



Food resource partitioning among sympatric populations of five species of freshwater fish (Characidae) in southern Brazil

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Abstract. We investigate interspecific and ontogenetic differences in the diet of five sympatric characid fish species in Rio Grande do Sul state, Southern Brazil. A total of 849 individuals were analyzed, sampled from January to December 2007. Smaller individuals of *Astyanax henseli* and *A. lacustris* consumed mainly allochthonous insects; vegetal items were added along their development. *Diapoma thauma* was specialized in allochthonous insects regardless of fish size. Smaller *B. iheringii* consumed allochthonous insects and sediment, shifting to algae with growth. Smaller *D. luetkenii* consumed allochthonous insects, while larger individuals feed mostly on vegetal matter. The high ingestion of allochthonous insects by *A. henseli*, *A. lacustris*, and *D. thauma* was responsible for their high diet overlap, which was increased for the *Astyanax* species due to their shared ingestion of vegetal matter. The small niche breadth allowed the identification of trophic specializations, suggesting that competition and food overlap are minimized by differences in the frequency/abundance of the consumed items. Therefore, whereas the characteristics of the aquatic environment and the riparian vegetation seem to offer enough food items to maintain these sympatric species, small trophic niche differences may contribute to reduce the potential inter and intraspecific competition, allowing these fish species to coexist.

Keywords: diet composition, ontogeny, interspecific differences, food overlap, coexistence.

Partição de recursos alimentares entre populações simpátricas de cinco espécies de peixes de água doce (Characidae) do sul do Brasil. Resumo: Diferenças interespecíficas e ontogenéticas na dieta de cinco espécies simpátricas de Characidae foram analisadas no estado do Rio Grande do Sul, Brasil. Ao todo 849 exemplares foram amostrados entre janeiro a dezembro de 2007. Os indivíduos menores de *Astyanax henseli* e *A. lacustris* consumiram principalmente insetos alóctones; itens vegetais foram adicionados ao longo do desenvolvimento. *Diapoma thauma*, independentemente do tamanho, consome principalmente insetos alóctones. Indivíduos menores de *Bryconamericus iheringii* consumiram insetos alóctones e sedimentos, mudando para algas com o crescimento. Indivíduos menores de *Deuterodon luetkenii* consumiram insetos alóctones enquanto os maiores consumiram matéria

vegetal. A alta ingestão de insetos alóctones por *A. henseli*, *A. lacustris* e *D. thauma* foi responsável pela alta sobreposição alimentar, aumentada nas espécies de *Astyanax* pela ingestão compartilhada de matéria vegetal. A pequena amplitude de nicho permitiu identificar especializações tróficas, sugerindo que competição e sobreposição alimentar são minimizadas por diferenças na frequência/abundância de itens consumidos. Portanto, enquanto as características do ambiente aquático e da vegetação ripária parecem oferecer alimentos suficientes para manter essas espécies simpátricas, pequenas diferenças de nicho alimentar podem contribuir para reduzir a competição inter e intraespecífica, permitindo a coexistência dessas espécies de peixes.

Palavras-chave: composição da dieta, ontogenia, diferenças interespecíficas, sobreposição alimentar, coexistência.

Introduction

Neotropical freshwater fish exhibit a great diversity of shapes, behaviors, and life-history traits that allow them to occupy a wide range of environments (Vari & Malabarba 1998). The different foraging tactics and strategies displayed by these fishes are good examples of such plasticity (Albert *et al.* 2020). This diversity allows fish to explore a wide range of the food resources available in their aquatic environment and its surroundings (Brandão-Gonçalves *et al.* 2009). They occupy all trophic levels within the food chain (Wootton 1992). However, how sympatric fish species with similar body morphology and niche coexist in a given environment is still not fully comprehended, mainly in highly diverse regions such as the neotropics.

Characidae includes more than 1,480 freshwater fish species and is the most diverse family of Characiformes in the neotropics (Fricke *et al.* 2021). They occur from southwest Texas and Mexico (North America) to Patagonia in South America (Nelson *et al.* 2016). Characins show a wide range of feeding habits (Teixeira 1989, Sabino & Castro 1990), which can vary seasonally (Graciolli *et al.* 2003) and ontogenetically (Mazzoni *et al.* 2010a, Dala-Corte *et al.* 2016b). On the other hand, studies have suggested that characins are typically omnivores and generalist species, exploring similar dietary niches (e.g. Bonato *et al.* 2017), which indicates that sympatric species of characid may present a high dietary niche overlap (Moraes *et al.* 2013, Barros *et al.* 2017).

Knowledge about the natural feeding habits of fish is fundamental for a better understanding of their trophic ecology, species behavior, and to predict how the species face natural and human-induced variability in environmental conditions and food availability (Wootton 1990). This knowledge can also provide insights into the main mechanisms that allow coexistence and competition for food

resources by numerous species within the same system (Goulding 1980). Furthermore, it can shed light on the interactions between fish and other organisms within aquatic communities (Hahn *et al.* 1997). In addition, studies on trophic ecology may allow inferences regarding the spatial distribution of fish in aquatic environments (Graciolli *et al.* 2003), and to better understand how a given species shifts its habitat occupation along the ontogenetic development and to understand whether different species show spatial aggregation or segregation (Wootton 1990).

The use of trophic resources, the way environmental resources are exploited, and the morphology can be strongly correlated (Mazzoni *et al.* 2010b). Therefore, sympatric and phylogenetically closely-related species with few anatomical differences are known to exhibit strong competitive potential (Wootton 1990). Thus, different habitat use and resource partitioning are expected for the coexistence of such species (Herder & Freyhof 2006, Brazil-Sousa *et al.* 2009). According to Pianka (1973), when resources are sufficient to maintain two or more populations of different species, there may be niche overlap. However, when food resources are limited, niche overlap leads to competition (Herder & Freyhof 2006), and potentially to competitive exclusion, although the use of the same resources could be minimized by strategies such as spatial or temporal segregation (Casatti 2002, Kotler & Brown 2007).

Studies have demonstrated that ontogeny influences the resource partitioning among coexisting species (Ross 1978, Borcharding *et al.* 2012). The size of consumed prey usually increases with fish size (Scharf *et al.* 2000, Cocheret De La Morinière *et al.* 2003, Sánchez-Hernández & Cobo 2012), and the prey types may also shift along with the ontogenetic development as a result of shifts in foraging abilities or habitat use (Mittelbach &

Persson 1998, Lukoschek & McCormick 2001, Nunn *et al.* 2012). For Neotropical characids, studies indicated that the populations undergo ontogenetic dietary shifts from terrestrial insects to fruits and leaves (*e.g.* Abelha *et al.* 2001, Drewe *et al.* 2004) or to increase the consumption of vegetation matter along the growth (Dala-Corte *et al.* 2016a). Ontogenetic differences in diet may lead to profound ecological consequences for fish by, for example, enhancing individual growth and lifetime reproductive output or reducing the risk of mortality (Sánchez-Hernández *et al.* 2019). However, the prevalence of ontogenetic changes in natural characid populations and how these changes relate to resource partitioning are still not well comprehended.

The present work describes and analyzes the diet of five sympatric characid species from the upper section of a river in southern Brazil, aiming to identify possible interspecific and ontogenetic differences that explain their coexistence. The studied characid species have been reported as omnivores with trophic plasticity, such as *Astyanax lacustris* (Lütken 1875) (Bastian *et al.* 2021), *Bryconamericus iheringii* (Boulenger 1887) (Dala-Corte *et al.* 2016a), and *Deuterodon luetkenii* (Boulenger 1887) (Graciolli *et al.* 2003), or were not yet studied regarding their feeding ecology in natural environment (*Astyanax henseli* Mello & Buckup 2006 and *Diapoma thauma* Menezes & Weitzman 2011). Diet overlap among these five sympatric characid species is still unknown for the studied region. However, studies conducted in other regions with other sympatric omnivorous and small-sized characid species have suggested that the species coexistence is only possible due to resource partitioning, such as found for Amazonian upland streams (Barros *et al.* 2017); for tributaries of the upper Paraná River (Silva *et al.* 2017); for the upper Uruguay River (Neves *et al.* 2018), and the lower Iguazu River (Pini *et al.* 2019). On the other hand, high diet niche overlap has been found in some cases, such as for two characid species in the Teles Pires and Juruena Rivers (Oliveira *et al.* 2021), suggesting that we still do not fully understand the drivers of species coexistence and resource partitioning in Neotropical characids. In addition, how ontogenetic shifts in diet of these sympatric and morphologically similar characids contributes to resource partitioning is yet poorly understood. Therefore, we hypothesized that all the characins would present a similar omnivorous diet, with a greater diet overlap occurring between the two

congeneric species of *Astyanax* due to their great phylogenetic proximity. In addition, we hypothesized that ontogenetic differences in diet would be evident only in the larger species (*A. henseli*, *A. lacustris*, and *B. iheringii*), which show a wider size range variation of individuals.

Material and Methods

Fish samplings were conducted monthly from January to December 2007 at the locality of Praia João Fernandes (29°45'51.59" S; 50°25'38.92" W), in an upper stretch of the Rio dos Sinos in the municipality of Caraá, Rio Grande do Sul state, southern Brazil (Fig. 1). The Rio dos Sinos basin is heavily impacted mainly owing to the untreated wastewater coming from growing urbanization and industrialization, especially leather and footwear industry (Figueiredo *et al.* 2010). However, the upper Rio dos Sinos is characterized by rural development and is much less impacted with greater native vegetation cover compared to the densely populated and heavily industrialized middle and lower sections (Figueiredo *et al.* 2010). Regional climate of South Brazil is subtropical with frequent and well distributed rainfall along the seasons. According to Köppen-Geiger climate classification (Beck *et al.* 2018), the region has a cfb climate type, humid subtropical, with hot and humid summers, and cool to mild winters. Water temperature during the sampling period ranged from 26.8°C (January) to 12.8°C (July) (Dala-Corte & Azevedo 2010). At the sampling site, the river ranges from 21 to 30 m in width and includes rapids interspersed by pools and relatively well-preserved riparian vegetation. In the stretches with rapids, the water flow is fast, the depth is less than one meter, and the bottom consists predominantly of stones of various sizes and gravel. In pools, the depth can exceed two meters, and the bottom is composed of sediments, organic matter, and leaves. The sampled section is close to the headwaters, located 20.8 km from the source, at an elevation of around 60 m above sea level (Dala-Corte & Azevedo 2010).

Sampling was performed by seine net (three hauls; 10x2 m net size; 5 mm mesh size), dip net (20 benthic samplings; 60x40 cm rim size; 2 mm mesh size), and gill net (12 h of exposure; 10x1.5 m net size for each mesh size of 15, 20, 25, 30, 35, 40 mm). Sampled fish were anesthetized with Eugenol (clove oil; 70 mg/L) and then fixed in 10% formalin solution. The fish specimens were transferred to 70% ethanol in the laboratory and identified to species level. Voucher specimens were cataloged in

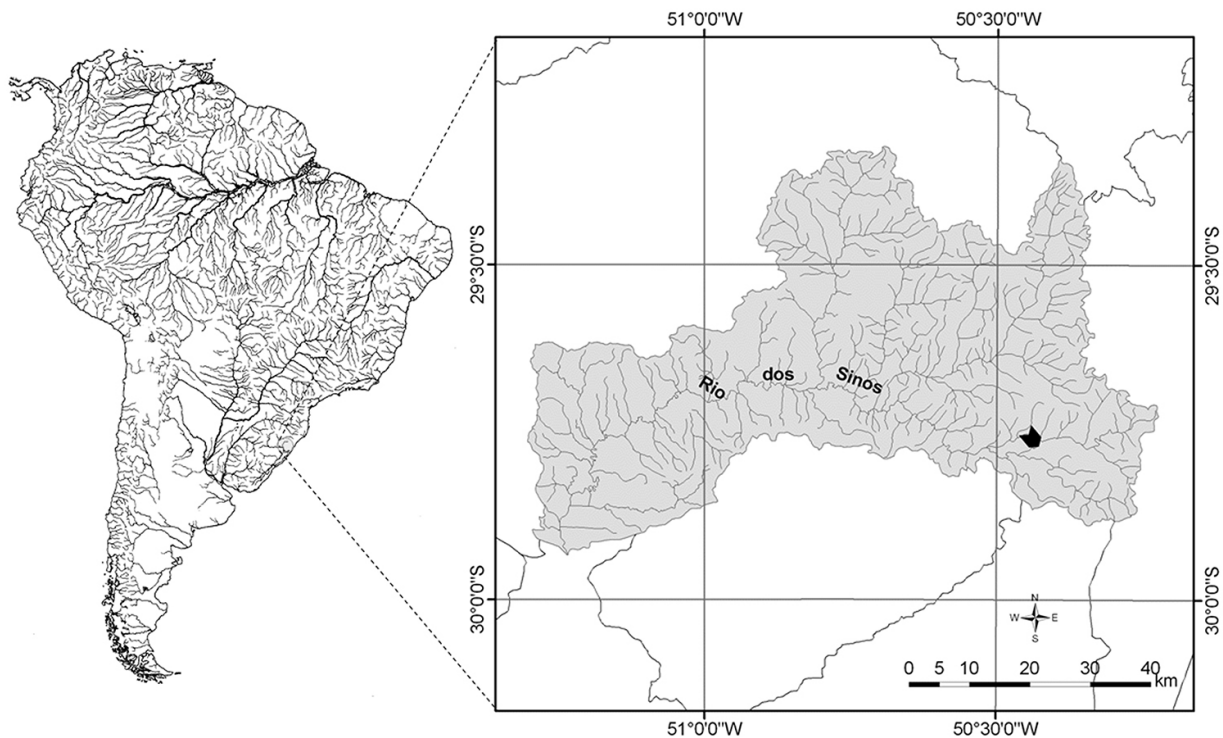


Figure 1. Sampling site location (indicated by an arrow in the zoom map) of characins in upper Rio dos Sinos, Cará municipality, Rio Grande do Sul state, Southern Brazil, sampled between January to December 2007.

the fish collection of Museu de Ciências Naturais, Divisão de Pesquisa e Manutenção de Coleções Científicas, Secretaria Estadual de Meio Ambiente e Infraestrutura do Rio Grande do Sul, Brazil.

Specimens were measured (standard length - SL; mm), weighed (total weight; g), and had their stomachs dissected and weighed. For diet analysis, stomach contents were observed and identified under a stereomicroscope. Food items were grouped into broad categories as follows: allochthonous insects (Allo Ins); autochthonous insects (Aut Ins); allochthonous invertebrates other than insects (Allo Inv); autochthonous invertebrates other than insects (Aut Inv); superior vegetal matter (SVM); sediment (Sed); Algae; fish parts (Fish); diverse organic items not included in the other categories (OM); and debris, inorganic matter (Deb). From the total, there were only 12 empty stomachs, which were not included in the subsequent analyses.

Stomach content analysis was based on the frequency of occurrence (FO, the number of stomachs with a particular food category divided by the total number of stomachs) (Hynes 1950) and volumetric frequency (VO, estimated according to the quantitative contribution of each item as determined by the number of squares occupied by each item on a scaled paper in relation to the total

number of squares occupied by all items) (Hyslop 1980; Dias *et al.* 2017). The relative importance of each food category was defined through the alimentary index (IA_i) (Kawakami & Vazzoler 1980), calculated according to the formula: $IA_i = [(Foi \times Voi) / \sum(Foi \times Voi)] \times 100$, where *i* = food item; Fo = frequency of occurrence; and Vo = volumetric frequency. Feeding data were analyzed for each population using descriptive statistics aiming to provide a general overview of the dietary composition of each species for the subsequent investigation of the ontogenetic influence on feeding preferences.

Astyanax henseli (MCN 18.893), *Astyanax lacustris* (MCN 20.034), *Bryconamericus iheringii* (MCN 20.033), *Diapoma thauma* (MCN 20.035) and *Deuterodon luetkenii* (MCN 20.036) were the five most abundant characids among the 39 fish species sampled at the study site in the upper Rio dos Sinos (R. B. Dala-Corte, unpublished data). The diet of the aforementioned species was analyzed according to standard length classes (SLCs) defined through the Sturges method (Vieira 1991), to determine possible influences of body size (ontogeny) on feeding habits (Table I). Size of the individuals captured for each species ranged as follows: *A. henseli* (27.4-88.9 mm); *A. lacustris*

(37.1-44.0 mm); *B. iheringii* (31.2-61.8 mm); *D. thauma* (26.4-48.6 mm); and *D. luetkenii* (28.5-43.3 mm).

Interspecific differences in diet and intraspecific ontogenetic differences in diet were tested through a Permutational Multivariable Analysis of Variance (PERMANOVA) with 999 permutations, based on a Bray-Curtis similarity matrix, using individual V_o values transformed as relative values per stomach. The PERMANOVA was performed with the functions *adonis* from the vegan package (Oksanen *et al.* 2020), for R environment (R Core Team 2020). To determine the contribution of the different food categories found using PERMANOVA, a similarity of percentage (SIMPER) (Clarke & Gorley 2006) was calculated using the food items as samples and species as factors. Later, averaged IA_i values were calculated per size class, which were used to generate a non-metric multidimensional scaling (NMDS) ordination intended to visualize intra and interspecific diet overlap, which was made with the function *metaMDS* of the vegan package (Oksanen *et al.* 2020).

The degree of diet specialization of each species was determined by calculating Levin's index (Krebs 1989) for trophic niche breadth using V_o values. To standardize the measurement of trophic niche, Hurlbert's Formula (Hurlbert 1978) was calculated, which can range from 0 to 1, as: $Ba_i = \{[1 / (n - 1)] / [(1 - \sum p_{ij}^2) - 1]\}$, where: Ba_i = standardized Levin's index for predator i ; p_{ij} = proportion of predator i diet that consists of prey j ;

and n = total number of alimentary items. Trophic niche breadths were classified as high (> 0.61), intermediary (0.41 to 0.6), or low (< 0.4) (Novakowski *et al.* 2008).

Diet overlap among species was determined through pairwise comparisons using the Morisita Index (Krebs 1989), which can range from 0 to 1, with 0 indicating a lack of diet overlap and 1 indicating complete overlap. Values equal to or higher than 0.6 indicate a significant diet overlap, as proposed by Amundsen *et al.* (2003).

Results

A total of 849 individuals were analyzed, being 332 *A. henseli*, 55 *A. lacustris*, 159 *B. iheringii*, 197 *D. thauma*, and 106 *D. luetkenii*.

Interspecific variation: Astyanax henseli and *A. lacustris* had a dietary preference for allochthonous insects ($IA_i = 89.06\%$ and 95.97% , respectively), which were very similar to *Diapoma thauma* ($IA_i = 98.93\%$). *Bryconamericus iheringii* consumed mainly algae ($IA_i = 66.52\%$), but complemented its diet with allochthonous insects and sediment ($IA_i = 15.1\%$, 12.58% , respectively). *Deuterodon luetkenii* had a tendency to herbivory, feeding mainly on superior vegetal matter ($IA_i = 85.68\%$), complemented with allochthonous insects ($IA_i = 12.65\%$). Other items such as allochthonous and autochthonous invertebrates, and fish had low representation among the species' diets (Table II). Values of F_o , V_o , and IA_i for the food items consumed by the five studied species are available in the Supplementary material (Table SI).

Table I. Standard length classes (SLC) intervals in millimeters for each of the five-studied characid species followed by the number of individuals analyzed in each class in parentheses.

	<i>Astyanax henseli</i>	<i>Astyanax lacustris</i>	<i>Bryconamericus iheringii</i>	<i>Diapoma thauma</i>	<i>Deuterodon luetkenii</i>
SLC1	< 27.4 (n = 25)	< 37.08 (n = 39)	< 31.16 (n = 11)	< 26.35 (n = 7)	< 28.48 (n = 19)
SLC2	27.41 - 37.64 (n = 75)	37.09 - 44.02 (n = 7)	31.17 - 37.29 (n = 23)	26.36 - 30.79 (n = 10)	28.49 - 33.43 (n = 38)
SLC3	37.65 - 47.88 (n = 71)	> 44.03 (n = 9)	37.3 - 43.42 (n = 45)	30.8 - 35.23 (n = 39)	33.44 - 38.38 (n = 21)
SLC4	47.89 - 58.12 (n = 57)		43.43 - 49.55 (n = 29)	35.24 - 39.67 (n = 62)	38.39 - 43.33 (n = 18)
SLC5	58.13 - 68.36 (n = 35)		49.56 - 55.68 (n = 18)	39.68 - 44.11 (n = 49)	> 43.34 (n = 49)
SLC6	68.37 - 78.6 (n = 32)		55.69 - 61.81 (n = 16)	44.12 - 48.55 (n = 24)	
SLC7	78.61 - 88.84 (n = 16)		> 61.82 (n = 16)	> 48.56 (n = 16)	
SLC8	> 88.85 (n = 21)				

The PERMANOVA analysis indicated interspecific differences in the diet of the five studied species ($F = 47.89$, $R^2 = 0.185$, $p < 0.001$), with allochthonous insects, superior vegetal matter, and algae being the main items responsible for the observed differences (Fig. 2). Nonetheless, despite these differences, *A. henseli*, *A. lacustris*, and *D. thauma* tended to show some diet overlap by their great ingestion of allochthonous insects (Figure 3).

In general, low niche breadths (lower niche breadth = higher specialization) were observed for *A. henseli* ($Ba=0.23$), *A. lacustris* ($Ba=0.21$), and *D. thauma* ($Ba=0.13$), indicating a trend towards dietary specialization. On the other hand, intermediate niche breadths were found for *D. luetkenii* and *B. iheringii* ($Ba=0.41$ and $Ba=0.48$, respectively), thus representing a relatively more generalistic diet. Regarding diet niche, high diet overlap was observed among *A. henseli*, *A. lacustris*, and *D. thauma* (Morisita index values of 0.99), due

to the predominance of allochthonous insects in the diet of these species (Tables II, III). All the other species pairs exhibited low diet overlaps (indices around 0.10 to 0.25) (Fig. 3).

Intraspecific variation: Differences in the diet of *A. henseli* were observed when comparing the different size classes (SLCs) ($R^2=0.05$, $p=0.003$). These differences were related to the greater ingestion of allochthonous insects and autochthonous insects in smaller SLCs, with a progressive increase of superior vegetal matter and a decrease in allochthonous insects in larger SLCs. *Astyanax lacustris* also showed a greater ingestion of allochthonous insects in smaller SLCs, which became progressively substituted by superior vegetal matter and fish in higher SLCs ($R^2=0.13$, $p=0.015$, $df=2,52$). For *D. thauma*, there was no significant difference in the diet among size classes ($R^2=0.03$, $p=0.564$, $df=6,188$).

Table II. Alimentary index (IAi%) of the food items consumed by five characid species. Values > 50.01% indicate the main food category (dark gray); between 1.01% and 50% (light gray) indicate additional food category; and < 1% indicate accidental food category (white). Allochthonous insects (Allo Ins); autochthonous insects (Aut Ins); allochthonous invertebrates (Allo Inv); autochthonous invertebrates (Aut Inv); superior vegetal matter (SVM); sediment (Sed); Algae; fish parts (Fish); diverse organic items (OM); debris, inorganic matter (Deb).

IAi	<i>Astyanax henseli</i>	<i>Astyanax lacustris</i>	<i>Bryconamericus iheringii</i>	<i>Diapoma thauma</i>	<i>Deuterodon luetkenii</i>
Allo Ins	89.07	95.97	15.11	98.93	12.65
Aut Ins	0.58	0.053	0.39	0.85	0.97
Allo Inv	0.03	0.01	<0.01	<0.01	<0.01
Aut Inv	0.31	0	0.33	<0.01	0.10
Fish	0.14	0.82	0.04	<0.01	<0.01
SVM	9.85	3.11	5.00	0.19	85.68
Algae	<0.01	0	66.53	<0.01	0
Sed	<0.01	0.02	12.58	<0.01	0.57
Deb	<0.01	0	<0.01	<0.01	0
OM	<0.01	0	<0.01	<0.01	<0.01

Table III. Morisita index for food overlap calculated from a paired comparison of five characid species from upper Rio dos Sinos.

	A. <i>henseli</i>	A. <i>lacustris</i>	B. <i>iheringii</i>	D. <i>thauma</i>	D. <i>luetkenii</i>
<i>A. henseli</i>	1				
<i>A. lacustris</i>	0.99	1			
<i>B. iheringii</i>	0.22	0.21	1		
<i>D. thauma</i>	0.99	0.99	0.2	1	
<i>D. luetkenii</i>	0.25	0.18	0.1	0.15	1

Bryconamericus iheringii exhibited non-significant but greater ingestion of allochthonous insects and sediment in the smaller SLCs, replaced by a higher

ingestion of algae in larger SLCs ($R^2=0.06$, $p=0.066$, $df=6,152$). Lastly, *D. luetkenii* exhibited a greater ingestion of allochthonous insects in the smaller SLCs and greater ingestion of superior vegetal matter in the larger SLCs ($R^2=0.15$, $p=0.001$, $df=4,96$). Smaller sizes tended to eat more insects or invertebrates, but *D. thauma* showed a homogeneous diet along its growth (Figure 3). The values of F_o , V_o and IAi according to SLC are provided in the Supplementary Material (Table SII).

Discussion

Our results indicated that the five small-sized characid fish species were able to feed on items of different origins, from different sources, but with a high ingestion of allochthonous insects, mainly by *A.*

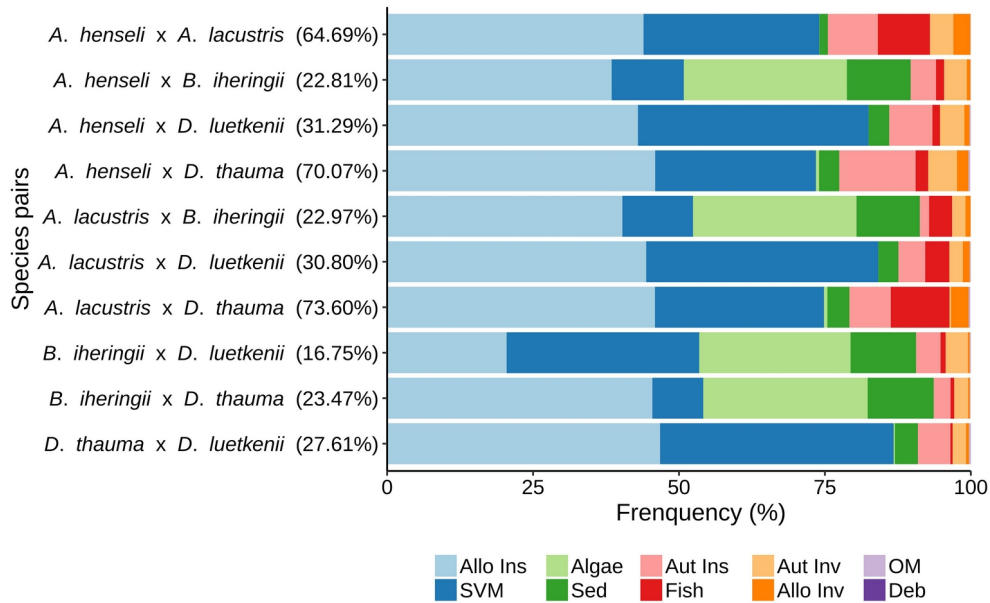


Figure 2. Interspecific differences in diet evaluated through similarity of percentage (SIMPER) analysis with paired comparisons for five characid species from upper Rio dos Sinos. Average similarity between species pairs are shown within parentheses. The contribution of each food item for the dissimilarity between species pairs are shown: allochthonous insects (Allo Ins); autochthonous insects (Aut Ins); allochthonous invertebrates (Allo Inv); autochthonous invertebrates (Aut Inv); superior vegetal matter (SVM); sediment (Sed); Algae; fish parts (Fish); diverse organic items (OM); debris, inorganic matter (Deb).

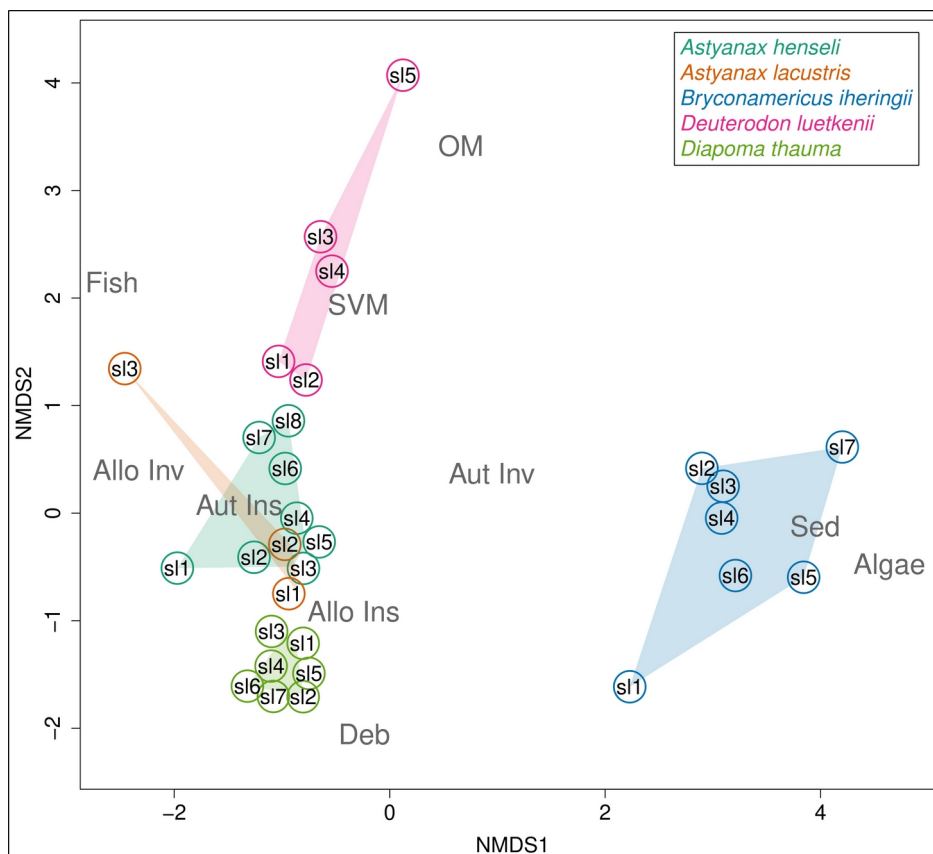


Figure 3. Non-metric multidimensional scaling (NMDS) ordination showing intra and interspecific diet overlap. Size classes (standard length classes - sl) represent mean values of IAI (diet important) for distinct size classes, with lower values respective to smaller size classes. Allochthonous insects (Allo Ins); autochthonous insects (Aut Ins); allochthonous invertebrates (Allo Inv); autochthonous invertebrates (Aut Inv); superior vegetal matter (SVM); sediment (Sed); Algae; fish parts (Fish); diverse organic items (OM); debris, inorganic matter (Deb).

henseli, *A. lacustris*, and *D. thauma*, generating a high diet overlap among these species. On the other hand, *B. iheringii* consumed a greater proportion of algae and *D. luetkenii* a greater proportion of superior (vascular) vegetal matter; thus, both showing a reduced diet overlap with the other species. In general, diet niche breadths for the five species were low, suggesting trophic specialization, which is in opposite to what is expected for these species according to the literature. These results only partially support our first hypothesis that all the characid species would present a high diet niche overlap, predominantly omnivorous, with a high similarity between the two *Astyanax* species due to their closer phylogenetic relationship. On the other hand, we did not find support for our second hypothesis that ontogenetic differences in diet would be more pronounced in larger species. Except for *D. thauma*, all the other four species showed ontogenetic shifts in their feeding preferences, as evidenced by diet differences among size classes. Juveniles tended to consume a greater proportion of animal origin matter and, progressively, replaced animal food items (insects and other invertebrates) by vegetal origin items (algae or superior vegetal matter) along with their growth. *Diapoma thauma*, on the other hand, showed a great specialization in allochthonous insects, which was maintained constant along its ontogenetic development. Furthermore, the higher ingestion of allochthonous items observed for all the species demonstrates the importance of the riparian vegetation in providing food for supporting the studied characid populations.

The results only partially support our first hypothesis that all the five characins would present a great diet overlap, mainly the two congeneric species of *Astyanax*. Although the diets of the species studied herein were relatively similar, quantitative analysis of the ingested food items and the short trophic niche breadths observed for the majority of these species suggested trophic preferences and diet niche segregation for some species. Such preference for a certain type of food resource may reflect specific morphological and/or behavioral adaptations. For instance, characteristics such as a shallow body, a small head, and a small subterminal (or terminal) mouth of *B. iheringii* indicate its ability or preference to occupy the benthic region and to consume items from the substrate bottom, mainly periphyton (Castro & Carvalho 2015). In addition, the relatively long intestine of this species may be serving to provide a more effective digestion of algae and other vegetal

materials, and sediment or detritus (Borges *et al.* 2006, Dala-Corte *et al.* 2016a). The presence of a greater variety of items in the stomachs of *B. iheringii* (insects, vegetal matter, sediment, and algae) compared to the other species studied may explain its intermediary niche breadth values, corroborating its generalist feeding behavior and remarkable adaptive capacity on feeding habits (Dala-Corte *et al.* 2016a).

A tendency for omnivory in *Deuterodon luetkenii* (former *Hyphessobrycon luetkenii*) has been reported in other populations of the species (Graciolli *et al.* 2003, Casciotta *et al.* 2005), but in our study the species consumed a great proportion of superior vegetal matter. In another river, close to the drainage where we conducted our study, Graciolli *et al.* (2003) also found that *D. luetkenii* ingested superior vegetal matter as the main food item, but in a much lower proportion compared to our study (17% versus 85%). This suggests that *D. luetkenii* can adjust its diet according to local environmental conditions and possibly to potential competition with other sympatric species.

The low niche breadth and feeding specialization towards allochthonous insects found for *D. thauma* corroborate the findings of Graciolli *et al.* (2003) for other species within the genus *Diapoma* Cope 1894. The authors reported that *D. speculiferum* Cope 1894 feeds mainly on allochthonous insects, even in autumn and winter when they tend to be less abundant, suggesting that *D. speculiferum* is a typical surface eater adapted to catch items from the water's surface before they sink. *Diapoma thauma* may also present a preference for catching food items on the surface, which may compensate for its diet overlap with the other two species of *Astyanax* Baird & Girard 1854 that consumed a great proportion of allochthonous insects. In addition, this result may suggest that riparian vegetation has an important contribution to the feeding ecology of *D. thauma*.

According to literature, the species of *Astyanax* have been described as having great trophic plasticity, being most commonly classified as omnivores (e.g. Castro & Casatti 1997, Lobón-Cervía & Benemann 2000, Graciolli *et al.* 2003, Oliveira & Benemann 2005, Esteves *et al.* 2008, Mazzoni *et al.* 2010b, Ferreira *et al.* 2012). The *Astyanax* species usually have a high efficiency at performing vertical movements, in addition to a high swimming capacity and efficient mouth traits, which together allow them to use a wide variety of resources (Prado *et al.* 2016). Differing from most

studies, the species of *Astyanax* (*A. henseli* and *A. lacustris*) in the present study consumed predominantly allochthonous insects. This preference is likely explained because allochthonous insects are the most caloric and probably the most abundant food item available in the environment. In addition, the high dietary overlap observed between the two *Astyanax* species indicates that both species have a high niche similarity and are potential competitors for exploiting similar habitats and food items. However, the existence of true competition needs to be further evaluated, because other factors not studied herein, such as spatial segregation at microhabitat scale or temporal segregation (feeding period), may diminish or even prevent competition.

When species that use the same resources coexist, we assume they explore resources differently, or that they consume the same but abundant resources (Pianka 1994). Sometimes, even small variations in diet can facilitate coexistence among species (Hynes 1970, Gatz 1979). These factors may explain the coexistence of the two studied species of *Astyanax* with a high diet overlap, even if both species tend to have similar pelagic habit. In addition, *D. thauma* had also a high diet overlap with the *Astyanax* species; however, *D. thauma* individuals are spatially segregated from the *Astyanax* in the river, occupying mostly the margins with dense shading from riparian vegetation (author's personal observation). *Bryconamericus iheringii*, on its turn, segregates spatially from the other species for its benthopelagic habit, sometimes occupying riffles with mid to strong flow, and probably foraging periphyton from the streambed (author's personal observation). Finally, *D. luetkenii* seems to overlap its habitat with the *Astyanax* species and *D. thauma*, but its diet was rather different from the other species as it consumed mainly superior vegetation matter. Therefore, niche segregation for these five similar sympatric species may be a plausible explanation that allows their coexistence. Conversely, Moraes *et al.* (2013) found high food overlap among four characid species in a stream of the upper Tocantins basin and inferred that resources were not limited and that the populations were not regulated by competition. Thus, an open question is to uncover the degree to which resource limitation or niche segregation contribute to define diet overlap and the coexistence of different fish species.

Our second hypothesis that ontogenetic shifts in diet would be more evident in larger species was not supported by the results. Only one small-sized

species (*D. thauma*) did not show ontogenetic variation in diet, while two others with similar size range (*A. lacustris* and *D. luetkenii*) showed a shift from invertebrates to vegetal items along with the growth. Even for *A. lacustris*, whose large and adult individuals were not in our samplings, presented shifts in its diet. These results may be explained by the different degree of diet specialization of the species. *Diapoma thauma* revealed a great diet specialization, with both juveniles and adults feeding basically on allochthonous insects only. The other two species (*A. lacustris* and *D. luetkenii*) are usually known as generalists, with a great potential for adaptation according to the available resources (Gracioli *et al.* 2003; Casciotta *et al.* 2005). In addition, except for *D. thauma*, all the other studied species (*A. henseli*, *A. lacustris*, *B. iheringii*, and *D. luetkenii*) can be inferred to be omnivorous and generalist according to the literature. However, contrary to the expectation, the species studied here showed a greater tendency to specialize in one type of food resource, which may be related to the amount and quality of resources available. Therefore, it seems that the ontogenetic variation in the characid populations can be affected by multiple factors, including the degree of specialization, the size range of the population, the presence of competition, and the amount of resources available.

Neotropical characids are reported to undergo ontogenetic dietary shifts from animal to vegetal source items, such as terrestrial insects to fruits and leaves (Drewe *et al.* 2004). For instance, Borges *et al.* (2006) found that *B. aff. iheringii* exhibited a decrease in the ingestion of animal items and an increase in the ingestion of algae with the growth. Our results partially corroborate the ontogenetic shifts in the diet of characids, as four out of the five studied species showed a clear change from animal to vegetal source items. Characid juveniles preyed mostly on insects and other invertebrates while adults included a larger proportion of algae or superior vegetal matter in their diets. These shifts during life stage transitions may increase resource partitioning and may be accompanied by a reduction in intraspecific competition within the fish population (Elliott 1967; Amundsen *et al.* 2003; Oscoz *et al.* 2006). However, the differences in the proportion of some food items found among some size classes of the studied species were not sufficient to change the general diet pattern of the species. On the other hand, they may represent a contribution to resource partitioning and may increase overall fitness of a given species, which could facilitate the

coexistence among the five sympatric characid species.

The findings of the present study support the inference that both intra and interspecific resource partitioning are important for the coexistence of the five similar characid species in the upper Rio dos Sinos. Intraspecific resource partitioning was clear when comparing juvenile and adult fish, but one specialized species did not present ontogenetic differences. Interspecific resource partitioning was not prevalent, as three out of five species showed high diet niche overlap. This suggests that the ecological characteristics of Rio dos Sinos offer food items in sufficient quantity and quality to maintain populations of multiple species of characid. In this regard, the riparian vegetation may be essential in promoting this coexistence, as allochthonous items were very important in the diet of the species. The degree of resource partitioning observed among similar fish species in the studied river site suggests that sympatric characid populations may adapt their diet according to the coexistence with other potential competing species. This adaptation may depend on the quality and quantity of food available, so some coexisting similar omnivorous characid species may present markedly different diets. In addition, the reduced intraspecific diet overlap observed in the most studied characins may reduce the impact that competition among individuals of the same or different species may have on these fish populations.

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Ethics statement

Collection of fish and other biological samples were conducted following all applicable

ethical regulations regarding experimentation with animals.

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Food resource partitioning among sympatric populations of five species of freshwater fish (Characidae) in southern Brazil

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Supplementary material

Table SI. Frequency of occurrence (Fo%), Volumetric frequency (Vo%), and Alimentary index (IAi%) of the food items consumed by five characid species from upper Rio dos Sinos. Unid. = unidentified; autoch = autochthonous; alloch = allochthonous.

Alimentary Items	<i>A. henseli</i>			<i>A. lacustris</i>			<i>B. iheringii</i>			<i>D. thauma</i>			<i>D. luetkenii</i>		
	Fo	Vo	IAi	Fo	Vo	IAi	Fo	Vo	IAi	Fo	Vo	IAi	Fo	Vo	IAi
Platyhelminthes	0.60	0.28	<0.01	0	0	0	0	0	0	1.01	0.02	<0.01	0	0	0
Mollusca	4.21	0.72	0.04	0	0	0	8.17	0.66	0.08	0	0	0	2.83	0.06	<0.01
Arachnida															
Araneae	3.91	0.49	0.03	3.63	0.90	0.04	1.88	0.07	<0.01	4.56	0.40	0.02	0.94	0.10	<0.01
Hydracarina	0.30	<0.01	<0.01	0	0	0	0.62	<0.01	<0.01	0	0	0	0	0	0
Collembola	0.30	<0.01	<0.01	0	0	0	0	0	0	0	0	0	0	0	0
Crustacea Unid.	0.30	0.01	<0.01	0	0	0	5.66	0.34	0.03	1.01	0.10	<0.01	2.83	0.09	<0.01
Microcrustacea	5.42	0.55	0.04	0	0	0	2.51	0.02	<0.01	0.50	<0.01	<0.01	9.43	0.14	0.02
Cladocera	0.90	0.01	<0.01	0	0	0	0	0	0	0	0	0	0	0	0
Insecta															
Blattodea	0.90	0.21	<0.01	0	0	0	0	0	0	0	0	0	0	0	0
Coleoptera	25.60	5.07	2.04	9.09	4.19	0.56	5.03	0.18	0.01	7.61	0.81	0.07	2.83	0.45	0.01
Curculionidae	0.60	0.06	<0.01	1.81	0.22	<0.01	0	0	0	0	0	0	0	0	0
Curculioniform															
larvae	0.60	0.31	<0.01	0	0	0	0	0	0	0	0	0	0	0	0
Elateridae larvae	0.30	0.01	<0.01	1.81	0.45	0.01	0	0	0	0	0	0	0	0	0
Unid. Coleoptera															
larvae	0.30	<0.01	<0.01	1.81	0.83	0.02	0	0	0	0	0	0	0	0	0
Dermaptera	0.60	0.01	<0.01	0	0	0	0	0	0	0.50	0.04	<0.01	0	0	0
Diptera	2.10	0.07	<0.01	3.63	0.11	<0.01	0.62	<0.01	<0.01	3.04	0.51	0.01	0.94	<0.01	<0.01

Alimentary Items	<i>A. henseli</i>			<i>A. lacustris</i>			<i>B. iheringii</i>			<i>D. thauma</i>			<i>D. luetkenii</i>		
	Fo	Vo	IAi	Fo	Vo	IAi	Fo	Vo	IAi	Fo	Vo	IAi	Fo	Vo	IAi
Brachycera Unid. Diptera	3.01	0.56	0.02	0	0	0	0	0	0	0.50	0.06	<0.01	0	0	0
larvae Unid. Diptera	0.30	<0.01	<0.01	0	0	0	0	0	0	0	0	0	0.94	0.01	<0.01
pupae	0.60	0.01	<0.01	0	0	0	0.62	0.01	<0.01	0	0	0	0	0	0
Culicidae Ephemeroptera	3.31	0.23	0.01	3.63	0.45	0.02	1.25	<0.01	<0.01	5.58	0.28	0.01	8.49	0.14	0.01
larvae (autoch) Ephemeroptera	6.92	0.16	0.01	0	0	0	0.62	0.01	<0.01	0	0	0	0	0	0
nymph (autoch)	6.02	0.52	0.05	0	0	0	10.06	0.40	0.06	8.12	0.49	0.04	7.54	0.38	0.04
Hemiptera (autoch) Hemiptera larvae	0.30	0.01	<0.01	0	0	0	0	0	0	1.52	0.05	<0.01	0	0	0
(autoch)	2.71	0.24	0.01	1.81	0.26	<0.01	6.91	0.09	0.01	3.55	0.09	<0.01	5.66	0.10	<0.01
Hemiptera (alloch) Sternorrhyncha	0	0	0	0	0	0	0	0	0	0.50	0.01	<0.01	0	0	0
(alloch) Auchenorrhyncha	0.30	0.12	<0.01	0	0	0	0	0	0	0	0	0	0	0	0
(alloch)	4.21	0.69	0.04	0	0	0	0.62	0.07	<0.01	1.52	0.06	<0.01	0	0	0
Hymenoptera	38.55	5.02	3.04	56.36	9.12	7.66	6.91	0.10	0.01	17.25	1.37	0.27	8.49	0.62	0.07
Isoptera	2.10	0.39	0.01	0	0	0	0	0	0	0	0	0	0	0	0
Lepidoptera Eruciform larvae	0.90	0.21	<0.01	0	0	0	0	0	0	0.50	0.17	<0.01	0	0	0
(alloch)	3.61	1.28	0.07	0	0	0	3.77	0.31	0.01	0	0	0	2.83	0.38	0.01
Odonata	0.60	0.19	<0.01	0	0	0	0.62	0.03	<0.01	1.52	0.03	<0.01	1.88	0.06	<0.01
Zygoptera Odonata nymph	1.20	0.84	0.01	0	0	0	0	0	0	0	0	0	0	0	0
(autoch)	3.91	0.80	0.05	0	0	0	2.51	0.28	0.01	5.07	1.93	0.11	1.88	0.14	<0.01
Orthoptera	1.20	0.07	<0.01	1.81	0.45	0.01	1.88	0.04	<0.01	0	0	0	0.94	0.13	<0.01
Ensifera	0.60	0.04	<0.01	0	0	0	0	0	0	0.50	0.01	<0.01	0	0	0
Thysanoptera	0.90	<0.01	<0.01	0	0	0	1.88	0.01	<0.01	0.50	0.01	<0.01	0	0	0
Unid. Insect larvae Unid. Insect	5.42	0.38	0.03	3.63	1.96	0.10	24.52	0.89	0.34	8.62	0.90	0.08	15.09	0.74	0.16
hatched pupae	1.80	0.04	<0.01	0	0	0	0.62	0.01	<0.01	0.50	0.01	<0.01	0.94	0.02	<0.01
Insect parts	89.75	55.34	78.10	89.09	64.37	85.42	61.63	10.70	10.27	95.43	90.12	99.07	49.05	7.82	5.69
Insect eggs	6.02	0.15	0.01	1.81	0.37	0.01	1.88	0.04	<0.01	2.03	0.21	<0.01	3.77	0.96	0.05
Unid. Arthropoda	0.60	0.22	<0.01	0	0	0	0	0	0	0	0	0	0	0	0
Fish	0.30	0.04	<0.01	0	0	0	0	0	0	0	0	0	0	0	0
Fish bones	0.30	0.01	<0.01	0	0	0	0	0	0	0	0	0	0	0	0
Fish scales	6.62	0.67	0.07	12.72	5.74	1.08	6.28	0.27	0.02	1.01	0.06	<0.01	1.88	0.14	<0.01
Ichthyoplankton Superior Vegetal	1.80	0.42	0.01	0	0	0	1.25	0.02	<0.01	0	0	0	0	0	0
Matter	47.28	21.67	16.11	32.72	10.20	4.97	49.68	7.04	5.45	12.69	1.71	0.25	74.52	84.20	93.04
Algae	0.30	<0.01	<0.01	0	0	0	79.24	45.99	56.77	0.50	0.10	<0.01	0	0	0
Unid. hair	1.50	0.01	<0.01	0	0	0	1.88	0.02	<0.01	0.50	0.08	<0.01	1.88	0.18	<0.01
Sediment	3.61	1.61	0.09	3.63	0.30	0.01	53.45	32.27	26.87	3.55	0.18	<0.01	17.92	3.03	0.80
Inorganic Matter	0.60	<0.01	<0.01	0	0	0	1.88	<0.01	<0.01	2.53	0.05	<0.01	0	0	0

Table SII. Alimentary index (IAi%) of the food categories found in the diet of each SLC of five characid species from upper Rio dos Sinos. Standard Length Class (SLC); allochthonous insects (Allo Ins); autochthonous insects (Aut Ins); allochthonous invertebrates (Allo Inv); autochthonous invertebrates (Aut Inv); fish parts (Fish); superior vegetal matter (SVM); Algae; sediment (Sed); debris, inorganic matter (Deb); diverse organic items (OM).

		Allo Ins	Aut Ins	Allo Inv	Aut Inv	Fish	SVM	Algae	Sed	Deb	OM
<i>A. henseli</i>	SLC1	83.73	11.69	0	0.03	0	4.52	0	0	0	0
	SLC2	94.12	0.69	0.18	0.06	<0.01	4.92	0	<0.01	0	0
	SLC3	95.17	0.52	0.03	0.39	0.08	3.79	0	0	<0.01	<0.01
	SLC4	92.76	0.64	0.08	0.42	0.12	5.93	<0.01	0.01	<0.01	<0.01
	SLC5	93.99	0.02	<0.01	0.33	0.10	5.47	0	0.05	0	<0.01
	SLC6	79.86	0.43	0	0.04	0.03	19.61	0	<0.01	0	0
	SLC7	73.90	0.32	0	0.27	1.98	23.50	0	<0.01	0	0
	SLC8	65.63	0.44	0	0.99	0.32	32.55	0	0.04	0	<0.01
<i>A. lacustris</i>	SLC1	97.44	0.02	0	0	0.16	2.34	0	0.03	0	0
	SLC2	93.77	0.73	0	0	0	5.48	0	0	0	0
	SLC3	51.20	0	1.60	0	21.60	25.60	0	0	0	0
<i>D. thauma</i>	SLC1	99.29	0	0	0	0	0.70	0	0	0	0
	SLC2	99.36	0	0.36	0.09	0	0	0	0.18	0	0
	SLC3	98.03	1.06	0	0	0	0.87	0	<0.01	0.01	0
	SLC4	98.98	0.84	<0.01	<0.01	0	0.14	<0.01	<0.01	<0.01	0
	SLC5	99.29	0.50	0.01	<0.01	<0.01	0.14	0	0.02	<0.01	<0.01
	SLC6	97.06	2.82	0.01	<0.01	0.01	0.06	0	0	<0.01	0
	SLC7	99.87	0.12	0	0	0	0	0	0	0	0
<i>B. iheringii</i>	SLC1	55.52	0.39	0	0	0	0.79	10.35	32.92	0	0
	SLC2	25.42	0.15	0	<0.01	0.04	11.73	48.74	13.90	<0.01	0
	SLC3	16.88	0.27	0	0.42	0.06	8.84	65.54	7.96	<0.01	0
	SLC4	21.65	0.42	0.03	1.00	0.02	6.05	58.34	12.45	0	<0.01
	SLC5	9.84	0.08	0	<0.01	0.01	1.34	75.37	13.32	0	0
	SLC6	21.05	1.80	0.02	1.40	0.16	2.96	58.12	14.46	0	0
	SLC7	2.31	0.06	0	0.06	<0.01	4.45	83.09	9.96	0	0.02
<i>D. luetkenii</i>	SLC1	36.42	1.90	0	0.36	0	61.30	0	0	0	0
	SLC2	46.25	1.28	0.03	0.36	0	51.43	0	0.62	0	<0.01
	SLC3	5.79	0.30	0	<0.01	0	93.80	0	0.10	0	0
	SLC4	9.40	1.21	0	0.08	0.01	88.49	0	0.71	0	0.07
	SLC5	0.04	0.22	0	0.04	0.06	97.85	0	1.76	0	0