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Dietary differentiation in relation to mouth and tooth morphology of a neotropical characid fish community

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ABSTRACT

The relationship between diet and mouth and tooth morphology among eleven characid species is evaluated herein. Specifically, we tested for: (1) significant differences among the diets and (2) corresponding variation of mouth and tooth morphology. Fishes were collected bimonthly during 2012 and 2013 using electrofishing techniques in the Alto Jacuí sub-basin. A total of 1525 stomachs were analyzed representing eleven species of characid fishes. A Permutational Multivariate Analysis of Variance (PERMANOVA) analysis showed significant interspecific differences among the diets, and Similarity Percentage (SIMPER) analysis indicated that the main food items that contributed to this differentiation were variation in the relative consumption of terrestrial and aquatic plants, terrestrial and unidentified aquatic insect, and adult Hymenoptera. Lastly, Constrained Principal Analysis on Coordinates (CAP) analyses showed that several morphological features were associated with dietary patterns. For example, sub-terminal mouth positions were correlated with the ingestion of benthic items (*i.e.*, aquatic insects and organic matter). Large mouths were associated with species that consume large items such as Decapoda (*e.g.*, *Aegla*) and fish. Species that showed a minor variation in tooth morphology along the outer row of the premaxilla, as well as those that have fewer teeth on the maxilla, consumed high proportions of plants and terrestrial insects. Species with intermediate and high numbers of cusps in the maxilla teeth tended to consume aquatic insects. Here, we demonstrated that eleven species of characid fishes had different diets and that those diets were correlated to a specific mouth and tooth morphology. Therefore, diet and oral morphology likely co-evolved such that divergence in trophic-related morphology likely facilitated dietary differentiation among characid fishes.

1. Introduction

Selective pressures in certain environments may generate much of the observed morphological diversity among species (Beaumord and Petrere, 1994). These pressures may cause phylogenetically similar species to adaptively diverge (Reilly and Wainwright, 1994) to avoid competition and thereby facilitate coexistence (Ross, 1986). However, Wootton (1990) emphasized that there may be evolutionary convergence in morphology of phylogenetically unrelated species that use similar food resources. More complex evolutionary changes of morphological characters that result in large changes in dietary patterns are often attributed to increased specialization (Kotrschal, 1989). Some authors emphasize the power of morphology to delimit trophic groups and understand, for example, the community trophic structure (Wiens and Rotenberry, 1980; Pouilly et al., 2003; Mise et al., 2013). Therefore, over the years many studies have sought to test this link between ecology and morphology (*i.e.* Chao and Musick, 1977; Yamaoka, 1982; Lauder and Clark, 1984; Balon et al., 1986; Motta, 1989; Winemiller et al., 1995; Santos et al., 2011; Dourado dos et al., 2015). Thus, we believe that using phylogenetically similar species, such as characid fishes, which have high diversity in their mouth and tooth morphologies and sometimes have a similar diets, provides a good system for investigating the ecomorphological influences on feeding habits.

The Characiformes belong to the Otophysi group, which represent about 75% of the Neotropical freshwater fishes (Malabarba and Malabarba 2014). Characiformes includes about 234 genera and

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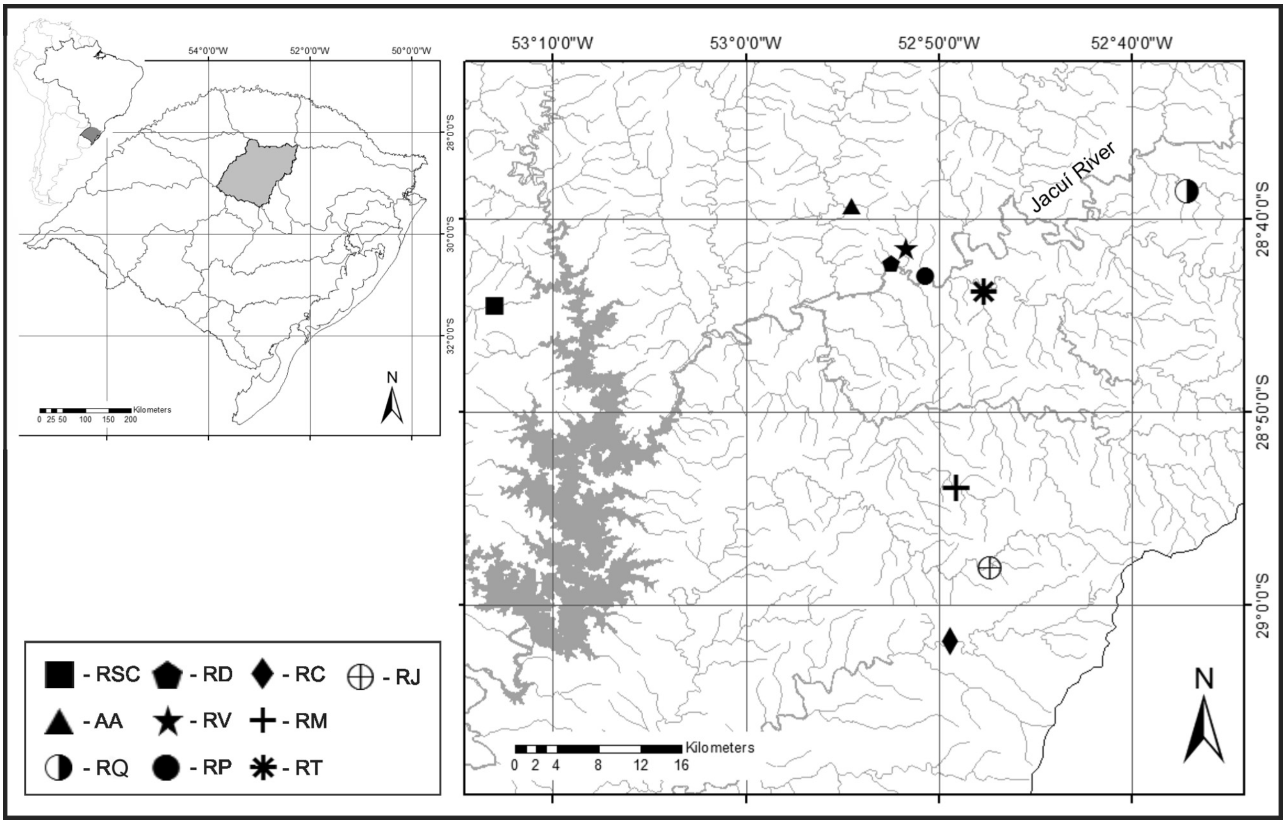

Fig. 1. Sampling streams in the Alto Jacuí sub-basin, state of Rio Grande do Sul, Brazil. RSC = Santa Clara River; RD = Divinéia River; RC = Caixões River; RJ = Jacuizinho River; AA = Angico Stream; RV = Valoroso Stream; RM = Morcego River; RQ = Quati River; RP = Paz Stream; RT = Turvo River.

Table 1
Taxonomic position (following Eschmeyer and Fricke, 2015) of eleven characid fishes in the Alto Jacuí sub-basin with their respective voucher numbers, species code and the number of stomachs analyzed for each species (these total number is based in the seven sampling realized).

Order/Family/Specie	Voucher Numbers	Species Code	Number of Stomachs
Characiformes			
Characidae			
Clade C[a]			
Astyanax lacustris (Lütken, 1875)	UFRGS 19977	AC	39
Astyanax laticeps (Cope, 1894a)	UFRGS 19328	AL	5
Astyanax obscurus (Hensel, 1870)	UFRGS 19329	AO	23
Astyanax procerus (Lucena et al., 2013a)	UFRGS 19329	AP	277
Astyanax xiru (Lucena et al., 2013a)	UFRGS 19323	AX	64
Oligosarcus jacuiensis (Menezes and Ribeiro, 2010)	UFRGS 19978	OA	10
Oligosarcus jenynsii (Günther, 1864)	UFRGS 19979	OE	5
Stevardiinae[b]			
Bryconamericus iheringii (Boulenger, 1887)	UFRGS 19974	BI	885
Bryconamericus sp.	UFRGS 17931	BY	156
Diapoma alburnus (Hensel, 1870)	UFRGS 19976	DA	58
Diapoma dicropotamicus (Malabarba and Weitzman, 2003)	UFRGS 19980	DD	3

[a] Sense Javonillo et al. (2010) and Oliveira et al. (2011).
[b] Sense Malabarba and Weitzman (2003).

2000 described species in the Neotropical region (Malabarba and Malabarba, 2010). Characidae is the family with the most species richness, with 146 genera, representing about 1096 valid species, 223 of which have been taxonomically described in the last ten years (Oliveira et al., 2011; Eschmemeyer and Fricke, 2015).

Characid fishes have highly heterogeneous ecologies due to their enormous taxonomic diversity (Lima et al., 2003). This family exhibits a wide range of body shape and body size, which varies from small fishes such as *Amazonspinther dalmata* Bührnheim et al. (2008) to large species such as the genera *Cynopotamus* Cuvier and Valenciennes (1850) and *Oligosarcus* Günther (1864), (Azevedo, 2010). Thus, the Characiformes can occupy many trophic niches including species that are piscivorous (*e.g.*, *Oligosarcus*), lepidophagus (*e.g.*, *Roeboexodon geryi* Myers, 1960 and *Roeboides bonariensis* (Steindachner, 1879)), and omnivorous (e.g., *Astyanax* Baird and Girard, 1854) (Lima et al., 2003; Javonillo et al., 2010; Neves et al., 2015). Additionally, these species ingest a wide variety of food items and range from generalists to specialists. Other morphological features, beyond body size, that permit characid fishes to explore many feeding habits are their tooth morphology. The Characiformes have a wide diversity of teeth arrangements on the premaxilla, maxilla and dentary. Additionally, tooth morphology also varies such that there are cusps on all or most teeth (Fink and Fink, 1981).

Because of their species richness, ecological diversity, and wide distribution, characid fishes have played an important role in the evolution of stream communities throughout Neotropical South America. Thus, in this study, we tested the hypothesis that species show different food preferences that corresponds to differences in their mouth and tooth morphologies such that the differentiation of these traits has facilitated their diversification into different trophic guilds. Therefore, the objectives of this study were to (i) describe the diet of the eleven Characidae species of the Alto Jacuí sub-basin; (ii) test if their diets are different as well as identify the items responsible for this differentiation; and (iii) test the relationship between mouth and tooth morphology and diet.

2. Materials and methods

2.1. Sampling

Fish samples were collected with authorization #34940 from register #3196382 from Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio). ICMBio is the agency linked to the Ministério do Meio Ambiente, and as such is responsible for issuing licenses to collect fish specimens according to law #11,516 of August 28, 2007, in Brazil. This study was approved by Ethics Committee on Animal Use of the Universidade Federal do Rio Grande do Sul (Permit #24434) and was conducted in accordance with protocols in their ethical and methodological aspects, for the use of fish. The committee follows National and International Norms and Guidelines, especially law #11,794 from November 8th, 2008, which describes the raising and use of animals for educational and research purposes.

The study was conducted in ten streams (Fig. 1) in northwest Rio Grande do Sul, which correspond to the Alto Jacuí sub-basin (Table A1). All streams are considered headwater streams and flow into the Jacuí River, which is one of the main tributaries to the Laguna dos Patos system. Fish were collected bimonthly in 2012 and 2013. For the sampling, we used electrofishing with three stages of 30 min each, in stretches of 50 m per sampling stream. After sampling, fish were euthanized with 10% eugenol (Vidal et al., 2008; Lucena et al., 2013b), fixed in 10% formalin. Fish were identified in the laboratory with identification keys and voucher specimens were deposited in the fish collection of the Departamento de Zoologia at the Universidade Federal do Rio Grande do Sul (Table 1). Only adult individuals were analyzed to avoid ontogenetic influence in the analyses. Individuals were dissected for stomach removal.

2.2. Diet composition and dietary differentiation

Stomach contents were identified under optical and stereoscopic microscopes to the lowest taxonomic level possible. Food items were identified using identification keys (*e.g.* Merritt and Cummins, 1996; Costa et al., 2006; Mugnai et al., 2010). Food items were then quantified according to the volumetric method (*i.e.*, the total volume of a food item consumed by the fish population given as a percentage of the total volume of all stomach contents (Hyslop, 1980)) using graduated test tubes and a glass counting plate (Hellawell and Abel, 1971).

We used Permutational Multivariate Analysis of Variance (PERMANOVA) with 9999 permutations (Anderson, 2001; Anderson et al., 2008) based on a Bray-Curtis dissimilarity (Legendre and Legendre, 1998) matrix to statistically test the existence of differences among the species' diets in the Alto Jacuí sub-basin. This analysis was based on the volumetric proportion of food items. If a difference was found, SIMPER (Clarke and Gorley, 2006) was applied to determine the food items responsible for the differences among species. These analyses were performed in PRIMER-E v6.1.16 with PERMANOVA+ v1.0.6 (Clarke and Gorley, 2006).

2.3. Mouth and tooth morphology

Measurements and characteristics of the mouth and teeth were based on published descriptions of characid species (see Table S1). The mouth and teeth features include counts and descriptions of shape. The choice of measurements was based on the characteristics that are hypothesized to be relevant to the diet among characids. For example, these features may determine what items can be ingested and how they are captured by species. These measurements included: mouth position (descriptive), mouth size (measured and descriptive), number of rows in premaxilla (quantitative), number of teeth in outer row (quantitative), number of cusps in outer row teeth (counted), number of teeth in inner row teeth (quantitative and descriptive), number of cusps in the inner row teeth (quantitative), number of teeth in maxilla (quantitative and descriptive), number of cusps in maxilla teeth (quantitative and descriptive), number of teeth in dentary (quantitative and descriptive), central cusp shape (descriptive), teeth shape (descriptive). For more descriptive information about measurements and characteristics see File S2. The 12 morphological mouth/tooth features chosen were categorized for CAP analysis (Table S3, Supporting Information).

2.4. Correlation between diet and mouth/tooth morphology

We performed a Constrained Principal Analysis on Coordinates (CAP) to determine the ratio of mouth/teeth morphological factors and diet of species. CAP is the canonical form of PCoA and can be applied to a matrix of distances (Bray-Curtis distance) between objects using any resemblance matrix. The CAP analysis permits comparison of two sets of matrices measured in the same sampling units (Legendre and Legendre, 1998; Legendre and Anderson, 1999). To facilitate the visualization of the CAP analysis subjects were grouped into their respective sampling units (*i.e.* species per stream and month sampled) and the items were grouped into trophic categories, only to improve the visualization (see Table 2). We used ANOVA analysis with 9999 permutations to test the significance of the CAP and the axes generated by this analysis and the correlation between variables, and deleting the possible correlated variables. All analyses were performed using R software (R Core Team, 2015) with the Vegan package (Oksanen et al., 2009).

3. Results

3.1. Diet composition and dietary differentiation

The contents of 1525 stomachs (Table S4) belonging to 11 Characidae species (Table 1) were analyzed. The species classification of Stevardiinae follows Thomaz et al. (2015), and the classification of *Astyanax lacustris* (Lütken, 1875) follow Lucena and Soares (2016). We recorded 58 different food items in the gut contents (Table 2). *Astyanax lacustris* consumed high proportions of terrestrial plants (36%), pieces of fish (15%) and terrestrial insects such as Hymenoptera and Lepidoptera (totaling 17.6%). The items consumed most by *Astyanax procerus* (Lucena et al., 2013a), were terrestrial (21.9%) and aquatic (19.7%) plants, and secondly Hymenoptera and unidentified terrestrial insects (totaling 21.5%). The diet of *Bryconamericus iheringii* (Boulenger, 1887) was based on benthic items as detritus (16%), unidentified aquatic insects (12%), organic matter (7.3%) and algae (7.1%). *Astyanax laticeps* (Cope, 1894a) fed mostly on Ephemeroptera (28.6%), followed by plants (terrestrial and aquatic with 21.4% of contribution) and both terrestrial and unidentified aquatic insects (14.3% each).

Table 2

Stomach content analysis (% by volume) for the species of Characidae in the Alto Jacuí sub-basin. AC = *Astyanax lacustris*; AL = *Astyanax laticeps*; AO = *Astyanax obscurus*; AP = *Astyanas procerus*; AX = *Astyanax xiru*; OA = *Oligosarcus jacuiensis*; OE = *Oligosarcus jenynsii*; BI = *Bryconamericus iheringii*; BY = *Bryconamericus* sp.; DA = *Diapoma alburnus*; DD = *Diapoma dicropotamicus*.

Origin and trophic categories of items	AC	AL	AO	AP	AX	OA	OE	BI	BY	DA	DD
Autochthonous											
Aquatic insects											
Chironomidae	0.0	0.1	0.0	0.2	*	0.0	0.0	0.6	3.2	2.1	2.0
Simuliidae	0.6	0.0	0.8	1.1	0.8	*	0.0	1.3	5.3	4.1	3.9
Ceratopogonidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	*	0.0	0.3	0.3
Psychodidae	*	0.0	0.0	*	0.2	0.0	0.0	*	*	0.0	0.0
Empididae	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.2	0.0	0.0
Stratiomydae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	*	0.0	0.0	0.0
Tabanidae	0.0	0.0	0.0	*	0.0	0.0	0.0	*	0.0	0.8	0.8
Tipulidae	0.0	0.0	0.0	0.0	*	0.0	0.0	*	0.0	0.0	0.0
Diptera pupae	0.5	0.0	0.5	0.2	0.1	0.0	0.0	0.3	0.2	2.3	3.2
Simuliidae pupae	0.0	0.0	0.0	*	*	0.0	0.0	0.1	0.1	*	*
Trichoptera larvae	0.1	0.0	1.2	1.3	0.2	0.0	0.0	5.5	**10.6**	**8.0**	**7.7**
Trichoptera pupae	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.3	0.2	0.2
Ephemeroptera	1.3	**28.6**	0.0	1.9	1.3	1.3	4.1	4.0	**48.5**	**39.7**	**37.9**
Plecoptera	0.0	0.0	0.0	0.1	0.7	0.0	0.0	1.1	3.3	1.2	1.2
Odonata nymph	0.0	0.0	0.0	0.6	0.0	0.0	0.0	2.2	1.2	2.0	1.9
Aquatic Coleoptera larvae	2.3	0.0	2.1	0.5	0.5	0.0	0.0	1.2	0.7	1.3	1.2
Aquatic Lepidoptera larvae	0.0	0.0	0.0	0.6	0.2	0.0	0.0	1.7	**12.7**	0.0	0.0
Lepidoptera pupae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0
Aquatic adult Hemiptera	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0
Unidentified aquatic insects	1.2	**14.3**	2.5	4.7	1.1	*	0.0	**12.0**	5.7	**11.3**	**10.8**
Other aquatic invertebrates											
Megaloptera	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.4	0.4
Aegla sp.	**9.7**	0.0	**22.4**	*	0.0	**16.9**	0.0	0.2	0.0	0.0	0.0
Aquatic Isopoda	0.0	0.0	0.0	0.3	0.0	0.5	0.0	0.7	0.0	0.0	0.0
Acari	0.0	0.0	0.0	*	*	0.0	1.0	*	0.0	*	*
Nematoda	0.0	0.0	0.0	0.6	0.0	0.0	0.0	0.0	0.1	0.0	0.0
Bivalvia	0.0	0.0	0.0	0.0	0.0	0.0	0.0	*	0.0	0.0	0.0
Gastropoda	0.0	0.0	0.0	0.5	0.0	0.0	0.0	0.6	0.1	0.0	0.0
Microcrustacea	0.0	0.0	0.0	*	0.2	0.1	0.0	0.2	0.0	0.0	0.0
Fish											
Fish	**15.9**	0.0	0.0	0.0	0.1	**60.1**	**79.4**	1.0	0.0	0.0	0.0
Scale	0.0	0.0	0.0	*	0.0	0.0	0.0	0.1	0.0	0.0	0.0
Other aquatic organisms											
Testae Amoebae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	*	0.0	0.0	0.0
Aquatic plants	0.0	**21.4**	0.1	**19.7**	**34.2**	0.0	0.0	**8.7**	0.0	5.2	4.9
Algae											
Diatomacea algae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	*	0.0	0.0
Filamentous algae	0.0	0.0	0.1	2.3	0.8	0.0	0.0	**7.1**	0.4	0.0	0.0
Organic matter											
Undetermined organic matter	0.0	0.0	0.0	3.9	3.8	0.0	0.0	**7.3**	0.3	0.0	0.0
Vegetal organic matter	0.0	0.0	0.5	2.4	0.0	0.0	0.0	1.7	0.7	0.0	0.0
Animal organic matter	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.9	0.4	0.0	0.0
Detritus	0.0	0.0	0.0	0.2	0.0	0.0	0.0	**16.4**	0.0	0.0	0.0
Sediment	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.8	0.4	0.0	0.0
Allochthonous											
Terrestrial insects											

Table 2 (*Continued*)

Origin and trophic categories of items	AC	AL	AO	AP	AX	OA	OE	BI	BY	DA	DD
Sarcophagidae larvae	0.0	0.0	0.0	1.0	**8.5**	0.0	0.0	0.0	0.0	0.0	0.0
Adult Diptera	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.6	0.0	1.2	1.1
Adult Orthoptera	0.0	0.0	0.8	0.3	0.1	0.0	0.0	*	0.0	0.0	0.0
Terrestrial adult Hemiptera	0.1	0.0	0.4	*	0.7	0.2	0.0	0.2	0.0	0.0	0.0
Adult Hymenoptera	**8.0**	0.0	**26.0**	**15.0**	4.1	3.0	0.6	1.7	0.4	7.5	**9.7**
Adult Coleoptera	**9.6**	0.0	4.1	4.5	0.6	**11.7**	0.0	1.7	0.5	2.9	2.8
Adult Lepidoptera	3.5	0.0	**19.8**	0.8	0.0	0.0	0.0	0.3	0.0	0.4	0.4
Terrestrial Lepidoptera larvae	1.7	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Adult Odonata	0.0	0.0	0.5	0.0	0.0	0.5	0.0	*	0.0	0.0	0.0
Adult Plecoptera	0.0	0.0	0.0	0.0	0.0	5.6	0.0	0.0	0.0	0.0	0.0
Adult Homoptera	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.3	0.0	0.0	0.0
Adult Neuroptera	0.0	0.0	0.0	0.0	0.0	0.0	0.0	*	0.0	0.0	0.0
Unidentified terrestrial insects	2.9	**14.3**	5.3	**6.5**	2.5	0.0	2.9	1.1	1.8	6.2	6.8
Other terrestrial organisms											
Diplopoda	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Oligochaeta	2.2	0.0	0.0	**6.3**	0.0	0.0	0.0	2.9	0.4	0.8	0.8
Aranae	3.4	0.0	0.6	0.9	0.0	0.0	0.0	0.4	0.0	0.2	0.2
Fur	0.0	0.0	0.0	0.0	*	0.0	0.0	*	0.0	0.0	0.0
Terrestrial plants											
Terrestrial plants	**36.3**	**21.4**	**12.0**	**21.9**	**39.3**	0.0	**12.0**	**13.7**	2.6	1.7	1.6
Pollen	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0

The asteristicks (*) indicates values less than 0.1%; bold values indicate the items most consumed.

Astyanax obscurus (Hensel, 1870) had a diet based on terrestrial insects such as Hymenoptera (26%) and Lepidoptera (19.8%) as well as crustaceans (*Aegla* sp.; 22.4%). *Astyanax xiru* (Lucena et al., 2013a) ingested mainly plants (39.3% terrestrial and 34.2% aquatic). *Diapoma alburnus* (Hensel, 1870), *Diapoma dicropotamicus* (Malabarba and Weitzman, 2003) and *Bryconamericus* sp. had higher consumption of Ephemeroptera (39.7%, 37.9% and 48.5%, respectively). *Oligosarcus jacuiensis* Menezes and Ribeiro (2010) and *Oligosarcus jenynsii* (Günther, 1864) were the species that most ingested fish with proportions of 60% and 79.4%, respectively (Table 2).

The existence of diet differentiation among the species (F = 13.5, *P* = 0.0001) was supported by PERMANOVA. The most significant food items that contributed to species' dietary differentiation were indicated by SIMPER. The main item that contributed to dietary differentiation among *Astyanax* species were plants. For two *Bryconamericus* species, aquatic insects, and the diets of two *Diapoma* species were differentiated by Diptera pupae, adult Hymenoptera and Ephemeroptera. Between *Oligosarcus* species, items such as Acari, Ephemeroptera and terrestrial plants contributed most to their dissimilarity (Table 3).

3.2. Correlation between diet and mouth/tooth morphology

This analysis was based on 196 sampling units (*i.e.* the respective species per stream and month sampled). Some morphological tooth features were correlated. In such cases, the less ecologically informative were removed from the analysis (number of rows in premaxilla, number of cusps in outer row teeth, number of cusps in the inner row teeth, number of teeth in dentary, central cusp shape, tooth shape.). Of the six remaining variables, five were significant: mouth position (F = 12.8, *P* = 0.0001), mouth size (F = 4.3, *P* = 0.0001), number of teeth in outer row (F = 8.4, *P* = 0.0001), number of teeth on the maxilla (F = 3.9, *P* = 0.0001), number of cusps in maxillary teeth (F = 2.7, *P* = 0.0001), and only the number of teeth in the inner row was non-significant (F = 1.5, *P* = 0.0760). The CAP explained 15.1% of the constrained variation of the food items. The CAP was significant (F = 5.6, *P* = 0.0001) as well as its first two axis (CAP1 – F = 14.5, *P* = 0.0001; CAP2 – F = 11.1, *P* = 0.0001). The explanations of the first two axes were 43.3% and 33.1%, respectively. The CAP confirms the significant differences found by PERMANOVA in the species' diet. The items indicated by SIMPER are the same that appear more isolated and are influencing the species in both axes of the CAP analysis (Fig. 2).

Mouth position separated the species with terminal mouths represented by negative scores (*i.e.* AL, AO, AP, AS, AX, OA and OI) from those with sub-terminal mouths represented by positive scores (*i.e.* BI and BY). The species with sub-terminal mouths (*i.e.* BI and BY) tended to eat more aquatic insects, which are benthic or eat items from the substrate such as detritus and organic matter, and those with terminal mouths ingested more quantities of terrestrial insects and plants because of being able to more easily capture these types of items on the surface of the water column. Mouth size separated the species with large mouths (OA and OI) from those having a small mouth (*i.e.* BI, BY, DA, DD). This situation was due to items of large size that can only be ingested by the species with large mouths. For example, species like OA and OE were consumed large items such as fish and terrestrial insects (*i.e.* Hymenoptera).

The number of teeth in the outer row grouped those species that have a similar minimum number of teeth in this row and had similar variation. The species (all *Astyanax* species) with small variation in the number of teeth had the highest ingestion of plants, which were mainly terrestrial plants. But those species with the largest number of teeth on the maxilla consumed more aquatic insects; however, species with the fewest teeth fed more on terrestrial items. Species with intermediate and more numerous cusps in maxillary teeth ingested more aquatic insects. Nevertheless, the smallest number of cusps in maxillary teeth seems to permit the consumption of large sized and terrestrial items (Fig. 1).

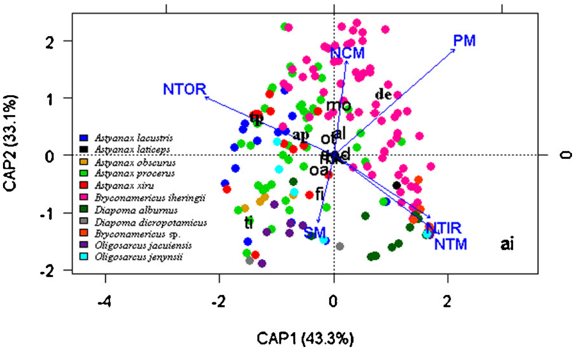

Fig. 2. Ordination of the Characidae species in the Alto Jacuí sub-basin, state of Rio Grande do Sul, Brazil, produced by the first two axes of the Constrained Principal Analysis on Coordinates (CAP1 and CAP2) applied to the correlation of six morphological tooth features and items ingested by the species. Morphological features: PM = mouth position, SM = mouth size, NTOR = number of teeth in outer row, NTIR = number of teeth in inner row, NCM = number of cusps on maxilla, NTM = number of teeth on maxilla. Items categories: ai = unidentified aquatic insects, ti = unidentified terrestrial insects, oa = other aquatic invertebrates, ot = other terrestrial invertebrates, mi = microcrustaceans, tp = terrestrial plants, ap = aquatic plants, al = algae, se = sediment, mo = organic matter, ta = Testae Amoebae, de = detritus, fi = fish.

4. Discussion

The characid assemblage of the Alto Jacuí sub-basin, in Neotropical Brazil, ingested a diverse supply of food resources. This finding supports the consensus that most Neotropical fish have highly variable diets (Lowe-McConnell, 1999), which is likely an adaptive response to heterogeneous environmental conditions (Winemiller, 1990). We demonstrate with our data that variation in feeding patterns in this characid assemblage are strongly related with the differentiation of morphological features. Thus, supporting the ecomorphology theory that morphological features of species should reflect their ecology and therefore predict the feeding habits of species (Gatz, 1979). Additionally, this pattern suggests that fishes with comparable morphological traits should use similar resources (Winemiller, 1991). According to Weitzman and Malabarba (1998), the numbers of teeth in a given row on the premaxilla has been one of the prominent sources supporting the recognition that Characidae is polyphyletic. The same authors emphasize that tooth shape and certain types of tooth arrangements, especially on the premaxilla, have been more successful in predicting relationships among characids. We observed that the morphological features of mouth and teeth may explain their dietary patterns. Some studies have obtained the same result indicating a link between morphology and diet (Motta et al., 1995; Winemiller et al., 1995; Piet, 1998; Fugi et al., 2001); however, others have not found this relationship (Barnett et al., 2006).

The characteristic that best separated the *Oligosarcus* species from the other species was mouth size. Carnivorous species must have sufficient gape that permits the ingestion of large items such as fishes and *Aegla* (Leach, 1820). This clear differentiation of carnivorous and piscivorous species from other dietary patterns is seen in many studies (Motta et al., 1995; Winemiller et al., 1995; Barnett et al., 2006; Dourado dos et al., 2015), which also indicated other features such as longer lower jaws, longer tooth size, an upturned mouth, and greater snout length that explain their dietary differentiation. Santos et al. (2011) verified the dietary differentiation of *Oligosarcus hepsetus* (Cuvier, 1829) from other species such that they explored lotic environments and had carnivorous feeding

Table 3

Dissimilarity of pairwise comparition and the contribution (%) of the food items obtained by SIMPER analyses for the 11 Characidae species sampling in the Alto Jacuí sub-basin. Diss = dissimilarity; ap = aquatic plants; ai = unidentified aquatic insects; ti = unidentified terrestrial insects; tp = terrestrial plants; ah = adult Hymenoptera; ac = adult Coleoptera; ep = Ephemeroptera; de = detritus; tr = Trichoptera, dp = Diptera pupae, si = Simullidae; ac = Acari; Fish = fi. AC = *Astyanax lacustris*; AL = *Astyanax laticeps*; AO = *Astyanax obscurus*; AP = *Astyanas procerus*; AX = *Astyanax xiru*; OA = *Oligosarcus jacuiensis*; OE = *Oligosarcus jenynsii*; BI = *Bryconamericus iheringii*; BY = *Bryconamericus* sp.; DA = *Diapoma alburnus*; DD = *Diapoma dicropotamicus*.

Species	Diss (%)	ap	ai	ti	tp	ah	ac	ep	de	tr	dp	si	fi	Species	Diss (%)	ap	ai	ti	tp	ah	ac	ep	de	tr	dp	si	fi	AC
ACxAL	84.5	25.4	11.2	10.1										ACxBY	94.3				17.4		6.2	17.7		7.7				
ACxAO	84.9				22.1	13.6	10.8							ALxBY	89.1		9.5		13.1			24.0		10.4				
ALxAO	91.0		12.6	10.0	18.8	12.9								AOxBY	95.7				8.5	9.3		20.2		9.0				
ACxAP	87.5				19.6	11.1								APxBY	90.2				8.3	8.0		17.5		8.5				
ALxAP	88.1	11.9	11.7	10.4	16.8	10.4								AXxBY	92.1	8.7			13.5	9.5		16.9						
AOxAP	89.3		10.0		12.7	14.6								BIxBY	86.1		10.3		9.7			14.3	6.1	8.6				
ACxAX	83.4	10.0			21.2	12.6								DAxBY	76.8		12.7					18.5		10.9		9.1		
ALxAX	86.0	15.0	10.2	10.0	20.9	13.3								DDxBY	94.6					14.4		20.5			17.0			
AOxAX	87.2	10.7			17.7	15.5								ACxOA	93.7				18.0	10.3	10.5						16.6	
APxAX	85.9	13.3			16.5	13.4								ALxOA	97.6				11.8	9.0		10.6					19.0	
ACxBI	87.2		10.2		15.4	6.1	6.1							AOxOA	93.9				7.5	13.9	10.4						17.1	
ALxBI	87.5		13.3		14.2			8.6	7.5					APxOA	94.6				6.8	11.6	8.2	7.6					15.3	
AOxBI	90.6		11.1		11.8	8.7			6.4					AXxOA	94.3	8.6			12.9	12.2	7.8						14.8	
APxBI	88.3	7.4	10.5		11.5	7.5		6.4						BIxOA	96.0		8.9		8.4	6.5	6.0	6.5					12.4	
AXxBI	87.5	9.4	10.0		13.9	8.6								DAxOA	92.2		10.3			9.2		14.0					15.6	
ACxDA	91.9		10.6		18.2	7.8		12.4						DDxOA	94.0					17.4					17.7		17.5	
ALxDA	87.7		15.8	8.7	13.0			17.4						BIxOA	93.7					7.2		18.1		7.6			15.3	
AOxDA	91.5		12.7		8.0	11.5		13.8						ACxOE	82.7				19.1			11.8					18.7	
APxDA	87.5	8.1	11.8			9.9		13.3						ALxOE	84.1			11.1	19.7			16.2					21.9	12.9
AXxDA	89.4	10.3	10.5		13.6	10.9		12.5						AOxOE	91.7				16.3	10.8		11.8					17.6	
BIxDA	85.3		11.6		9.5			11.2		6.8				APxOE	89.5				15.6	9.0		11.3					16.5	
ACxDD	92.6			10.2	20.7	16.7					17.4			AXxOE	86.5				17.5	10.5		11.2					16.5	
ALxDD	94.6			14.8	13.8	20.1					24.0			BIxOE	89.0		9.0		12.7			9.5					13.8	6.7
AOxDD	90.0			11.2		21.6					20.5			DAxOE	89.6		9.3		14.3			13.5					16.3	
APxDD	90.9			11.2	8.0	17.9					17.8			DDxOE	94.9				15.4	14.3		11.6			16.2		17.5	
AXxDD	90.0		10.2	10.5	15.3	17.6					16.9			BYxOE	85.7				14.8			16.0					17.1	9.0
BIxDD	95.3		9.8	7.2	9.5	11.5					13.1			OAxOE	88.8				14.5			12.6						24.0
DAxDD	90.5		11.6	9.8		16.2		14.2			17.6																	

habits, which they linked to morphological features such as higher relative height of the mouth and mouth aspect.

The species of genus *Bryconamericus* (Eigenmann et al., 1907) were separated from the others mainly by having a sub-terminal mouth allowing greater intake of benthic items such as detritus, organic matter and benthic aquatic insects. The species of genus *Diapoma* Cope (1894b); despite having a terminal mouth, eat more benthic items too. This is probably related to the shape of the body, which is elongate and allows them to more efficiently exploit the bottom of streams and among rocks. Although tooth number in the outer row of the premaxilla has been identified as crucial in dietary differentiation, it does not seem to distinguish the species analyzed here. Maybe it is not the number that defines this separation. Although *Bryconamericus* and *Diapoma* both have a large range in the number of teeth (3–6) on the premaxilla, they have another feature in common, which is the angle of these teeth. This angle is greater than in *Astyanax*, which have teeth that project more externally (Malabarba and Malabarba, 1994) and may allow the species to forage along the substrate and the spaces between rocks. In contrast, *Bryconamericus* scrapes algae from surfaces. The high number of teeth on the maxilla may also be responsible for this foraging behavior by further facilitating eating algae.

Astyanax species, in general, have similar diets as the other species, characterized primarily by consumption of items (animal and plant) of terrestrial origin. The more superior position of the mouth in *Astyanax* permits them to forage from the surface water and eat floating terrestrial insects as well as drift resources in the water column. Furthermore, according to Peretti and Andrian (2008), the consumption of Hymenoptera and Coleoptera by *Astyanax* is explained by the type of teeth. The insertion, which almost forms a right angle (90°) to its premaxilla and dentary, does not allow scraping substrates, but makes it easier to bite and tear plants and ingest terrestrial insects. Therefore, *Astyanax* may be considered as browsers that bite off pieces and tear plants above the substrate, usually by pointing the head upward (Jones, 1968; Loureiro-Crippa and Hahn, 2006; Mise et al., 2013). In contrast, *Bryconamericus* are grazers that ingest algae from close to the substrate and may ingest some of the substrate. This type of species feeds by pointing the head down and applying their lips and teeth to the substrate, so they can feed by rasping and suction (Jones, 1968; Orciolli and Bennemann, 2006; Oosterom et al., 2013).

In conclusion, with this work we describe the trophic ecology of several recently described species and reinforced the hypothesis of the Characidae as a diverse family that exploits distinct habitats and associated broad trophic spectrum. The species showed varied diets. This ecological variability is possibly due to the diversity of morphological features exhibited among the species. Thereby, with this study we demonstrate that variation in mouth and tooth morphology likely facilitated the differentiation of feeding habits in this characid assemblage.

We hope that with this effort in adding biological and ecological information, in the near future, we can have more clear and objective answers about the evolutionary patterns within the Characidae. Because many questions still remain unresolved in many taxonomic levels of the Characiformes, mainly in the named "Clade C" (Vari and Malabarba, 1998). Recently, Thomaz et al. (2015) established the Stevardiinae as monophyletic, synonymized *Hypobrycon* Malabarba and Malabarba (1994) with *Bryconamericus* with, and designated *Cyanocharax* Malabarba and Weitzman (2003) as *Diapoma*. This evolutionary similarity is consistent with our dietary data such that we observed similar insectivorous diets among this sub-group including *D. alburnus*, *D. dicropotamicus* and *Bryconamericus* sp. With greater understanding of the relationships within these groups, we can infer with more certainty, for example, why species of *Astyanax* have similar diets. This pattern may be due to ancient diversification in the presence of ecological opportunity as has been shown with other groups of Neotropical fishes (López-Fernández et al., 2012) or a more recent diversification resulting from high competition among ecologically similar species.

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Appendix A.

Table A1
Geographic coordinates, elevation and localization of the sampled streams and their respective codes in the Alto Jacuí sub-basin.

Stream	Code	Geographic Coordinates	Elevation (m)	Locality
Caixões River	RC	29°01'54.4"S, 052°49'25.1"W	420	Guanxuma, Espumoso
Jacuizinho River	RJ	28°58'02.9"S, 052°47'20.3"W	513	Depósito, Espumoso
Morcego River	RM	28°53'55.0"S, 052°49'05.6"W	461	São Domingos, Espumoso
Turvo River	RT	28°43'47.0"S, 052°47'40.4"W	351	Santo Antônio, Espumoso
Quati River	RQ	28°38'31.8"S, 052°37'07.9"W	439	Mormaço
Santa Clara River	RSC	28°44'30.1"S, 053°13'03.0"W	439	Santa Clara, XV de Novembro
Valoroso Stream	RV	28°41'32.0"S, 052°51'41.5"W	376	Teutônia, Tapera
Divinéia Stream	RD	28°42'16.7"S, 052°52'25.9"W	350	Teutônia, Tapera
Paz Stream	RP	28°42'57.3"S, 052°50'41.7"W	378	Vila Paz, Tapera
Angico Stream	AA	28°39'17.9"S, 052°54'31.1"W	368	São Rafael, Tapera

Appendix B. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.jcz.2017.01.003.

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