

Longitudinal and ontogenetic changes in feeding patterns of an insectivorous Crenuchidae in streams of southern Brazil

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Abstract

Longitudinal and ontogenetic changes in feeding patterns of an insectivorous Crenuchidae in streams of southern Brazil. The genus *Characidium* has the highest species richness within the Crenuchidae family and the Characidiinae subfamily. *Characidium pterostictum* holds immense importance due to its widespread distribution in South America, especially in the hydrographic systems of the Uruguay River. The objective of this study is to describe the feeding biology of *Characidium pterostictum* in streams of the Ijuí River basin (Uruguay River system) in southern Brazil and to identify potential spatial and ontogenetic variations in its diet. Samples were collected from three tributaries of the Ijuí River. Food items were identified and quantified using the volumetric method and frequency of occurrence. *Characidium pterostictum* was characterized as an insectivorous fish, a specialization previously reported in Characidiinae. There was a slight difference in feeding patterns based on variations in standard length and sampling sites. Ontogenetic analysis showed that *C. pterostictum* expands its feeding spectrum as it develops. The consumption of autochthonous items such as insect remains (Ephemeroptera, Trichoptera, and Chironomidae) as the primary component of diet indicates that this fish species requires extensive preservation of the watercourses it inhabits.

Key words: *Characidium pterostictum*, Autochthonous resources, Aquatic insects, Fish ecology

Resumen

Cambios longitudinales y ontogénicos en las pautas de alimentación de una especie insectívora de la familia Crenuchidae en arroyos del sur del Brasil. El género *Characidium* es el más rico en especies de la familia Crenuchidae y la subfamilia Characidiinae. *Characidium pterostictum* reviste una inmensa importancia debido a su amplia distribución en América del Sur, en especial en los sistemas hidrográficos del río Uruguay. El objetivo del presente estudio es describir la biología alimentaria de *Characidium pterostictum* en los arroyos de la cuenca del río Ijuí (sistema del río Uruguay) en el sur del Brasil, así como determinar las posibles variaciones espaciales y ontogénicas de su dieta. Se recogieron muestras en tres afluentes del río Ijuí. Se identificaron y cuantificaron los alimentos utilizando el método volumétrico y la frecuencia de presencia. *Characidium pterostictum* se caracterizó como un pez insectívoro, una especialización que ya se había observado en la subfamilia Characidiinae. Existe una ligera diferencia en las pautas de alimentación en función de las variaciones en la longitud estándar de los individuos y los sitios de muestreo. El análisis ontogénico demostró que *Characidium pterostictum* amplía el espectro alimentario a medida que se va desarrollando. El consumo de alimentos autóctonos (restos de insectos, efemerópteros, tricópteros y quironómidos) como principal componente de la dieta indica que esta especie de pez necesita la conservación intensiva de los cursos de agua en los que vive.

Palabras clave: *Characidium pterostictum*, Recursos autóctonos, Insectos acuáticos, Ecología de los peces

Introduction

Among freshwater fishes, the order Characiformes is one of the most diverse in the Neotropical region, comprising approximately 33% of the total species richness (Malabarba and Malabarba 2014). This order is distributed across Africa, South America, Central America, and the southern part of North America. The Crenuchidae family is composed of 116 valid species (Fricke et al 2023), found in a range from the east of Panama to the east of Argentina. These fish inhabit numerous freshwater drainages throughout the Neotropical region (Buckup 2003). Within this family, the Characidiinae subfamily is notably the most diverse, with 111 species (Fricke et al 2023). These small fishes exhibit a wide range of habitats, ranging from lowland streams to fast-flowing streams (Buckup 1993).

The genus *Characidium* Reinhardt 1867, has the highest species diversity within the Characidiinae subfamily, with 85 valid species. It shares the same wide geographic distribution as the Crenuchidae family (Buckup et al 2007, Oliveira-Silva et al 2022, Fricke et al 2023). Among the species in this genus, *Characidium pterostictum* Gomes 1947, is known for its distribution in South America, from the Ribeira de Iguapé River to the Uruguay River basin, encompassing Brazil, Uruguay, and Argentina. In the state of Rio Grande do Sul, Brazil, this species can be found in three hydrographic systems: in the drainages of the River Tramandaí, the Laguna dos Patos, and the River Uruguay (Buckup and Reis 1997). *Characidium pterostictum* is typically found in streams or small rivers with rocky bottoms and clear, fast-flowing water (Buckup and Reis 1997).

In the Uruguay River Basin, a study was conducted to sample streams in three sections (upper, middle, and lower) of the Ijuí River sub-basin, spanning from upstream to downstream along the longitudinal gradient. This study revealed that the species *C. pterostictum* ranked among the five most abundant species out of the six sites sampled over the course of one year (Cavalheiro and Fialho 2020). In fact, this species alone accounted for 19% of all individuals collected in this study and was recognized as one of the dominant species across the three sampled sections of the sub-basin (Cavalheiro and Fialho 2020). Dominant species play a crucial role in their respective habitats, exerting a significant influence over the entire community. Additionally, it is essential to highlight that *C. pterostictum* is a common species in several lotic ecosystems in South Brazil, being dominant in its microhabitat and niche, as supported by examples from the literature (Uieda et al 1997, Aranha et al 2000, Motta and Uieda 2004, Braga 2005, Gomiero and Braga 2008, Braga and Gomiero 2009, Rolla et al 2009, Cavalheiro and Fialho 2020).

One aspect that directly affects the structure and composition of populations is feeding behavior (Barreto and Aranha 2006). Thus, understanding the interactions of these populations within the fish community depends on various factors, such as the breadth of the feeding niche, the position in the trophic chain, ontogenetic and ecomorphological variations, quantification of interactions such as predation and competition, resource partitioning, and feeding selectivity (Esteves

et al 2021). The strategies species use to obtain energy through feeding vary depending on the species and habitat (Wootton 1990, Gerking 1994). Freshwater fishes are known to present several feeding specializations (Aranha et al 2000). Generalist species have a broad spectrum of diet, while in contrast, specialists have a relatively restricted diet, focusing on a small number of species (Gerking 1994). Insectivory specialization has been reported in the Characidiinae subfamily, with a predominant consumption of immature insects. This same pattern is particularly evident in *Characidium* species (Uieda et al 1997, Aranha et al 2000, Motta and Uieda 2004, Braga 2005, Gomiero and Braga 2008, Braga and Gomiero 2009, Rolla et al 2009).

Most teleosts display considerable feeding versatility (Abelha et al 2001). Several studies have reported ontogenetic dietary changes as a common pattern among neotropical freshwater fishes (Motta and Uieda 2004, Adite et al 2005, Wolff et al 2009, Cavalheiro and Fialho 2016, Dala-Corte et al 2016, Dias et al 2017, Cavalheiro and Fialho 2019). The variation in feeding habitats during a species' development illustrates an adaptation related to reduced competition, meeting physiological needs associated with migration, sexual maturation, and reproduction (Braga and Braga 1987, Motta and Uieda 2004). The food spectrum can thus be influenced by both environmental conditions and species biology (Abelha et al 2001).

The objective of the present study was to investigate the feeding behavior of *Characidium pterostictum* in the streams of the Ijuí River sub-basin and to understand aspects of its biology. We hypothesized that, although the Characidiinae subfamily generally exhibits an insectivorous diet, *C. pterostictum* presents similar dietary changes to those observed in other neotropical fish, with different phases of its life cycle showing different specialization in certain food items. Additionally, we examined the hypothesis that the species' diet varies across different locations within the basin, influenced by their position along the upstream-to-downstream gradient.

Material and methods

Study area

Samples of *C. pterostictum* were collected from three streams within the Ijuí River basin, located in the northwest region of the Rio Grande do Sul State, southern Brazil. With drainage of 10,649.13 km², the Ijuí River basin is situated in the middle portion of the Uruguay River hydrographic network. The selection of streams aimed to represent different sections of the Ijuí River sub-basin, including the upper, middle, and lower portions along the longitudinal gradient, progressing from upstream to downstream areas near the mouth of the Ijuí River sub-basin in the Uruguay River (fig. 1).

The Ijuí River is one of the primary tributaries on the left bank of the Uruguay River Basin (Pereira et al 2014, Silva et al 2018). The region's climate features an average annual temperature ranging between 17 and 20°C, with an average annual rainfall ranging from 1,700 to 1,800 mm (Wollmann and Galvani 2012). Land use is mainly agricultural, focusing on direct cultivation,

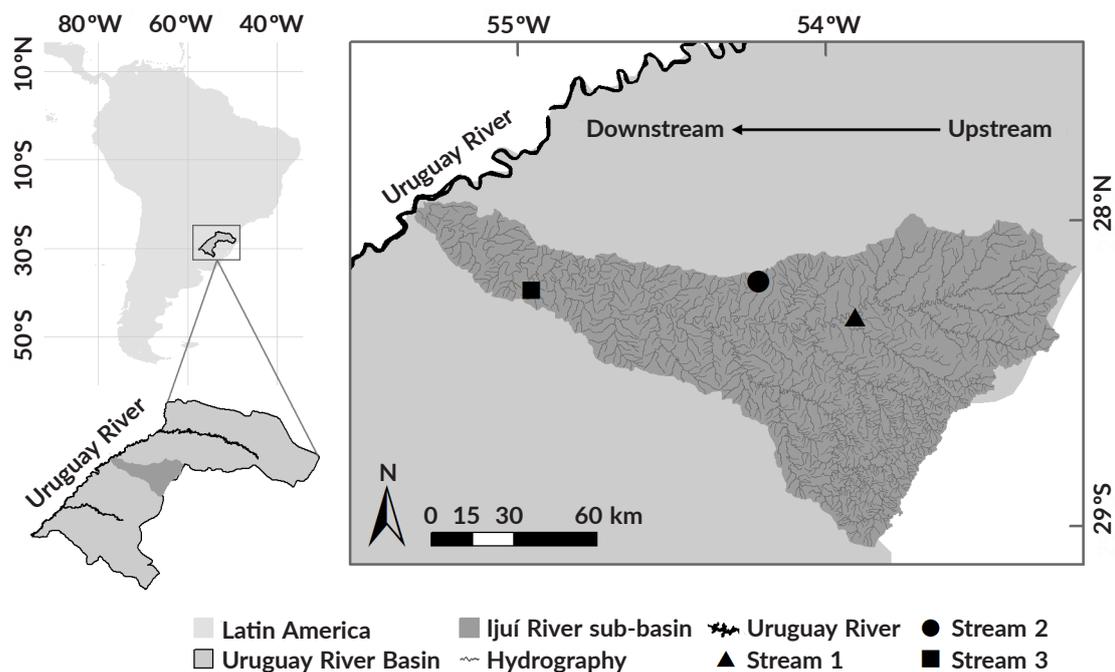


Fig. 1. Location of the sampled streams in the Ijuí River sub-basin and their respective positions within the Uruguay River hydrographic basin, Brazil. The figure shows the sites sampled for *Characidium pterostictum*.

Fig. 1. Ubicación de los arroyos donde se recogieron las muestras en la subcuenca del río Ijuí y sus respectivas posiciones dentro de la cuenca hidrográfica del río Uruguay, en el Brasil. La figura muestra los sitios en los que se recogieron muestras de *Characidium pterostictum*.

particularly of crops such as soybeans, maize, and wheat. During the spring and summer months, farmers cultivate beans, soybeans, and corn, while the winter season witnesses a shift to wheat and oats as primary crops (Melo et al 2010, Silva et al 2018). The sub-basin features fairly homogeneous relief forms characterized by gentle hills and deepening river valleys, sculpted in volcanic rocks with well-developed soils (Scheren and Robaina 2019). Associated with the hills, there are common depressions that form springs and small river courses in the drainage network (Scheren and Robaina 2019).

The first sampled stream ($28^{\circ} 18' 58.4''$ S, $53^{\circ} 54' 7.9''$ W) is in the upper portion of the sub-basin (upstream) and features narrower margins. The second stream ($28^{\circ} 12' 06.2''$ S, $54^{\circ} 13' 06.9''$ W) represents the middle portion of the sub-basin and has an intermediate width between its margins. The third stream ($28^{\circ} 13' 40.8''$ S, $54^{\circ} 57' 24.8''$ W) is situated in the lower portion of the sub-basin (downstream) and is characterized by large stones and broader margins. In these three environments, there are only remnants of riparian, these consisting of narrow strips of trees along the stream margins (fig. 2). Human activities near the streams primarily involve agriculture, with soybean crops, and cattle farming.

Sampling

Samples of *C. pterostictum* were collected bimonthly from July 2015 to May 2016 in the three streams,

resulting in a total of six expeditions for each stream. The sampling was conducted using electric fishing, with an hour of sampling effort per sampling site along a stretch of approximately 100 m. In the field, individuals were anesthetized and euthanized using 10% eugenol (Jenkins et al 2014) and then fixed in 10% formalin. In the laboratory, specimens were selected and identified before being preserved in 70% alcohol. Voucher specimens were deposited in the ichthyological collection of the Departamento de Zoologia, Universidade Federal do Rio Grande do Sul, Brazil (voucher lots: UFRGS 24564, UFRGS 24565, UFRGS 24566).

Fieldwork and sampling were conducted under a scientific collection permit (Permit Number 48291-1) issued by the Instituto Chico Mendes de Conservação da Biodiversidade, Ministério do Meio Ambiente, Brasília (Distrito Federal, Brazil). This study was carried out in accordance with approved protocols for ethical and methodological aspects of fish use by the Ethics Committee on Animal Use of the Universidade Federal do Rio Grande do Sul, Brazil (Permit Number 35495).

Data analysis

To conduct the analysis, all captured individuals were included, except in cases where the number exceeded 40 specimens per sampling unit. When more than 40 fish were collected in a sampling unit, a random subset of 40 individuals was selected to represent the entire range of standard lengths (SL). The fish under



Fig. 2. Sites sampled for *Characidium pterostictum* in the Ijuí River sub-basin, RS, Brazil: A, stream 1 (28° 18' 58.4" S, 53° 54' 17.9" W); B, stream 2 (28° 12' 06.2" S, 54° 13' 06.9" W); and C, stream 3 (28° 13' 40.8" S, 54° 57' 24.8" W).

Fig. 2. Sitios en los que se recogieron muestras de *Characidium pterostictum* en la subcuenca del río Ijuí, en Río Grande del Sur (Brasil): A, arroyo 1 (28° 18' 58,4" S, 53° 54' 17,9" O); B, arroyo 2 (28° 12' 06,2" S, 54° 13' 06,9" O); C, arroyo 3 (28° 13' 40,8" S, 54° 57' 24,8" O).

analysis were measured by their standard length (SL) in millimeters and subsequently dissected. Stomach contents were carefully examined using a dissecting microscope and identified based on established taxonomic references (McCafferty 1983, Mugnai et al 2010, Segura et al 2011). The food items were quantified using the volumetric method (VO%) (Hynes 1950) in conjunction with the frequency of occurrence (FO%) (Hyslop 1980). Each food item was quantified by determining the area it occupied on graph paper, with a fixed height of 1 mm.

The VO% and FO% data were calculated for each stream and the different sized groups of individuals, creating a data matrix for the subsequent multivariate analyses. Additionally, percentage volume and frequency of occurrence were calculated for the total number of individuals collected. This broader analysis provides an overview of the species' feeding biology that could be used for comparison with other species of Characidiinae. To achieve this, we considered the total volume of food found in all dissected stomachs.

To investigate potential ontogenetic variations, the specimens were divided into three body size categories: small (SL ≤ 32.96 mm), medium (SL 32.97 mm to 47.18 mm), and large (SL ≥ 47.19 mm). These categories were determined based on the grouping of fish into small, medium, and large-size classes using Sturges' rule (Sturges 1926).

To assess changes in diet composition across sampling sites and potential intraspecific ontogenetic influences, we conducted permutational multivariate analysis of variance (permanova; $\alpha < 0.05$) (Anderson 2001). The analysis was based on a Bray-Curtis dissimilarity matrix (Borcard et al 2011), which accounts for both presence/absence and abundance data. This dissimilarity matrix was constructed using the VO% and FO% data per individual. Permanova analysis was chosen for this test due to its ability to handle non-normal data and its suitability for testing multiple factors (Anderson 2001), making it compatible with diet data analysis.

The indicator value index (IndVal) with randomization (Borcard et al 2011) was used to investigate potential associations between food items and specific body size categories or sampling sites of *C. pterostictum*. IndVal compares the abundances and

relative frequencies of food items between groups (Cardoso et al 2013). The statistical significance of such associations is confirmed through a permutation test (De Caceres 2013). A higher IndVal (Stat) indicates a strong association between a particular food item and a specific group (De Caceres 2013). In the test, components A (comp A) and B (comp B) ranged from 0 to 1, representing the probability of a food item being restricted to a specific group and the probability of that food item being present in all sampled stomachs of that group, respectively (De Caceres 2013).

Canonical analysis of principal coordinates (CAP) was used to compare diet composition about standard length size classes and sampling sites (Legendre and Anderson 1999, Anderson and Willis 2003). This ordering method was selected due to its ability to use a distance matrix (using the Bray-Curtis metrics), enabling assessment of the relationships between principal coordinates (dietary data) and variables (size categories or sampling sites) through redundancy analysis (RDA). Moreover, it performs a permutation test that does not rely on assumptions of data normality (Legendre and Anderson 1999). To determine the significance of the ordering analysis and its respective axis and terms, we conducted an analysis of variance (ANOVA) with permutation tests ($\alpha < 0.05$) (Legendre and Anderson 1999).

All statistical tests were performed using the R Project for Statistical Computing software, version 3.4.1. The Permanova, CAP, and Anova analyses were implemented using the statistical package Vegan, version 2.4–5 (Oksanen et al 2017). The IndVal test was conducted using the Indicspecies package, version 1.7.6 (De Caceres and Legendre 2009).

Results

A total of 480 specimens of *C. pterostictum* were captured during the sampling process, 378 of which were dissected and their stomachs were analyzed. The stomachs in of 372 of these individuals contained food. Analysis of stomach contents revealed the presence of 24 different items (table 1). The most frequently consumed items in the overall sample, regardless of the sampling site and size, were insects, Ephemero-

Table 1. Food items consumed by *Characidium pterostictum* in streams of the Ijuí River sub-basin, RS, Brazil. The table presents volume (VO%) and frequency of occurrence (FO%) data considering the total contents of the analyzed stomachs.

Tabla 1. Alimentos consumidos por *Characidium pterostictum* en los arroyos de la subcuenca del río Ijuí, en Río Grande del Sur (Brasil). En la tabla se presentan datos de volumen (VO%) y frecuencia de presencia (FO%) considerando el contenido total de los estómagos analizados.

| Autochthonous | VO (%) | FO (%) | Allochthonous | VO (%) | FO (%) | Undetermined origin | VO (%) | FO (%) |
|-------------------------------|--------|--------|---------------|--------|--------|--|--------|--------|
| Chelicerata (Acarina) | 0.4 | 5.11 | Lepidoptera | 3.24 | 10.22 | Plant material | 0.02 | 0.27 |
| Crustacea (<i>Aegla</i> sp.) | 0.18 | 0.27 | | | | Detritus | 0.13 | 1.61 |
| Ceratopogonidae | 1.26 | 15.05 | | | | Remains of unidentified organic matter | 1.84 | 13.71 |
| Chironomidae | 10.91 | 55.38 | | | | | | |
| Empididae | 0.02 | 0.27 | | | | | | |
| Psychodidae | 3.01 | 14.25 | | | | | | |
| Simuliidae | 4.93 | 15.59 | | | | | | |
| Tabanidae | 0.11 | 0.54 | | | | | | |
| Diptera pupae | 0.09 | 0.81 | | | | | | |
| Other Diptera | 0.59 | 7.26 | | | | | | |
| Plecoptera | 6.63 | 12.1 | | | | | | |
| Trichoptera | 14.13 | 41.67 | | | | | | |
| Ephemeroptera | 19.3 | 33.6 | | | | | | |
| Hemiptera | 0.04 | 0.27 | | | | | | |
| Dryopidae | 0.14 | 0.27 | | | | | | |
| Psephenidae | 1.66 | 0.81 | | | | | | |
| Other Coleoptera | 0.47 | 2.96 | | | | | | |
| Odonata | 0.47 | 0.81 | | | | | | |
| Insects remains | 30.34 | 85.22 | | | | | | |
| Scale | 0.09 | 1.08 | | | | | | |
| Total (VO%) | 94.77 | | | 3.24 | | | 1.99 | |

tera, Trichoptera, and Chironomidae (autochthonous items). These items accounted for more than 70% of the ingested food volume by *C. pterostictum*, with a high frequency of occurrence (table 1).

Food items not belonging to the insect group showed occasional occurrence and were consumed in only small amounts (Chelicerata, *Aegla* sp., scale, detritus, and plant material) (VO: 2.55%). Additionally, *C. pterostictum* fed predominantly on autochthonous items. A small percentage of the ingested food was of terrestrial origin (Lepidoptera, VO: 3.24%, FO: 10.22%) or undetermined (VO: 1.99%) (table 1).

Feeding patterns differed depending on the sampling site (Permanova, $F: 11.16$, $R^2: 0.07$, $p: 0.0001$) and standard length (Permanova, $F: 15.53$, $R^2: 0.05$, $p: 0.0001$). The IndVal test for the sampling site revealed that Ephemeroptera and insect remains (autochthonous items) were associated with Stream 1 due to their higher volume and frequency of occurrence at that site (table 2). No food items were specifically associated with Stream 2, as the proportions of the items were like those found at the other sampling site (table 2). In Stream 3, there was a 71% probability of fish captured in this area having Chironomidae in their stomach contents. Additionally, Psychodidae (autoch-

thonous) and Lepidoptera (allochthonous) were food items associated with Stream 3 as they were restricted to the stomachs of that specific sampling site (IndVal, component A: 1.00; table 2). These items were rarely consumed by *C. pterostictum*. These differences in species' food composition concerning the sampling site can also be observed in the analysis of principal coordinates (fig. 3).

Ontogenetic analysis revealed specific food items associated with large fish. Among these, autochthonous items included insect remains, Trichoptera, Simuliidae, Ephemeroptera, Plecoptera, Psychodidae, and Psephenidae. Additionally, we found allochthonous items such as Lepidoptera, along with remains of unidentified organic matter (table 3). It is of note that autochthonous Psephenidae was exclusively associated with large fish as it was found only within this size category (IndVal, component A: 1.00; table 3). Allochthonous Lepidoptera, an occasional item, had a probability of approximately 60% occurring in the stomachs of large individuals (IndVal, component A: 0.57; table 3), thus being associated with this group of fish size class. The association of other items with large fish was due to their higher volume or frequency of occurrence in this size class.

Table 2. Indicator values (IndVal) of food items consumed by collection points of *Characidium pterostictum*. The table displays the components A (Comp A) and B (Comp B) in the test, ranging from 0 to 1, indicating the probability of a food item being restricted to a specific group and the probability of all sampled stomachs of that group containing the food item. The test statistic (Stat) represents the association between a given food item and a specific group. (* $\alpha < 0.05$).

Tabla 2. Valores del indicador (IndVal) de los alimentos consumidos por cada punto de recogida de *Characidium pterostictum*. En la tabla se muestran los componentes A (Comp A) y B (Comp B) en la prueba, que oscilan entre 0 y 1, que indican la probabilidad de que un alimento esté limitado a un grupo determinado y la probabilidad de que dicho alimento se encuentre en todos los estómagos analizados. La prueba estadística (Stat) representa la asociación entre un alimento determinado y un grupo específico. (* $\alpha < 0,05$).

| | Comp A | Comp B | Stat | p-value |
|-------------------------------|--------|--------|------|---------|
| Stream 1 | | | | |
| Insect remains | 0.68 | 0.78 | 0.73 | 0.007* |
| Ephemeroptera | 0.63 | 0.67 | 0.65 | 0.006* |
| Trichoptera | 0.42 | 0.44 | 0.43 | 0.59 |
| Ceratopogonidae | 0.39 | 0.22 | 0.30 | 0.39 |
| Stream 2 | | | | |
| Remains of unidentified | | | | |
| organic matter | 0.49 | 0.16 | 0.28 | 0.56 |
| Other Diptera | 0.44 | 0.11 | 0.23 | 0.39 |
| Odonata | 0.95 | 0.01 | 0.12 | 0.21 |
| Diptera pupae | 0.70 | 0.01 | 0.10 | 0.60 |
| Dryopidae | 1.00 | 0.007 | 0.09 | 0.40 |
| Plant material | 1.00 | 0.007 | 0.09 | 0.40 |
| Stream 3 | | | | |
| Chironomidae | 0.75 | 0.71 | 0.73 | 0.004* |
| Psychodidae | 1.00 | 0.24 | 0.49 | 0.02* |
| Lepidoptera | 1.00 | 0.17 | 0.41 | 0.04* |
| Plecoptera | 0.80 | 0.15 | 0.35 | 0.13 |
| Simuliidae | 0.46 | 0.15 | 0.26 | 0.89 |
| Chelicerata (Acarina) | 0.68 | 0.06 | 0.21 | 0.53 |
| Other Coleoptera | 0.63 | 0.03 | 0.14 | 0.73 |
| Scale | 1.00 | 0.02 | 0.13 | 0.34 |
| Detritus | 0.61 | 0.02 | 0.11 | 0.91 |
| Tabanidae | 1.00 | 0.01 | 0.10 | 0.55 |
| Psephenidae | 0.52 | 0.01 | 0.07 | 1.00 |
| Crustacea (<i>Aegla</i> sp.) | 1.00 | 0.004 | 0.07 | 1.00 |
| Empididae | 1.00 | 0.004 | 0.07 | 1.00 |
| Hemiptera | 1.00 | 0.004 | 0.07 | 1.00 |

No specific foods were found to be associated with medium and small-size classes. However, the analysis of principal coordinates indicates a modification in feeding habits from small to larger fish in *Characidium pterostictum*. This analysis shows medium-sized individuals as intermediaries, in terms of food, between small and large fish (fig. 4).

Discussion

The dominance of autochthonous insects in the diet of *Characidium pterostictum* confirms our hypothesis that

Table 3. Indicator values (IndVal) of food items consumed by standard length size classes (SL) of *Characidium pterostictum*. The table includes small (SL ≤ 32.96 mm), medium (SL 32.97 mm to 47.18 mm), and large (SL ≥ 47.19 mm) size categories. The components A (Comp A) and B (Comp B) in the test vary from 0 to 1, indicating the probability of a food item being restricted to a specific group and the probability of all sampled stomachs of that group containing the food item. The test statistic (Stat) represents the association between a given food item and a specific group. (* $\alpha < 0.05$).

Tabla 3. Valores del indicador (IndVal) de los alimentos consumidos por clase de longitud estándar (SL) de *Characidium pterostictum*. En la tabla se incluyen las categorías de talla pequeña (SL $\leq 32,96$ mm), mediana (SL 32,97 mm a 47,18 mm) y grande (SL $\geq 47,19$ mm). Los componentes A (Comp A) y B (Comp B) en la prueba oscilan entre 0 y 1 e indican la probabilidad de que un alimento esté limitado a un grupo determinado y la probabilidad de que dicho alimento se encuentre en todos los estómagos analizados. La prueba estadística (Stat) representa la asociación entre un alimento determinado y un grupo específico. (* $\alpha < 0,05$).

| | Comp A | Comp B | Stat | p-value |
|--|--------|--------|------|---------|
| Small (SL ≤ 32.96 mm) | | | | |
| Plant material | 1.00 | 0.01 | 0.09 | 0.52 |
| Tabanidae | 0.74 | 0.01 | 0.08 | 0.84 |
| Medium (SL 32.97 mm to 47.18 mm) | | | | |
| Ceratopogonidae | 0.42 | 0.18 | 0.28 | 0.37 |
| Diptera pupae | 1.00 | 0.02 | 0.13 | 0.24 |
| Odonata | 1.00 | 0.02 | 0.13 | 0.23 |
| Scale | 0.61 | 0.02 | 0.10 | 0.58 |
| Detritus | 0.43 | 0.02 | 0.09 | 0.93 |
| Empididae | 1.00 | 0.01 | 0.08 | 1.00 |
| Hemiptera | 1.00 | 0.01 | 0.08 | 1.00 |
| Dryopidae | 1.00 | 0.01 | 0.08 | 1.00 |
| Large (SL ≥ 47.19 mm) | | | | |
| Insects remains | 0.60 | 0.91 | 0.74 | 0.0001* |
| Trichoptera | 0.62 | 0.66 | 0.64 | 0.0001* |
| Simuliidae | 0.84 | 0.38 | 0.57 | 0.0001* |
| Ephemeroptera | 0.58 | 0.51 | 0.55 | 0.0001* |
| Chironomidae | 0.40 | 0.60 | 0.49 | 0.23 |
| Plecoptera | 0.77 | 0.24 | 0.43 | 0.0003* |
| Psychodidae | 0.63 | 0.22 | 0.37 | 0.004* |
| Remains of unidentified | | | | |
| organic matter | 0.48 | 0.24 | 0.34 | 0.02* |
| Lepidoptera | 0.57 | 0.15 | 0.29 | 0.049* |
| Other Diptera | 0.49 | 0.13 | 0.25 | 0.057 |
| Psephenidae | 1.00 | 0.04 | 0.21 | 0.007* |
| Chelicerata (Acarina) | 0.54 | 0.06 | 0.18 | 0.41 |
| Other Coleoptera | 0.51 | 0.04 | 0.15 | 0.44 |
| Crustacea (<i>Aegla</i> sp.) | 1.00 | 0.01 | 0.12 | 0.18 |

this species tends to be insectivory. This specialization has been reported in several studies on Characidiinae -for *C. pterostictum* and also for other species of *Characidium* (Uieda et al 1997, Aranha et al 2000, Motta and Uieda 2004, Braga 2005, Gomiero and Braga 2008, Braga and Gomiero 2009, Rolla et al 2009). For example, similar findings have been observed in other studies involving other species of *Characidium* such as *C. lanei* Travassos 1967, *C. lauroi* Travassos

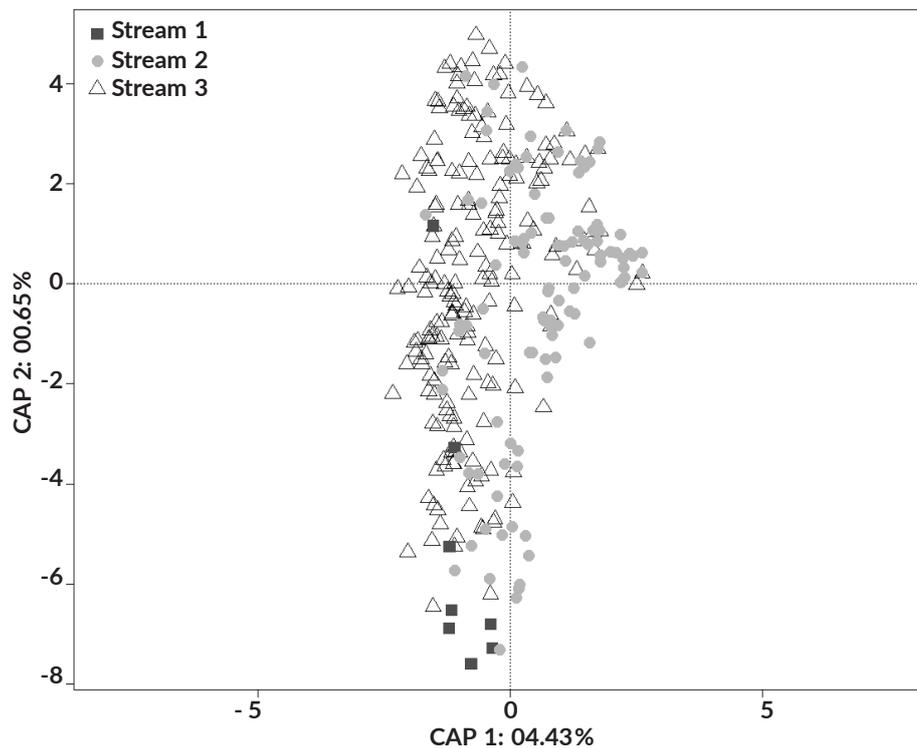


Fig. 3. Diet composition of *Characidium pterostictum* associated with the collection points based on Canonical Analysis of Principal Coordinates (CAP).

Fig. 3. Composición de la dieta de *Characidium pterostictum* asociada con los puntos de recogida basada en el análisis canónico de coordenadas principales (CAP).

1949, *C. alipioi* Travassos 1955, and *C. schubarti* Travassos 1955 in which autochthonous insects were also crucial on diet (Aranha et al 2000, Motta and Uieda 2004, Braga 2005).

Insect larvae of benthic origin, such as Chironomidae, Ephemeroptera, Plecoptera, and Trichoptera, represented the most frequent food ingested by *C. pterostictum*, regardless of size or sampling site. These insects are also crucial for other species of the genus, as indicated in the literature: *Characidium gomesi* Travassos 1956 and *C. oiticica* Travassos 1967 have a high preference for these items and are consequently classified as benthic insectivores (Rolla et al 2009). Similarly, the food preference estimated for *C. alipioi* and *C. lauroi* indicated that these species are benthic insectivorous due to the consumption of Diptera and Trichoptera larvae and Ephemeroptera nymphs, respectively (Braga and Gomiero 2009). Regardless of seasonality, Chironomidae and Simuliidae larvae were the most important items in the diet of *C. pterostictum* in the mid-stream of Paraná State (southern Brazil), while Chironomidae larvae and Ephemeroptera nymphs were the most important items for *C. lanei*, except in the summer (Aranha et al 2000). Species that rely on autochthonous insects indirectly depend on the quality of habitats surrounding watercourses, as the life cycles of these emerging aquatic insects (Ephemeroptera, Plecoptera, and Trichoptera, for example) are closely

linked to riparian vegetation, where they spend part of their adult life. These emerging aquatic insects play a significant role in material cycling and trophic transfers in aquatic environments, serving as crucial bioindicators of water and habitat quality in streams, as they occur in clean and well-oxygenated waters (Bispo et al 2006). Aquatic insects like Ephemeroptera, Plecoptera, and Trichoptera are very sensitive to environmental perturbations such as modifications to riparian forests and siltation of substrate and stream beds (Bispo et al 2006). Therefore, *C. pterostictum*, like other insectivorous fish species, requires protection of its habitats. Such protection should consider not only the environmental quality of the streams but also the integrity of adjacent riparian vegetation (Cavalheiro and Fialho 2016, Cavalheiro and Fialho 2019). Recognizing that the effects of predator diversity extend beyond the predators' habitat and can propagate to adjacent ecosystems due to the cascade effect between aquatic and terrestrial food webs, underscores the interconnectedness of riparian habitats (Wesner 2012). This highlights their significance in sustaining healthy fish populations and an overall ecosystem balance (Wesner 2012). The significance of riparian vegetation for fish diet is well recognized in various studies (Gomiero and Braga 2008, Borba et al 2008, Ferreira et al 2012, Souza and Lima-Junior 2013, Silva et al 2014, Leite et al 2015).

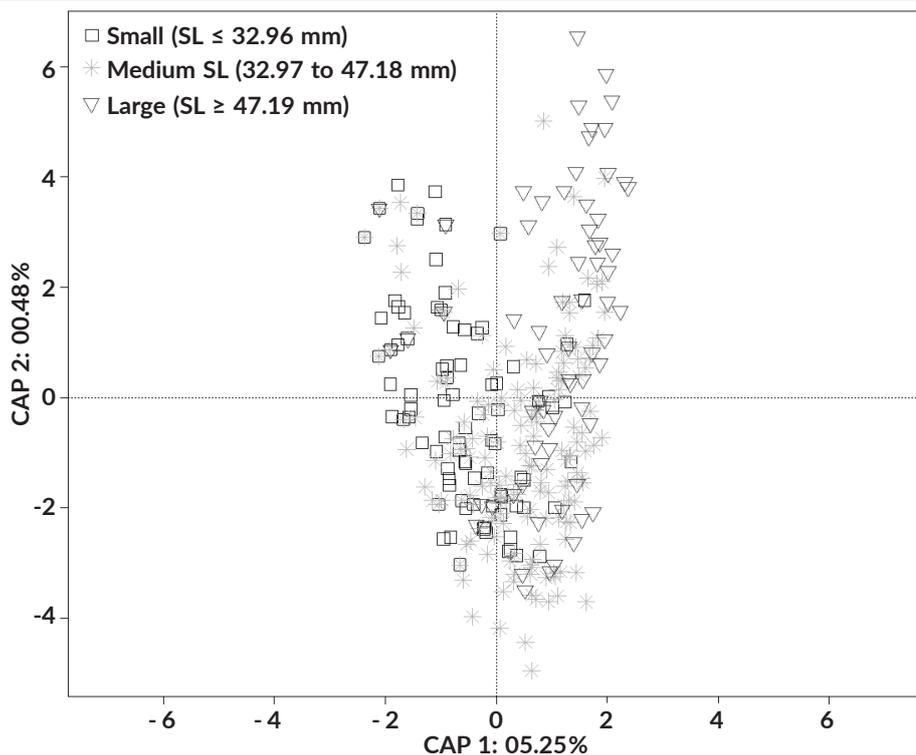


Fig. 4. Diet composition of *Characidium pterostictum* associated with the size classes based on Canonical Analysis of Principal Coordinates (CAP).

Fig. 4. Composición de la dieta de *Characidium pterostictum* asociada a las clases de talla basada en el análisis canónico de coordenadas principales (CAP).

These comparisons suggest a pattern in the classification of the genus *Characidium* within trophic guilds, regardless of the sampling location (in the state of Brazil) or seasonality/time (year) in which the fish are captured. This feeding behavior does not appear to change, despite the great diversity of habitats or variations in sampling seasons, although variations in the types of prey consumed can be observed. Therefore, in our study as well, we classified *C. pterostictum* as an insectivorous benthic fish. Other studies have also shown that *Characidium zebra* Eigenmann 1909 has a high frequency of occurrence of insects and is characterized as an insectivorous-benthophagous species (Gomiero and Braga 2008). In contrast, *C. rachovii* Regan 1913 exhibits an invertivorous habit, with a strong inclination towards larvivory, primarily consuming immature aquatic insects (Bastos et al 2013).

Specialist species like *Characidium pterostictum* maintain their diets based on specific food categories, regardless of their habitat distribution (Braga and Gomiero 2009). In our study, we found that *C. pterostictum* exhibits a benthic habitat, as indicated by its food preferences. These fish are commonly found in environments of riffles and rapids, and possess physical characteristics such as a streamlined body, ventrally positioned pectoral and pelvic fins, and a specialized mouth shape and position that facilitate food capture among submerged stones in hard-to-reach areas for

other fish species (Aranha et al 2000). Consequently, they primarily feed on larvae and insects that inhabit these environments, capturing them through suction rather than biting (Braga 2005). These factors likely explain why autochthonous insects were the main dietary items for *C. pterostictum* in our analyses.

Based on the sampling sites that we identified in our analyses, changes in the diet of *C. pterostictum* may be influenced by various factors, including seasonality and resource availability. The dietary changes identified through Permanova primarily center around the substitution of prey within the category of aquatic insects (as indicated by the significant associations found in the IndVal analysis). Consequently, our data are insufficient to support the hypothesis that diet variations are impacted by the position from upstream to downstream in the sub-basin. As previously discussed, this species consistently demonstrates a well-established feeding pattern, consuming aquatic insects, regardless of the sampling site (Uieda et al 1997, Aranha et al 2000, Motta and Uieda 2004, Braga 2005, Gomiero and Braga 2008, Braga and Gomiero 2009, Rolla et al 2009, Bastos et al 2013).

Our analysis indicates that *C. pterostictum* exhibits modifications in certain food items as it progresses through its life cycle, akin to other freshwater Neotropical fish species. This differentiation in dietary preferences within a species is often influenced

by variations in energy demands and morphological limitations (Abelha et al 2001). Such differential use of food resources is a common strategy among freshwater fish species, aimed at mitigating trophic niche overlap between juvenile and adult individuals (Rudolf and Lafferty 2011, Russo et al 2014, Cavalheiro and Fialho 2016, Dala-Corte et al 2016, Cavalheiro and Fialho 2019). Throughout our study, we observed a discernible shift in the feeding behavior of *C. pterostictum*, characterized by a decrease in the consumption of smaller-sized items, such as autochthonous Chironomidae, and a concurrent increase in the intake of larger insects, including autochthonous Simuliidae, Trichoptera, Ephemeroptera, Plecoptera, Psychodidae, and Psphenidae. This transition indicates an expansion of the species' food spectrum, a phenomenon that is integral to enhancing predator-prey encounter rates (Houde 1997). Consequently, as the fish progress in size, we anticipate a corresponding increase in the size and diversity of their prey spectrum (Houde 1997). Moreover, the disparity in food consumption between larger and smaller fish individuals may also contribute to the broadening of the food spectrum and the diversity of ingested items across the species' ontogeny. The observed functional variation among different stages of the life history within a population, often attributed to ontogenetic niche changes (Rudolf and Rasmussen 2013, Rudolf et al 2014), involves modifications in the quantity and types of prey consumed by a species as it grows. These niche changes and functional differences among individuals of the same species also play a crucial role in shaping the structural dynamics of communities (Hertz et al 2016). Indeed, the size of individuals (ontogenetic stage), their niche variations, and resulting functional roles are key factors contributing to intraspecific diversity within ecosystems (Rudolf and Rasmussen 2013, Rudolf et al 2014).

Similarly, in the case of *C. schubarti*, ontogenetic changes in the consumption of aquatic insects are observed, reflecting the patterns identified in our study with *C. pterostictum*. Smaller fish in the *C. schubarti* population primarily feed on Chironomidae (Motta and Uieda, 2004). On the other hand, *Characidium rachovii* demonstrates a subtle increase in the diversity of consumed prey during development, accompanied by a slight expansion in niche breadth influenced by ontogenetic factors as the species grows (Polesel and Poi 2016).

In conclusion, *Characidium pterostictum* is an insectivorous fish that primarily feeds on autochthonous insects. As the species grows, it broadens its dietary spectrum and prey size diversity, showing variation within the insectivorous range. Smaller-sized fish consume autochthonous Chironomidae, while larger fish consume other autochthonous insects, with minimal dietary variation across different sampling sites. Consequently, the variations in feeding patterns observed in *Characidium pterostictum* are closely linked to the specific environmental conditions of each sampling site and the ontogenetic stage of the fish. Therefore, understanding the intricate interplay between habitat characteristics, prey availability, and fish ontogeny is essential for effectively managing and conserving *C. pterostictum* populations in their natural habitats.

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Author contributions

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Conflicts of interest

The authors declare no conflict of interest.

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