance of food items.

Differences in morphology and diet between species were tested with a permutational multivariate analysis of variance (PERMANOVA) for each group of traits, with 999 permutations, using dissimilarities among species in their respective distance matrices. One PERMANOVA was applied for morphology and another one for diet. The variance of morphology and diet was calculated using morphological data and relative abundance of food items to test the niche width for each species. The Pianka Niche Overlap Index (Krebs 1989) was also calculated using relative abundance of food items in order to evaluate the overlap in the partitioning of the food resources.

To evaluate the relationship between morphology and diet, a Mantel test correlation was applied on Euclidean distances between individuals in the morphological and dietary 4-dimensional PCA spaces (Manna et al. 2019). Positive correlation with significant relationship reveals that morphology explains feeding niche, so a graphical example with hypothetical data was developed to facilitate the comparisons with our results (Figure 4a). All analyses were performed in the R statistical and programming environment (R 3.1.0., R Development Core Team 2014), with the "vegan" (Dixon 2003), "ade4" (Dray & Dufour 2007), and "spaa" (Zhang 2013) packages.

Table 1. Morphological data of twenty specimens of *H. punctatus* (HP) and *P. maculicauda* (PM) from Mato Grosso stream, Saquarema, Rio de Janeiro, Brazil. SD = standard deviation.

Character	Range							
	Minimum		Maximum		Mean		SD	
	HP	PM	HP	PM	HP	PM	HP	PM
Body measurements (mm)								
Standard length (Sl)	53.85	33.38	91.03	39.75	71.07	37.34	12.879	1.867
Body height (Bh)	8.90	4.92	18.14	6.67	12.36	5.93	2.926	0.486
Body width (Bw)	14.20	6.2	25.30	8.95	18.15	8.13	3.114	0.745
Body area (Ba) (mm²)	479.27	164.22	1602.13	256.79	914.01	222.17	389.188	22.520
Midline height (Mh)	4.94	2.8	8.36	4.38	6.19	3.85	1.110	0.436
Head measurements (mm)								
Head length (Hl)	13.67	8.09	20.73	10.23	16.98	8.98	2.511	0.621
Head height (Hh)	7.65	3.24	14.21	5.01	10.38	4.42	2.029	0.401
Eyes midline height (Emh)	6.25	2.6	10.96	3.25	8.17	3.02	1.607	0.155
Fin measurements (mm)								
Pectoral fin length (Pfl)	15.55	9.18	29.48	11.12	20.77	10.24	4.130	0.624
Pectoral fin width (Pfw)	8.57	4.35	14.54	6.51	11.77	5.34	2.382	0.672
Pectoral fin area (Pfa) (mm²)	86	25	310	43	160.35	32.1	65.13	5.035
Caudal fin length (Cfl)	18.97	8.86	36.06	12.88	26.16	11.46	4.372	1.225
Caudal fin height (Cfh)	15.87	8.29	33.90	12.27	23.21	10.69	4.193	1.188
Caudal fin area (Cfa) (mm²)	185	48	720	76	353.1	64.85	143.526	8.028
Dorsal fin area (Dfa) (mm²)	165	27	708	40	338.8	32.65	152.404	4.356
Caudal peduncle measurements (mm)								
Caudal peduncle length (Cpl)	17.35	10.04	31.90	12.90	23.29	11.80	4.37	0.897
Caudal peduncle width (Cpw)	3.25	1.6	9.11	2.67	4.97	2.39	1.887	0.268
Caudal peduncle height (Cph)	4.63	2.43	9.43	3.9	6.18	1.93	1.601	0.234
Mouth measurements (mm)								
Mouth width (Mw)	4.8	2.27	8.72	3.05	6.16	2.66	1.087	0.248
Mouth height (Mh)	3.95	1.68	8.03	2.46	5.21	1.93	1.233	0.234

Results

1. Habitat use

The ANOSIM revealed significant differences in the physical characteristics between the two studied habitats "stream channel" and "stream bank" (R = 0.712; p < 0.001). Sand and mud were the most abundant substrate types registered in both habitats totalling 97.4% in stream channel and 84.5% in stream bank. The mean values of water flow and depth were 0.37 m/s and 30.6 cm in stream channel and 0.2 m/s and 24.1 cm in stream bank, respectively. Water flow and stream depth were highly correlated (t = 5.379; df = 308; p < 0.001) revealing that habitats with higher water flow were also the habitats with higher depth. Relationship between habitat use and fish abundance revealed a positive correlation for *Hypostomus punctatus*, indicating that a high number of individuals was using habitats with higher values of water flow (Figure 2a) and no correlation for *Parotocinclus maculicauda* was found (Figure 2b).
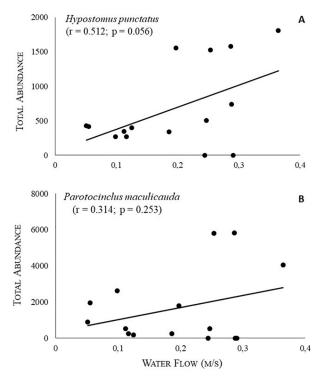

Figure 2. Correlations between total abundance and water flow for (A) *H. punctatus* and (B) P. *maculicauda*.

2. Morphology and feeding ecology between studied species

The intestine content analysis showed nine types of food items for *P. maculicauda* and seven for *H. punctatus*. Sediment and organic matter were the main items for both species, whereas plant debris, diatom and filamentous algae showed a high frequency of occurrence but low volumetric values (Table 3).

PCA showed morphological differences between the species (Figure 3a). The first axis explained 57.24% of the total variance and the second axis 15.21%. Intestine length, the relative area of the dorsal fin, the relative mouth height, the index of ventral flattening, and the relative mouth width were the principal attributes responsible for the separation of the species (Table 2). For diet, PCA showed feeding similarity between species (Figure 3b and Table 4) and values of diet traits did not vary between sampled months for both species (*H. punctatus* – F = 2.612; p = 0.111 and *P. maculicauda* – F = 0.8; p = 0.373).

PERMANOVA results revealed significant differences between species for morphology (F = 112.64; p < 0.001) corroborating PCA results. However, as the opposite from PCA results, diet was significantly different between species (PERMANOVA – F = 6.553; p < 0.001). Finally, the variance in the use of food resources was higher for *H. punctatus* (9.567) than for *P. maculicauda* (0.037) and niche overlap tended to 1 (0.981) showing an overlapping trend between the studied species.

3. Morphological-dietary relationships

Mantel test correlations between morphological dissimilarity and diet dissimilarity among individuals were not significant for *H. punctatus* (R = -0.213; p = 0.76) (Figure 4b) and for *P. maculicauda* (R = -0.2005; p = 0.964) (Figure 4c). Both correlations were weak and revealed that morphology did not explain the diet in both studied species.

Discussion

The physical differences between stream channel and stream bank observed in this study allowed two different habitats to be explored by both loricariid species, corroborating the high diversity of habitats previously registered in Neotropical streams (Manna et al. 2017). Our results revealed that total abundance of *H. punctatus* was higher in stream channel confirming that this species used the stream channel with more frequency. Species of the same family (close-related species) generally present niche segregation (MacArthur 1972, Kirchhof et al. 2010), and this was one of our initial hypotheses when the habitat use by the two studied species was considered. However, *Parotocinclus maculicauda* and *Hypostomus punctatus* from Mato Grosso stream explored similar food resources in both of them. Many studies in the literature have shown that the species of Loricariidae consume mainly vegetal items (e.g. Menezes 1949, Nomura et al. 1975, Casatti & Castro 2006, Casatti et al. 2005) but diet composition in the Loricariidae species is variable (Garavello & Garavello 2004). Some species have been classified as iliophagous, with a low frequency of algae and high values for detritus and sediment in the diet (Buck & Sazima 1995, Albrecht & Silveira 2001, Mazzoni et al. 2010) and even with a variable diet composed by detritus, sponges, bryozoans, and bryophytes (Delariva & Agostinho 2001). Vegetal items, such as diatoms and filamentous algae, and periphyton colonize various types of substrate in aquatic environments, especially composed by hard structure (e.g. stones and gravel) (Azim et al. 2005). Our results revealed that "stream channels" and "stream banks" were composed mainly by sand and mud, which are soft substrates, affecting the availability of periphyton to be consumed by fish and explain the high amount of sediment consumed by the studied species. Diet in stream-dwelling fish can be largely dependent of the environment where the individuals inhabited in the moment of fish sampling (Lobón-Cerviá et al. 2016, Dias et al. 2017) explaining the diet composed by a large amount of sediment in the two studied Loricariidae species.

Loricariidae species are specialized in the way they explore the environment and frequently present morphology adapted to explore specific resources like detritus or periphyton (Agostinho et al. 1997,
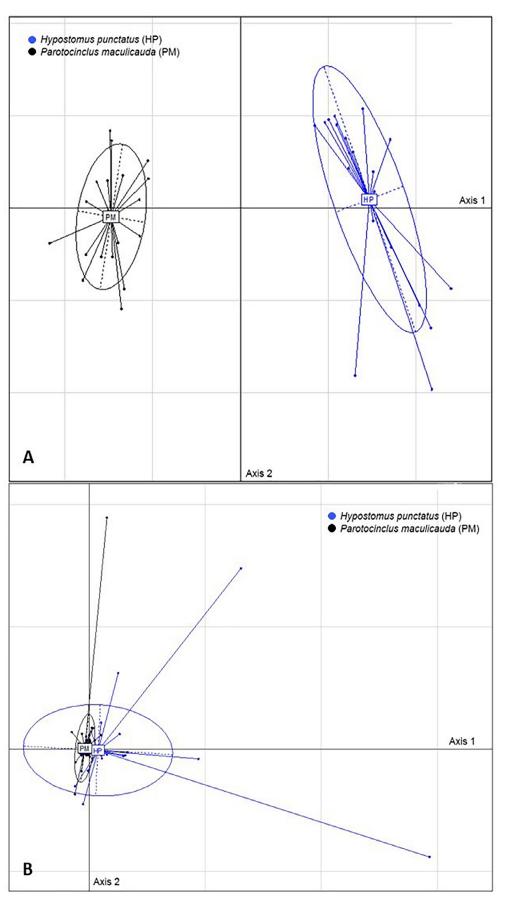
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Figure 3. Principal component analysis (PCA) for *H. punctatus* (HP; blue circles) and P. *maculicauda* (PM; black circles) from the Mato Grosso Stream according to (a) 16 ecomorphological traits identified in Table 2 and (b) diet traits identified in Table 4.

Table 2. Percent of total variance explained by components and scores, and average values of 16 ecomorphological attributes for 20 specimens of *H. punctatus* and 20 of *P. maculicauda* from the Mato Grosso Stream, Saquarema, Rio de Janeiro, Brazil.

Ecomorphological	PCA		Average value (mm)	
Attribute (mm)	Factor 1	Factor 2	*Parotocinclus maculicauda*	*Hypostomus punctatus*
Relative head length (= Sl / Hl)	-0.212	0.622	0.240	0.238
Caudal fin aspect ratio (= Cfh^2 / Cfa)	-0.386	0.417	1.768	1.603
Compression index (= Bh / Bw)	-0.436	-0.795	0.724	0.676
Pectoral fin aspect ratio (= Pfl / Pfw)	-0.587	-0.366	1.929	1.768
Relative caudal peduncle length (Cpl / Bl)	0.633	0.091	0.316	0.327
Relative eye position (= Emh / Hh)	0.689	-0.225	0.685	0.777
Relative depth (= Bh / Bl)	0.723	-0.485	0.159	0.172
Relative area of pectoral fin (Pfa / Ba)	0.801	0.431	0.142	0.177
Caudal peduncle compression index (Cph / Cpw)	-0.801	0.464	1.513	1.287
Mouth aspect ratio (= Mh / Mw)	0.806	-0.363	0.725	0.837
Relative area of caudal fin (= Cfa / Ba)	0.826	0.370	0.293	0.390
Relative mouth width (= Mw / Bl)	0.902	0.272	0.071	0.087
Index of ventral flattening (= Mh / Bh)	-0.914	0.165	0.648	0.508
Relative mouth height (= Mh / Bl)	0.955	-0.061	0.052	0.072
Relative area of dorsal fin (= Dfa / Ba)	0.958	0.192	0.147	0.376
Intestine length	0.968	-0.028	3.960	12.476
Predicted Eigenvalues (Broken-stick)	**9.159**	**2.435**		
Percent of Total Variance Explained	**57.24**	**15.21**		

Table 3. Volume (Vo), Frequency of Occurrence (Fo), and Alimentary Index (AIi) of each food item registered for *H. punctatus* and *P. maculicauda* from the Mato Grosso stream, Saquarema, Rio de Janeiro, Brazil.

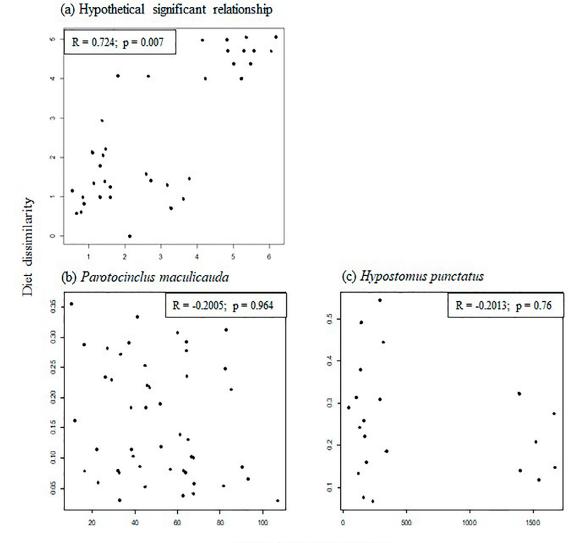| Standard Length (minimum-maximum)	*Parotocinclus maculicauda* (N = 117) 2.5 ± 4.8 cm			*Hypostomus punctatus* (N = 62) 2.2 ± 6.5 cm		
Item	Vo	Fo	AIi	Vo	Fo	AIi
Aquatic larvae	0.07	0.85	0.001	0.00	0.00	0.00
Cyanobacteria	0.01	2.56	<0.001	0.003	3.23	<0.001
Scale	0.14	2.56	0.004	0.00	0.00	0.00
Unidentified	0.01	2.56	<0.001	0.01	6.45	0.001
Filamentous algae	0.47	48.72	0.23	0.32	29.03	0.09
Plant debris	1.24	63.25	0.79	1.94	80.65	1.58
Diatom algae	0.99	88.89	0.89	1.69	96.77	1.65
Detritus	41.06	100	41.49	38.32	100	38.58
Organic matter	56.01	100	56.60	57.72	100	58.11

Hahn et al. 1997) playing an important role for nutrient cycling in aquatic ecosystems (Capps & Flecker 2013, Santos et al. 2016). Large dorsal fins and maneuverability to sustain in the rapids is one of their main ecomorphological features and was also registered in the studies developed by Pagotto et al. (2011). The mouth position and shape can allow the species to explore benthonic microhabitats by grazing (Casatti 2002, Garavello & Garavello 2004). Microscopic algae grow on stones, twigs, or submerged vegetation (Bicudo & Bicudo 1970), and the physical parameters of the streams can influence the composition and structure of the diatom communities (Sinitean et al. 2012). The stream site has suffered strong environmental changes resulted from sand extraction and presented a lot of sand, mud substrata, and an absence of stones in stream bank (Mazzoni et al. 2010, Lobón-Cerviá et al. 2016). These changes could be influencing the availability of algae and hence explain the low volume of algae in the diet of the two studied species. We suggest that the environmental changes have forced changes in the natural feedings habits and caused the similar diet of the two studied species with high amount of sediment in their diet composition.

Although the two studied species are morphologically closely related, the results of the present study revealed significant differences in the morphological attributes between them. *Hypostomus punctatus* showed higher values for its mouth characteristics and a lower value

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Table 4. Percent of total variance explained by components and scores, and average values of seven diet traits for 117 specimens of *Parotocinclus maculicauda* and 62 of *Hypostomus punctatus* from the Mato Grosso Stream, Saquarema, Rio de Janeiro, Brazil.

Diet traits (V%)	PCA		Average value (Volume - mm³)	
	Factor 1	Factor 2	*Parotocinclus maculicauda*	*Hypostomus punctatus*
Aquatic larvae	0.001	-0.511	0.005	0.000
Cyanobacteria	0.009	0.011	<0.001	<0.001
Scale	0.013	0.052	0.010	0.000
Unidentified	0.014	0.185	<0.001	0.002
Filamentous algae	-0.053	-0.788	0.035	0.059
Plant debris	-0.451	-0.225	0.092	0.365
Diatom algae	-0.501	0.119	0.073	0.318
Detritus	-0.514	0.088	3.065	7.216
Organic matter	-0.524	0.077	4.182	10.869
Predicted Eigenvalues (Broken-stick)	**3.478**	**1.154**		
Percent of Total Variance Explained	**36.65**	**12.82**		

Figure 4. Correlation between dissimilarity in morphology and diet for the two studied species. The top panel show a significant correlation computed on with hypothetical data (a). Bottom panels show results computed on individual's data for *P. maculicauda* (b) and *H. punctatus* (c). Values of Mantel's correlation test are provided at the top of each panel.

for ventral flattening, whereas *P. maculicauda* presented a lower value for the relative area of the dorsal fin. A larger mouth with modified oral lips is used for temporary substrate attachment (Casatti et al. 2001) and provides better foraging performance in turbulent water (Casatti et al. 2005). Furthermore, low ventral flattening is an important factor that indicates a better ability to remain fixed on the river bed (Mahon 1984). The larger size of the dorsal fin on *H. punctatus* enables faster movement and is used for propulsion, braking, and stabilization in turbulent waters (Breda et al. 2005). These differences between the two studied species can explain the higher frequency of *H. punctatus* in the stream channel when compared to *P. maculicauda*. Thus, despite their use of similar food resources, we suggest that these loricariids are spatially segregating in the studied stream, facilitating their coexistence, as it has been reported in other studies (Leitão et al. 2015, Celestino et al. 2017).

The weak correlation between morphological variability and diet dissimilarity registered for both species suggests that specialized morphology described for Loricariidae species (Schaefer & Lauder 1986, Delariva & Agostinho 2001) was not enough to explain feeding habits of the studied species. Correlations between diet and morphology were already related as weak relationships revealing that morphology is not a good proxy for diet (e.g. Ibañez et al. 2007, Manna et al. 2019). Versatility in the diet for Neotropical fishes can explain this absence of significant relationship between morphology and diet, since fish are able to change feeding habits according to environmental conditions (Manna et al. 2012, Lobón-Cerviá et al. 2016). Additionally, some studies revealed the morphological adaptation of the digestive system (e.g. intestine length) to process detritus during digestion in loricariid species (Agostinho et al. 1997, Hahn et al. 1997) which can explain the consumption of sediment and organic matter by studied species. Moreover, our results revealed that feeding overlap was high and that morphology did not explain feeding habits. The studied site is impacted with siltation along the entire stream bank, which seems to explain why studied species do not have a high range of prey to capture and consequently, showed high feeding overlap and weak dietary-morphological relationships.

Intraspecific variability in trophic morphology between related species has been frequently documented in the literature (Binning & Chapman 2010, Griffen & Mosblack 2011). Trophic variance was higher for *H. punctatus* which reflect higher individual variation in the use of food resources when compared to *P. maculicauda*. This difference can be explained by the larger body size of *H. punctatus* that allows it to explore a larger spatial area and different microhabitat types, especially the stream channel, where there is high turbulence (personal field observations). Buck & Sazima (1995) have previously proposed that Loricariidae species exploit the same type of substrata and present similar foraging habits. Although PERMANOVA revealed significant differences in the diet between studied species, these observations reflect our results, as *H. punctatus* and *P. maculicauda* in the Mato Grosso stream displayed almost complete trophic niche overlap. Furthermore, the high consumption of sediment and organic matter seems to explain the higher feeding overlap between species (Abilhoa et al. 2016) while the differences in the consumption of algae and plant debris are driving the differences detected in PERMANOVA. These variations in trophic resource utilization can be also explained by the differences in how species are exploring their foraging habitats (Pagotto et al. 2011). These results may be explained by certain physical characteristics of

the study site, such as high amount of sand and mud (Mazzoni et al. 2010, Lobón-Cerviá et al. 2016).

The differences in morphological traits, expressed by the differences in ventral flattening should be causing species segregation according to habitat use. However, the morphology did not explained trophic similarity revealed between species, which is probably reflected by the high consumption of sediment and organic matter in both species' diet. Thus, our results suggest that the environmental conditions were more important for the diet composition when compared to the similar and specialized morphology of studied loricariids, and that studied species are segregating in habitat use to facilitate their coexistence.

Acknowledgments

Author contributions

Luisa Resende Manna: conceived the ideas and designed methodology; collected the data; analyzed the data; led the writing of the manuscript.

Jean Carlos Miranda: collected the data; analyzed the data;

Carla Ferreira Rezende: conceived the ideas and designed methodology;

Rosana Mazzoni: conceived the ideas and designed methodology; led the writing of the manuscript.

All authors contributed critically to the drafts and gave final approval for publication.

Conflicts of interest

The authors declare that they have no conflict of interest related to the publication of this manuscript.

Ethics

This study was performed in strict accordance with the recommendations of the Ethical committee of Rio de Janeiro State University (CEUA/012/2013) and sampling was compiled with current Brazilian laws (collecting permit IBAMA/MMA 02022.002475/2006-10, authorization number 118/2006 – DIFAP/IBAMA).

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