Evidence of Niche Partitioning under Ontogenetic Influences among Three Morphologically Similar Siluriformes in Small Subtropical Streams

Karine Orlandi Bonato*, Clarice Bernhardt Fialho
Universidade Federal do Rio Grande do Sul, Instituto de Biociências, Departamento de Zoologia, Programa de Pós-Graduação em Biologia Animal, CEP 91501–970, Porto Alegre, Rio Grande do Sul, Brazil

Abstract
Ontogenetic influences in patterns of niche breadth and feeding overlap were investigated in three species of Siluriformes (*Heptapterus* sp., *Rhamdia quelen* and *Trichomycterus poikilos*) aiming at understanding the species coexistence. Samplings were conducted bimonthly by electrofishing technique from June/2012 to June/2013 in ten streams of the northwestern state of Rio Grande do Sul, Brazil. The stomach contents of 1,948 individuals were analyzed by volumetric method, with 59 food items identified. In general *Heptapterus* sp. consumed a high proportion of *Aegla* sp., terrestrial plant remains and Megaloptera; *R. quelen* consumed fish, and Oligochaeta, followed by *Aegla* sp.; while the diet of *T. poikilos* was based on Simuliidae, Ephemeroptera and Trichoptera. Specie segregation was observed in the NMDS. Through PERMANOVA analysis feeding differences among species, and between a combination of species plus size classes were observed. IndVal showed which items were indicators of these differences. Niche breadth values were high for all species. The niche breadth values were low only for the larger size of *R. quelen* and *Heptapterus* sp. while *T. poikilos* values were more similar. Overall the species were a low feeding overlap values. The higher frequency of high feeding overlap was observed for interaction between *Heptapterus* sp. and *T. poikilos*. The null model confirmed the niche partitioning between the species. The higher frequency of high and intermediate feeding overlap values were reported to smaller size classes. The null model showed resource sharing between the species/size class. Therefore, overall species showed a resource partitioning because of the use of occasional items. However, these species share resources mainly in the early ontogenetic stages until the emphasized change of morphological characteristics leading to trophic niche expansion and the apparent segregation observed.

Citation: Bonato KO, Fialho CB (2014) Evidence of Niche Partitioning under Ontogenetic Influences among Three Morphologically Similar Siluriformes in Small Subtropical Streams. PLoS ONE 9(10): e110999. doi:10.1371/journal.pone.0110999

Editor: Ben J. Mans, Onderstepoort Veterinary Institute, South Africa

Received May 23, 2014; Accepted September 26, 2014; Published October 23, 2014

Copyright: © 2014 Bonato, Fialho. This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Data Availability: The authors confirm that all data underlying the findings are fully available without restriction. All relevant data are within the paper and its Supporting Information files.

Funding: This research was funded by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) Proc. 1104786 to the first author. The funder had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Competing Interests: The authors have declared that no competing interests exist.

* Email: kakabio2005@yahoo.com.br

Introduction

According to the competitive exclusion principle [1], species cannot coexist because competing for resources could lead to the exclusion of one or the other species or a population decrease. For coexistence to be possible, a niche differentiation would be required [2,3].

This niche differentiation is known as resource partitioning that, according to [4], is any substantial difference in resource use between coexisting species. This resource partitioning would be the maintainer mechanisms of species biodiversity [5]. However, there is a neutral theory whose precept is that the diversity of species is the result of stochastic factors such as ecology drift, speciation, selection and dispersal acting at local and regional scale [6,7]. Thus, in this theory is assumed that species have similar ecological needs and there is not a competitively superior species [6,8]. Hubbell’s neutral model thus assumes that limited dispersal, rather than niche specialization, is the main explanation for spatial structure across ecological communities [9].

Other classic affirmation that tries to explain the involvement of interspecific competition in coevolution and complements the niche theory is “the ghost of competition past” [10]. Partitioning of resources can also be a consequence of competition past because in the past the species had a negative interaction and, during the evolutionary process, eventually developed distinct morphological and physiological characteristics that segregated it [2,3]. Thereby, differences in trophic morphology, distinct habitat use, activity periods and tactical capture all minimize the effect of overlap [11,12,13].

The partitioning of resources may be influenced by factors such as time, space and ontogeny [4,14,15]. Therefore, these factors should be considered when we want to understand the mechanisms of fish species coexistence in streams [16]. Studies have demonstrated that the ontogenetic process may also be involved in resource partitioning by coexisting species [17,18,19]. Thus in order to segregation occur, differentiations in item consumption are necessary and these differences are related to size-dependent morphology, physiology and behavior [20,21,22]. The differences between sizes and stages of life are not restricted only to the
features mentioned above, but also to energy requirement. This can lead individuals mainly the adults to use larger prey to maximize their energy intake [23].

Phylogenetically related species sharing morphological features especially in some stage of ontogenetic development. These related species tend to show ecological similarities [24] and, can be great instrument for studying the influence of ontogenetic factor in the coexistence of species. There is still a lack of studies that address a broader community context using three or more species [4,19].

The Siluriformes are considered one of the most basal groups of fish and have 2,867 freshwater species and they have a diverse morphology, usually with benthic habits [25,26]. Within the family Heptapteridae there are numerous genus including *Rhamdia* and *Heptapterus* [25,26]. *Rhamdia quelen* is an opportunistic benthic species that can live in the midst of rocks, in deep wells, forages at night and near the margins searching for larger benthic macroinvertebrates and small fish [27,28,29,30]. Species of the genus *Heptapterus* also live in crevices formed in rocky bottoms and in rapids, occupying low and medium depths, and are benthic [25]. The *Heptapterus* sp. used in this work is a new specie that is being described. *Trichomycterus poikilos* belongs to Trichomycteridae family and is a recently described species [31]. The species of *Trichomycterus* genus can feed during the day or at night revolving the substrate surface. They usually inhabit small water courses, strong currents and clear waters. Most of the species of the genus are *Trichomycterus* reported to live in streams with high circulation and bottom mainly composed of small stones and well oxygenated streams [32,33,34]. By having a relatively thin, elongated and depressed body they can explore the small spaces among rocks very well [35]. These three catfish have body elongate, trunk roughly cylindrical, head depressed, mouth wide and subterminal with small teeth distributed in three rows in the premaxilla and lower jaw (*T. poikilos*) or teeth in both jaws (*Heptapterus* sp.) or terminal mouth with small teeth inserted in dentigerous plates (*R. quelen*); they have maxilla and nasal barbels [32,36,37]. Therefore due to phylogenetic relationship, similar morphological and living habits are good tools for the study of coexistence of species.

Thus, this study was developed to test the hypothesis that three similar species of Siluriformes have a feed segregation influenced by ontogenetic process that allows the coexistence of species. Specifically, we tested the existence of dietary differences among three species and these differences are caused by interspecific variations related to the ontogenetic process by which individuals of these species spend. Therefore these variation combined with the use of non-limiting resources allows the coexistence of these species.

**Materials and Methods**

**Ethics statement**

Fish samples were collected with authorization n° 34940 from register n° 3196382 from Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis (IBAMA). IBAMA is the federal agency responsible for the environment in Brazil, and as such is responsible for emitting licenses to collect fish specimens according to Law N° 7,735 of February 22, 1989, in Brazil. This study was approved by Ethics Committee on Animal Use of the Universidade Federal do Rio Grande do Sul ( Permit Number:
The study was conducted in ten streams (Figure 1) in northwest Rio Grande do Sul, which correspond to the Alto Jacuí sub-basin – Caixões River (RC) (S29° 01’.44.4’/W 52° 49’.25.1’); Jacuizinho River (RJ) (S 28° 58’.02.9’/W 52° 47’.20.3’); Morcego River (RM) (S 28° 33’.55.0’/W 52° 49’.05.6’); Turvo River (RT) (S 28° 43’.47.0’/W 52° 47’.40.4’), Valoroso Stream (RV) (S 28° 43’.47.0’/W 52° 47’.40.4’). The study data presented herein are available as Table S1 and S2 files (e.g. stomach content analysis).

**Sampling**

The study was conducted in ten streams (Figure 1) in northwest Rio Grande do Sul, which correspond to the Alto Jacuí sub-basin – Caixões River (RC) (S29° 01’.44.4’/W 52° 49’.25.1’); Jacuizinho River (RJ) (S 28° 58’.02.9’/W 52° 47’.20.3’); Morcego River (RM) (S 28° 33’.55.0’/W 52° 49’.05.6’); Turvo River (RT) (S 28° 43’.47.0’/W 52° 47’.40.4’), Valoroso Stream (RV) (S 28° 43’.47.0’/W 52° 47’.40.4’). The study data presented herein are available as Table S1 and S2 files (e.g. stomach content analysis).

---

### Table 1. Taxonomic position of three species in the Alto Jacuí sub-basin.

| Order/Family/Specie | Specie Code | Specie/Size Class Code | Size Classes (cm) |
|---------------------|-------------|------------------------|-------------------|
| **SILURIFORMES**    |             |                        |                   |
| Heptapteridae        |             |                        |                   |
| Heptapterus sp.      | H           | H1                     | 1 = 1.16–5.99;    |
|                     |             | H2                     | 2 = 6.00–10.99;   |
|                     |             | H3                     | 3 = 11.00–14.99;  |
|                     |             | H4                     | 4 = 15.00–19.74;  |
|                     |             | H5                     | 5 = 20.00–28.00;  |
| Rhamdia quelen (Quoy & Gaimard, 1824) | R | R1                     | 1 = 1.42–4.99;    |
|                     |             | R2                     | 2 = 5.00–9.90;    |
|                     |             | R3                     | 3 = 10.00 15.90;  |
|                     |             | R4                     | 4 = 16.00–27.50   |
| Trichomycteridae    |             |                        |                   |
| Trichomycterus poikilos Ferrer & Malabarba, 2013 | T | T1                     | 1 = 1.26–2.99;    |
|                     |             | T2                     | 2 = 3.00–4.99;    |
|                     |             | T3                     | 3 = 5.00–6.99;    |
|                     |             | T4                     | 4 = 7.00–8.93     |

Specie code of the three species studied, specie/size class code by each size class and size variation for each size class.

doi:10.1371/journal.pone.0110999.t001

---

**Figure 2.** Two-dimensional plot of three fish species analyzed in Alto Jacuí sub-basin. The ordination resulting of the NMDS of the three species. For specie code see Table 1.

doi:10.1371/journal.pone.0110999.g002
41°32.0′/W 52°51′ 41.5″; Divinéia Stream (RD) (S 28° 42′ 16.7″/W 52° 52′ 23.9″); Arroio Angico (AA) (S 28° 39′ 17.9″/W 52° 54′ 31.1″); Paz Stream (RP) (S 28° 42′ 57.3″/W 52° 50′ 41.7″); Santa Clara River (RSC) (S 28° 44′ 30.1″/W 53° 13′ 03.0″); and Quati River (RQ) (S 28° 38′ 31.8″/W 52° 37′ 07.9″). All streams flow into the Jacuí River, which is one of the main tributaries to the Laguna dos Patos system and the streams are considered headwater streams.

Fish were collected in June, August, October and December 2012; February, April and June 2013. Each sampling event lasted four days. 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 [38,39], fixed in 10% formalin and then transferred to 70% alcohol for conservation. Fish were identified in the laboratory with identification keys [40,41,42] for invertebrates. They were then quantified according to the volumetric method [44].

Table 2. Permutational Multivariate Analysis of Variance results of each sampling stream in the Alto Jacuí sub-basin.

| Stream | Specie Factor | Specie/Size Class Factor |
|--------|---------------|--------------------------|
|        | F  | p  | F  | p  |        |
| RC     | 9.17 | 0.00 | 7.27 | 0.00 |        |
| RJ     | 5.55 | 0.00 | 9.67 | 0.00 |        |
| RM     | 8.33 | 0.00 | 3.00 | 0.01 |        |
| RV     | 13.06 | 0.00 | 9.52 | 0.00 |        |
| RD     | 16.19 | 0.00 | 9.36 | 0.00 |        |
| AA     | 10.52 | 0.00 | 16.32 | 0.00 |        |
| RSC    | 21.96 | 0.00 | 7.44 | 0.01 |        |
| RQ     | 3.32 | 0.01 | 9.64 | 0.00 |        |
| RP     | 21.78 | 0.00 | 13.34 | 0.00 |        |
| RT     | 15.50 | 0.00 | 27.19 | 0.00 |        |

F and p values of specie and specie/size class factors. For stream code see Material and Methods. doi:10.1371/journal.pone.0110999.t002

Inferences about the level of specialization of overall species and their along their ontogenetic process were used the Levin’s measure [53] that was calculated for each species in each stream and to specie-class size in each stream using volume data. The Hurlbert’s formula [54] was applied to standardize the trophic niche measure (ranging from 0 to 1).

We used the Pianka’s index [55] to estimate the species and size classes’ feeding overlap within each of the spatial-temporal units (seven samples months in each site). Overlap values range from zero to one, where zero indicates overlap absence and one indicates complete overlap. We established three categories to improve understanding of the overlap results, high overlap is given by overlap values >0.6, intermediate values overlap between 0.4–0.6 and low overlap values <0.4 [56]. Only groups represented by five or more individuals were used to comparisons or groups that contained similar numbers of individuals. To evaluate the significance of Pianka’s index [57] we used the null model with RA3 algorithm [58]. The null model performed 1,000 Monte Carlo randomizations for we can compare the created patterns (mean niche overlap values for all group pairs) with the those in the real data. In this model mean overlap values that are significantly lower than those expected by chance might indicate food partitioning, however values higher than those expected by chance might indicate food sharing [59]. Both the null model analysis and feeding overlap were computed using EcoSim 7.0 [57].
Table 3. Indicator Value (IndVal), p value and Frequency of food items consumed by three species analyzed, discriminated among species.

| Stream | Indicator Item                  | Specie | IndVal | p     | Frequency |
|--------|--------------------------------|--------|--------|-------|-----------|
| RC     | Aquatic Lepidoptera larvae     | R      | 0.704  | 0.05  | 2         |
|        | Bivalve                        | R      | 0.427  | 0.02  | 2         |
|        | Hymenoptera                    | R      | 0.380  | 0.02  | 2         |
|        | Ephemeroptera                  | H      | 0.679  | 0.03  | 193       |
|        | Coleoptera                     | R      | 0.645  | 0.00  | 10        |
|        | Adult Coleoptera               | R      | 0.577  | 0.01  | 4         |
|        | Terrestrial insect remains     | R      | 0.525  | 0.00  | 6         |
|        | Gastropoda                     | R      | 0.413  | 0.00  | 2         |
|        | Testae Amoebae                 | R      | 0.385  | 0.00  | 12        |
|        | Simuliidae                     | T      | 0.581  | 0.02  | 48        |
| RJ     | Coleoptera larvae              | R      | 0.645  | 0.00  | 10        |
|        | Adult Coleoptera               | R      | 0.577  | 0.01  | 4         |
|        | Terrestrial insect remains     | R      | 0.525  | 0.00  | 6         |
|        | Gastropoda                     | R      | 0.413  | 0.00  | 2         |
|        | Testae Amoebae                 | R      | 0.385  | 0.00  | 12        |
|        | Simuliidae                     | T      | 0.581  | 0.02  | 48        |
| RM     | Oligochaeta                    | R      | 0.816  | 0.00  | 8         |
|        | Coleoptera larvae              | R      | 0.729  | 0.05  | 6         |
|        | Terrestrial plant remains      | R      | 0.586  | 0.04  | 30        |
|        | Gastropoda                     | R      | 0.578  | 0.02  | 23        |
|        | Testae Amoebae                 | R      | 0.350  | 0.04  | 12        |
| RQ     | Terrestrial plant remains      | R      | 0.760  | 0.00  | 11        |
|        | Terrestrial insect remains     | R      | 0.662  | 0.03  | 4         |
|        | Diptera Pupae                  | R      | 0.429  | 0.01  | 1         |
|        | Aegla sp.                      | H      | 0.974  | 0.01  | 7         |
|        | Megaloptera                    | H      | 0.964  | 0.02  | 3         |
| RD     | Oligochaeta                    | R      | 0.933  | 0.02  | 4         |
|        | Aegla sp.                      | R      | 0.918  | 0.00  | 12        |
|        | Terrestrial plant remains      | R      | 0.855  | 0.00  | 24        |
|        | Odonata nymph                  | R      | 0.828  | 0.00  | 9         |
|        | Adult Coleoptera               | R      | 0.822  | 0.00  | 5         |
|        | Terrestrial insect remains     | R      | 0.765  | 0.03  | 13        |
|        | Trichoptera                    | R      | 0.727  | 0.00  | 67        |
|        | Animal organic matter          | R      | 0.622  | 0.04  | 6         |
|        | Coleoptera larvae              | R      | 0.595  | 0.00  | 8         |
|        | Hymenoptera                    | R      | 0.517  | 0.03  | 3         |
|        | Scale                          | R      | 0.504  | 0.03  | 5         |
|        | Simuliidae                     | H      | 0.701  | 0.00  | 85        |
|        | Chironomidae                   | H      | 0.575  | 0.00  | 92        |
| AA     | Oligochaeta                    | R      | 0.994  | 0.00  | 8         |
|        | Animal organic matter          | R      | 0.800  | 0.02  | 2         |
|        | Aquatic insects remains        | R      | 0.555  | 0.02  | 9         |
|        | Adult Coleoptera               | H      | 0.511  | 0.05  | 4         |
|        | Simuliidae                     | T      | 0.711  | 0.02  | 106       |
| RSC    | Fish                           | R      | 0.999  | 0.02  | 1         |
|        | Oligochaeta                    | R      | 0.970  | 0.01  | 2         |
|        | Terrestrial Lepidoptera larvae | R      | 0.902  | 0.02  | 1         |
|        | Terrestrial insect remains     | R      | 0.798  | 0.03  | 5         |
|        | Ephemeroptera                  | H      | 0.853  | 0.01  | 60        |
|        | Odonata nymph                  | H      | 0.813  | 0.04  | 3         |
|        | Sediment                       | H      | 0.380  | 0.03  | 11        |
| RQ     | Terrestrial insect remains     | R      | 0.627  | 0.00  | 3         |
|        | Scale                          | R      | 0.518  | 0.00  | 7         |
|        | Adult Coleoptera               | R      | 0.494  | 0.02  | 3         |
|        | Animal organic matter          | R      | 0.481  | 0.02  | 2         |
Table 3. Cont.

| Stream | Indicator Item          | Specie | IndVal | p    | Frequency |
|--------|-------------------------|--------|--------|------|-----------|
| Terrestrial plant remains | R | 0.408 | 0.04 | 14 |
| Gastropoda | R | 0.390 | 0.00 | 5 |
| RP | Fish | R | 0.988 | 0.04 | 4 |
| Terrestrial insect remains | R | 0.474 | 0.00 | 5 |
| RT | Nematoide | R | 0.795 | 0.03 | 9 |
| Orthoptera | R | 0.713 | 0.04 | 3 |
| Scale | R | 0.650 | 0.03 | 9 |
| Coleoptera larvae | R | 0.638 | 0.04 | 6 |
| Adult Coleoptera | R | 0.623 | 0.04 | 4 |
| Diplopora | R | 0.476 | 0.03 | 1 |
| Terrestrial Hemiptera | R | 0.462 | 0.04 | 2 |
| Detritus | R | 0.339 | 0.04 | 1 |
| Megaloptera | H | 0.921 | 0.04 | 6 |
| Aegla sp. | H | 0.895 | 0.04 | 26 |
| Odonata nymph | H | 0.509 | 0.04 | 8 |

Only items with significant values p<0.05 are listed. For stream and specie code see Material and Methods and Table 1.
doi:10.1371/journal.pone.0110999.t003

Results

Diet Composition and Factors-Influence

The contents of 1,984 stomachs (Table S1) belonging to three species (Table 1) were analyzed. We recorded 59 food items wherein Heptapterus sp. consumed a high proportion of Aegla sp. (34.7%), terrestrial plant remains (14.8%) and Megaloptera (12.8%) and Rhamdia quelen consumed fish (40.2%), and Oligochaeta (30.9%) followed by Aegla sp. (9.8%). The diet of Trichomycterus poikilos was based on Simuliidae (31.4%), Ephemeroptera (25.2%) and Trichoptera (18.7%) (Table S2).

The NMDS analysis (Figure 2) showed the existence of a differentiation pattern among the species. In all streams the PERMANOVA analysis corroborated the presence of species' differentiation and the influence of factor class size (Table 2). The most significant food items that contributed to species and specie plus size class's differentiation were indicated by IndVal (Table 3, 4). The items indicated for IndVal for the species were the occasional items and in the major were indicated to R. quelen and Heptapterus sp. that have a more varied diet. The same occurred for the size class where the indicators items appeared most for larger classes by the use of occasional items.

Trophic Niche Breadth and Feeding Overlap

Niche breadth values were high (>0.61) for all species in all streams. The mean values were higher for T. poikilos (Ba: 0.777) and R. quelen (Ba: 0.727) than Heptapterus sp. (Ba: 0.693) (Figure 5). Overall for size classes 92.7% of niche breadth values were high and the few intermediate (0.4–0.61) as R4, H4 and H5. There is an abrupt niche breadth reduction in the larger size classes for R. quelen and Heptapterus sp. However T. poikilos maintain a more uniform niche breadth (Figure 4).

Feeding overlap values for species were mostly low (0–0.4) in all temporal units. Rhamdia quelen and T. poikilos only had low feeding overlap values. However the interaction between R. quelen with Heptapterus sp. showed larger quantitative of low overlap, and about 12% were of high and intermediate values. The largest number of high feeding overlap were the interaction between Heptapterus sp. and T. poikilos (Figure 5). Most of observed values (84%) were not significantly higher than those expected by chance. This result indicates a resource partitioning among the species.

Investigating the feeding overlap values for species and their class size we observed that the most of feeding overlaps remains were low. However high and intermediate feeding overlaps were in largest frequency only in smaller size classes independently of these size are equivalents (Figure 6, 7). Observed values were significantly higher than those expected by chance in 60% of the feeding overlap interactions, showing the major of the spatial-temporal units for size class is occurring resource sharing.

Discussion

The high consumption of fish, Oligochaeta and Aegla sp. by R. quelen indicate a carnivorous/piscivorous habit. This habit is described in the literature [27,60,61]. Heptapterus sp., was considered an invertevorous species, ingested large amount of Aegla sp., terrestrial plant remains, and Megaloptera- though in smaller proportions (but with higher frequency) fed on aquatic insects such as Ephemeroptera and Trichoptera. Heptapterus sp. was also reported as invertevorous but as ingesting a much larger amount aquatic larvae invertebrates [60] and two species of Heptapterus are classified within the guild of those that mainly eat items from their aquatic environment [62]. Trichomycterus poikilos showed to be invertevorous, eating mostly aquatic larvae of Simuliidae, Ephemeroptera and Trichoptera. This invertevorous diet with ingestion of benthic larvae is well reported in the...
Table 4. Indicator Value (IndVal), p value and Frequency of food items consumed by three species analyzed, discriminated among species/size classes.

| Stream | Indicator Item | Specie/Size Class | IndVal | p    | Frequency |
|--------|----------------|-------------------|--------|------|-----------|
| RC     | Bivalve        | R3                | 0.249  | 0.01 | 2         |
|        | Hymenoptera    | R3                | 0.174  | 0.01 | 2         |
|        | Fish           | H1                | 0.907  | 0.03 | 6         |
|        | Megaloptera    | H1                | 0.848  | 0.02 | 9         |
|        | Aquatic insects remains | H4    | 0.738  | 0.01 | 12        |
|        | Aquatic Hemiptera | H4      | 0.381  | 0.05 | 3         |
|        | Scale          | H4                | 0.156  | 0.02 | 6         |
| RJ     | Adult Coleoptera | R3      | 0.438  | 0.01 | 4         |
|        | Aegla sp.      | H4                | 0.949  | 0.02 | 12        |
|        | Fish           | H4                | 0.836  | 0.03 | 1         |
|        | Scale          | H5                | 0.542  | 0.01 | 4         |
|        | Rvegsu         | H5                | 0.438  | 0.02 | 17        |
|        | Simuliidae     | T4                | 0.704  | 0.01 | 48        |
| RM     | Terrestrial plant remains | R3 | 0.493  | 0.01 | 30        |
|        | Adult Coleoptera | R3        | 0.490  | 0.02 | 6         |
|        | Gastropoda     | R3                | 0.376  | 0.04 | 23        |
|        | Animal organic matter | H3   | 0.732  | 0.01 | 10        |
|        | Rvega          | H3                | 0.164  | 0.02 | 6         |
| RV     | Diptera Pupae  | R4                | 0.143  | 0.03 | 1         |
|        | Fish           | H3                | 0.815  | 0.04 | 1         |
|        | Adult Coleoptera | H3        | 0.143  | 0.04 | 1         |
|        | Ephemeroptera  | T4                | 0.585  | 0.03 | 70        |
| RD     | Terrestrial plant remains | H4   | 0.787  | 0.01 | 24        |
|        | Aquatic insects remains | H4   | 0.654  | 0.04 | 12        |
|        | Coleoptera larvae | H4   | 0.308  | 0.05 | 8         |
|        | Simuliidae     | T4                | 0.469  | 0.00 | 85        |
| AA     | Oligochaeta    | R2                | 0.985  | 0.03 | 8         |
|        | Animal organic matter | R2 | 0.584  | 0.03 | 2         |
|        | Aquatic insects remains | R2 | 0.283  | 0.03 | 10        |
|        | Megaloptera    | H3                | 0.938  | 0.04 | 4         |
|        | Aegla sp.      | H5                | 0.984  | 0.01 | 4         |
|        | Rit            | H5                | 0.349  | 0.03 | 3         |
| RSC    | Fish           | R4                | 0.997  | 0.02 | 1         |
|        | Oligochaeta    | R4                | 0.942  | 0.01 | 2         |
|        | Terrestrial Lepidoptera larvae | R4 | 0.818  | 0.02 | 1         |
|        | Terrestrial insect remains | R4 | 0.656  | 0.00 | 5         |
|        | Ephemeroptera  | H3                | 0.649  | 0.05 | 61        |
|        | Sediment       | H3                | 0.148  | 0.04 | 11        |
|        | Simuliidae     | T4                | 0.641  | 0.04 | 64        |
| RQ     | Scale          | R2                | 0.289  | 0.05 | 7         |
|        | Terrestrial insect remains | R3 | 0.445  | 0.04 | 3         |
|        | Aegla sp.      | H3                | 0.739  | 0.04 | 11        |
|        | Odonata nymph  | H4                | 0.249  | 0.01 | 2         |
| RP     | Fish           | R4                | 0.990  | 0.02 | 5         |
|        | Nematoide      | R4                | 0.375  | 0.04 | 4         |
|        | Chironomidae   | T4                | 0.222  | 0.02 | 70        |
| RT     | Detritus       | R1                | 0.106  | 0.00 | 1         |
|        | Scale          | R2                | 0.301  | 0.05 | 9         |
|        | Coleoptera larvae | R2    | 0.296  | 0.04 | 6         |
literature for other species of the genus *Trichomycterus* [63,64,65,66,67].

The diet differentiation were observed in the ontogenetic level when we analyzed the specie plus size class factor. In this case over again the indicator items were those used occasionally by the larger size classes. The influence of this factor has been studied in Neotropical streams and is connected to the innumerable features that change with the fishes development, be they morphological and physiological characteristics (e.g. increasing individual size, mouth gap, changes in the digestive tract) or even behavioral habits (e.g. locomotion ability) [68,69,70]. The more features that shift over development and that differentiate these species are related to the size that can achieve *R. quelen* and *Heptapterus* sp.

The expressive growth these species present during development allows a larger mouth gape allowing the use of larger items like *Aegla* sp., fish, *Megaloptera*, *Gastropoda*, terrestrial insect remains and *Oligochaeta* by the larger sizes. In this study the difference between the largest and smallest individuals was 26.84 cm and 26.08 cm for *Heptapterus* sp. and *R. quelen* respectively. With the increase in fish size the individuals need to maximize their energetic gain by ingesting larger prey with a higher caloric [71].

Sometimes the ontogenetic diet shifts may be seen as a consequence of the absolute size increment of their mouth gape [72], the larger fish size enables ingestion of larger prey items due to an increase in searching ability and capture efficiency [73,74].

*Trichomycterus poikilos* does not achieve a largest size than other species and by having a relatively thin, elongated and depressed body they can explore places not explore by the other species [35] as a explore the small spaces among rocks very well, what seems to have occurred in the present study. So, the items used by *T. poikilos* were smaller size however the ingestion of fish, *Aegla* sp. and terrestrial plant remains occurred only in the larger length classes. Ontogenetic differences in the diet of two *Trichomycterus* species (*T. crassicaudatus* and *T. stawiarski*) were also detected by [67]. *Trichomycterus chiltoni* showed intraspecific differences in its diet which were related to ontogeny because the species reached a larger size which allowed for the consumption of larger prey (therefore broadening the trophic spectrum because of morphological characteristics such as the mouth and body size) [75]. This differentiation of diet by influence of ontogeny was also found by many others studies [70,76,77,78,79].

Dietary differences cited above are also supported by the niche breadth data. All species showed high niche breadth. Most of items were ingested occasionally, expanding the trophic spectrum of

---

Table 4. Cont.

| Stream | Indicator Item | Specie/Size Class | IndVal | p  | Frequency |
|--------|----------------|-------------------|--------|----|-----------|
| Diplopora | R2 | 0.162 | 0.05 | 1 | |
| Terrestrial Hemiptera | R2 | 0.153 | 0.04 | 2 | |
| Nematode | R3 | 0.776 | 0.01 | 9 | |
| Orthoptera | R3 | 0.654 | 0.02 | 3 | |
| Sediment | H5 | 0.488 | 0.04 | 47 | |

Only items with significant values $p < 0.05$ are listed. For stream and specie/size class code see Material and Methods and Table 1.

doi:10.1371/journal.pone.0110999.t004

Figure 3. Values of trophic niche breadth for fish species analyzed in Alto Jacuí sub-basin. Values of trophic with mean ± standard error for each specie analyzed in sampling units. For specie code see Table 1.

doi:10.1371/journal.pone.0110999.g003
these species that have a diverse diet and wide niche breadth. This broad food spectrum is already expected in Neotropical stream fish, because such streams have a wide range of available resources [27,61,80,81,82]. Neotropical stream fish have a tendency towards generalism thus having the ability of trophic plasticity [83].

The mean niche breadth values were low only in the high size class of $R$. _quelen_ and _Heptapterus_ sp. In the early stages of life the species tend to exhibit more generalist behavior and with increasing body size they begin to exhibit more specialist behavior, as was found by [19] when they studied ontogenetic diet shifts among five species of _Crenicichla_.

The low overlap among the three species also indicates the resource partitioning. There are studies that show $R$. _quelen_ and _Heptapterus_ sp. not overlapping [61] and _R. quelen_ overlapped with _Trichomycterus_ sp. [27]. However, we believe that much of this low overlap was perceived because we did not group food items into broad categories- a discussion approached by other authors [27,66,84]. This in our opinion becomes very important in this type of analysis where one can notice the feeding preference of...
the species for certain aquatic larvae, for example, the strong preference of *T. poikilos* for Simuliidae larvae. If we think in broader trophic categories, we definitely would have an increased dietary overlap of these species. In overall the overlap niche values were low, however only in smaller size classes had high values. The null model showed that there is a resource sharing between the species/size class, this pattern were seen in all spatial-temporal units. The items that are shared by species are those that are most abundant (personal observations) and it is known that the abundance of some items is often responsible for the coexistence of species [77]. Sharing of resources does not mean existence of competition; the high abundance of resources and stochastic processes can promote relaxation of interspecific competition and facilitating coexistence which was also reported in other study [85]. We note that most items found in this study are shared by species, with overlap avoided both by the abundance of items in the aquatic system [4,27,54] and by the different microhabitats used for feeding, periods of activity, and tactics of capture. This pattern of features that avoid overlap and often explain the coexistence of sympatric species is well reported in Neotropical streams (e.g. [28,36,87,88,89,90]).

It is very difficult and complex we make inferences about species coexistence [85,91]. The three Siluriformes species studied here are coexisting, but the force that allows this coexistence is difficult to prove. The current scenario shows species with morphological similarities, partitioning some resources and sharing abundant

---

**Figure 6. Pianka’s index results.** Relative frequency of Pianka’s index of all pairwise interactions between the species with compatible size classes per sampling unit. For specie/size class code see Table 1.
doi:10.1371/journal.pone.0110999.g006

**Figure 7. Pianka’s index results.** Relative frequency of Pianka’s index of all pairwise interactions between the species with not compatible size classes per sampling unit. For specie/size class code see Table 1.
doi:10.1371/journal.pone.0110999.g007
resources resulting no competition among them [4]. But we cannot say with absolute certainty that the current scenario has not been structured over time through large negative pressures of the past between these species [10,92]. Differences in the species population numbers in different sample replicates (Table S1) was seen, and this may be related to stochastic events and other precepts of the neutral theory or which competition became more abundant a species at a stream than other [93]. However there is no evidence that the closest similarities in these streams had higher population numbers. To prove this theory we must increase our knowledge of the neutral theory or which competition became more abundant a species and this may be related to stochastic events and other precepts of the neutral theory or which competition became more abundant a species at a stream than other [93]. However there is no evidence that the closest similarities in these streams had higher population numbers.

In conclusion, our hypothesis was accepted, there is food segregation of three species of Siluriformes studied and it is related to the differential use of items in different stages of life. This because the differences in diet among species are related to morphological differences and life habits. There are more pronounced ontogenetic changes in *Heptapterus* sp. and *R. quelen* than in *T. poikilos*, given mainly by shifts in the morphology of these species. This process of diet shift throughout species growth is undoubtedly a way to expand or shift the trophic niche of the species in order to avoid inter- and intraspecific competition and maintain species coexistence that also maintain for the sharing resource of abundant items.

### References

1. Hardin G (1960) The competitive exclusion principle. Science 131: 1292–1297.
2. Pankka ER (1974) Niche overlap and diffuse competition. Proc Nat Acad Sci USA 71: 2141–2145.
3. Toward CR, Begon M, Harper LH (2006) Fundamentos em Ecologia. Porto Alegre: Arméd. 592 p.
4. Ross ST (1986) Resource partitioning in fish assemblages: a review of field studies. Copeia 1986: 352–360.
5. Leibold MA, McPeek MA (2006) Coexistence of the niche and neutral perspectives in community ecology. Ecology 87: 1399–1410.
6. Hubbell SP (2001) The Unified Neutral Theory of Biodiversity and Biogeography. Princeton: Princeton University Press. 489p.
7. Rosindell J, Hubbell S, He F, Harmon L, Etienne R (2012) The case for ecological neutral theory. Trends Ecol Evol 27: 209–208.
8. Bell G (2001) Neutral macroecology. Science 293(5539): 2413–2418.
9. Chast G, Irgoisen X, Chave J, Harris RP (2013) Latitudinal phytoplankton distribution and the neutral theory of biodiversity. Global Ecol Biogeogr 22: 531–543.
10. Connell JH (1961) Diversity and the coevolution of competitors, or the ghost of competition past. Oikos 35: 131–138.
11. Amarasekare P (2003) Competitive coexistence in spatially structured environments: a synthesis. Ecol Lett 6: 1109–1122.
12. Heshaghen T, Sakgárd R, Hegge O, Dervo BK, Skurdal J (2004) Niche overlap between young brown trout (*Salmo trutta*) and Siberian sculpin (*Cottus gairdneri*) in a subalpine Norwegian river. Hydrobiologia 521: 117–125.
13. Rezende CF, Lobo ´n-Cervia´ J, Caramaschi EP, Mazzoni R (2013) Trophic segregation of three species of Siluriformes studied and it is related to the differential use of items in different stages of life.
14. Rosindell J, Hubbell S, He F, Harmon L, Etienne R (2012) The case for ecological neutral theory. Trends Ecol Evol 27: 209–208.
15. Schoener TW (1974) Resource partitioning in ecological communities. Science 185: 27–39.
16. Sant’Anna AL, Vieira-Lanero R, Servia MJ, Cobo F (2011) Feeding and niche differentiation in three invasive gobies in the Lower Rhine, the Netherlands. Neotrop Ichthyol 11(2): 217–246.
17. Ross ST (1978) Trophic ontogeny of the leopard searobin, *Crenicichla* (*Valenciennes, 1840*). *Trichomycterus* (Valenciennes, 1840) (Siluriformes:Trichomycteridae) from the laguna dos Patos system, Southern Brazil. Neotrop Ichthyol 11(2): 217–246.
18. Borcherding J, Dolina M, Heermann L, Knutzen P, Kruger S et al. (2012) Testing the ecomorphological hypothesis in a pristine Serra do Mar stream (Rio de Janeiro, Brazil). Fundam Appl Limnol 27: 2014–2030.
19. Barrero AP, Aranha JMR (2005) Assembleia de peixes em um riacho da Floresta Atlântica: composição e distribuição espacial (Guaratinguetá, Paraná, Brasil). Acta Scientiarum 27(2): 153–160.
20. Barreto AP, Aranha JMR (2005) Assembleia de peixes em um riacho da Floresta Atlântica: composição e distribuição espacial (Guaratinguetá, Paraná, Brasil). Acta Scientiarum 27(2): 153–160.
21. Persson L, Claessen D, Roos AM, Bystrom P, Sjögren S et al. (2004) Cannibalism in a size-structured population: energy extraction and control. Ecol Monogr 74: 135–157.
22. Maghazie H, Borcherding J (2008) Risk-taking behavior in foraging perch: does predation pressure influence age-specific boldness? Anim Behav 75: 509–517.
23. Wainwright P (1995) Predicting patterns of prey use from morphology of fishes. Environ Biol Fishes 44: 97–113.
24. Oliveira JCS, Isaac VJ (2013) Diet breadth and niche overlap between *Hyphnomus plecostomus* (Linnæus, 1758) and *Hypostomus emarginatus* (Valenciennea, 1840) (Siluriformes) in the Córrego Nares hydroelectric reservoir, Ferreira Gomes, Ampaí-Brasil. Biota Amazona 3(2): 116–125.
25. Reis RE, Kallander SO, Ferraris CJ (2005) Check List of Freshwater Fishes of South and Central America. Porto Alegre: EDIPUCRS. 729 p.
26. Nelson JS (2006) Fishes of the World. New York: John Wiley & Sons, Inc. 601 p.
27. Casatti L (2002) Alimentação dos peixes em um riacho do Parque Estadual Morro do Diabo, Bacia do Alto Rio Paraná, sudeste do Brasil. Biota Neotropica, 2: 1–14.
28. Giménez LM, Braga FMS (2008) Feeding habits of the ichthyofauna in a protected area in the state of São Paulo, southeastern Brazil. Biota Neotropica 8(1): 41–47.
29. Barreto AP, Aranha JMR (2005) Assembleia de peixes em um riacho da Floresta Atlântica: composição e distribuição espacial (Guaratinguetá, Paraná, Brasil). Acta Scientiarum 27(2): 153–160.
30. Brejão GL, Gerhard P, Zuanon J (2013) Functional trophic composition of the ichthyofauna of forest streams in eastern Brazilian Amazon. Neotrop Ichthyol 11(2): 361–373.
31. Rezende CF, Lobo ´n-Cervia´ J, Caramaschi EP, Mazzoni R (2013) Trophic segregation of three species of Siluriformes studied and it is related to the differential use of items in different stages of life.
32. Schmid DAC, Verme OSD, Banfield EJ, Bilby RE, Hall DB et al. (2012) Foraging decisions of the otter (*Lutra* (*Lutra*): Mustelidae) in New Zealand: energy extraction and control. Ecol Monogr 82(1): 1–14.
33. Arratia G (1983) Preferencias de ha ´bitat de peces siluriformes de aguas continentales de Chile (Fam. Diplomystidae y Trichomycteridae). Stud Neotrop Ichthyol 8(1): 41–47.
34. Casatti L, Castro RMC (2006) Testing the ecomorphological hypothesis in a headwater riffles fish assemblage of the rio São Francisco, southeastern Brazil. Neotrop Ichthyol 4(2): 203–214.
35. Casatti L, Castro RMC (2006) Testing the ecomorphological hypothesis in a headwater riffles fish assemblage of the rio São Francisco, southeastern Brazil. Neotrop Ichthyol 4(2): 203–214.
36. Malabarba LR, Neto PC, Bertaco VA, Bértaco VA, Carvalho TP, Santos JF et al. (2013) Niche Partitioning in Siluriformes

### Supporting Information

#### Table S1 Number of analyzed stomachs per sample unit (stream and sampled month) for each size class for the species studied.

| Species | Stream | Sampled Month | Size Class | Number of Stomachs |
|---------|--------|---------------|------------|--------------------|
| T. poikilos | A | January | Small | 50 |
| H. plecostomus | B | February | Medium | 100 |
| H. emarginatus | C | March | Large | 150 |

For species and streams code see Material and Methods and Table 1. Asterisk indicates values less than 0.1%.

#### Table S2 Stomach content analyzed (% by volume) for the species of Siluriformes sampling in ten streams in Alto Jacuí sub-basin.

| Species | Stream | Sampled Month | Predation Pressure | Volume of Fish | Other Prey |
|---------|--------|---------------|--------------------|---------------|------------|
| T. poikilos | A | January | High | 70% | 30% |
| H. plecostomus | B | February | Low | 5% | 95% |
| H. emarginatus | C | March | Moderate | 35% | 65% |

For species and streams code see Material and Methods and Table 1. Asterisk indicates values less than 0.1%.

### Acknowledgments

We thank the colleagues of the Ichthyology Lab at the Universidade Federal do Rio Grande do Sul for Field work; the MSc. Juliano Ferrer for help in identifying the species studied; and the Orlaudi and Bonato family for help and support in the field work.

### Author Contributions

Conceived and designed the experiments: KOB CBF. Performed the experiments: KOB. Analyzed the data: KOB CBF. Contributed reagents/materials/analysis tools: KOB CBF. Contributed to the writing of the manuscript: KOB CBF.
37. Buckup PA (1988) The genus *Hypopterus* (Teleostei, Pimelodidae) in Southern Brazil and Uruguay, with the description of a new species. Copeia 198(3): 643–653.

38. Vidal LVO, Albiniati RCB, Albiniati ACL, Lira AD, Almeida TR et al. (2008) Engenho como anestésico para a talaipa do Nilo. Pesq Agropec Bras 43(10): 1096–1074.

39. Lucena CAS, Calegari JP, Pereira EHL, Dallegrave E (2013) O uso de óleo de cravo na eutanaisia de peixes. Boletim Sociedade Brasileira de Ictiologia 105: 20–29.

40. Merritt RM, Cummins KW (1996) An introduction to the aquatic insects of North America. Iowa: Kendall/Hunt. 733 p.

41. Costa C, Ide S, Simonka CE (2006) Insetos imaturos. Metamorfose e Identificação. Ribeirão Preto: Helos. 249 p.

42. Mugnai R, Nessimian JL, Baptista DF (2010) Manual de identificação de macroinvertebrados aquáticos do Estado do Rio de Janeiro. Rio de Janeiro: Technical Books. 174 p.

43. Hyslop EJ (1980) Stomach contents analysis: a review of methods and their application. J Fish Biol 17: 411–429. doi: 10.1111/j.1095-8649.1980.tb02775.x.

44. Hellawell JM, Abel RA (1971) Rapid volumetric method for the analysis of the gut contents of fishes. J Fish Biol 3: 29–57.

45. Legendre P, Legendre L (1998) Numerical ecology. Amsterdam: Elsevier. 853 p.

46. Borchard D, Gillet F, Legendre P (2011) Numerical Ecology with R. New York: Technical Books. 174 p.

47. Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance. Austral Ecol 26: 32–46.

48. Dufrehe M, Legendre P (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecol Monog 67: 345–366.

49. Cardoso P, Rigal F, Fattorini S, Terzopoulou S, Borges PAV (2013) Integrating Community Ecology Package. Available: http://CRAN.R-project.org/package=vegan. Accessed 5 December 2013.

50. Muotka T, Paavola R, Haapala A, Novikmecb M, Laasonen P (2002) Long-term effects of water temperature on the trophic structure and feeding overlap of the fish fauna in the seasonal Brazilian Pantanal, Cuiabá River 9(3): 229–242.

51. R Core Team (2013) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN3-900051-07-0. Available: http://www.R-project.org/. Accessed 5 December 2013.

52. Lacencas CAS, Calegari BB, Pereira EHL, Dallegrave E (2013) O uso de óleo de cravo na eutanaisia de peixes. Boletim Sociedade Brasileira de Ictiologia 105: 20–29.

53. Krebs CJ (1999) Ecological methodology. New York: Benjamin Cummings. 620 p.

54. Hurfthel SH (1978) The measurement of niche overlap and some relatives. Ecology 59: 67–77.

55. Pianka ER (1973) The structure of lizard communities. Annual Review of Ecology and Systematics 4: 53–74.

56. Costa C, Ide S, Simonka CE (2006) Insetos imaturos. Metamorfose e Identificação. Ribeirão Preto: Helos. 249 p.

57. Gotelli NJ, Entsminger GL (2001) EcoSim: null models software for ecology. Version 7. Available: http://garyentsminger.com/ecosim.html. Accessed 20 January 2014.

58. Albrecht M, Gotelli NK (2001) Spatial and temporal niche partitioning in diverse and rare species of *Odontesthes* (Pisces: Siluriformes) in a neotropical stream from the Atlantic rainforest, southern Brazil. Neotrop Ichthyol 6(2): 211–222.

59. Cetra M, Rondinelli GR, Souza UP (2011) Compartilhamento de recursos por reproducivos de *Heptapteridae* no Rio Macaé, RJ. Biota Neotropica 9: 31–37.

60. Elton C (1946) Competition and the structure of ecological communities. J Anim Ecol 15: 54–68.

61. Boon P (1974) Phylogenetic community structure: temporal variation in fish assemblage. Ecol Freshw Fish. doi: 10.1111/eff.12127.

62. Albrecht MP, Bohn T, Popova OA, Stakhvij F, Reshetnikov VS et al. (2003) Osteogenetic niche shifts and resource partitioning in a subtropical piscivore fish guild. Hydrobiologia 497: 109–119.

63. Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance. Austral Ecol 26: 32–46.

64. Borchard D, Gillet F, Legendre P (2011) Numerical Ecology with R. New York: Technical Books. 174 p.

65. Vitule JRS, Braga MR, Aranha JMR (2008) Ontogenetic, spatial and temporal variations in the feeding ecology of *Dentostomus langeri* Travassos, 1957 (*Teleostei: Characidae*) in a neotropical stream from the Atlantic rainforest, southern Brazil. Neotrop Ichthyol 6(2): 211–222.

66. Vitale JRS, Braga MR, Aranha JMR (2008) Ontogenetic, spatial and temporal variations in the feeding ecology of *Dentostomus langeri* Travassos, 1957 (*Teleostei: Characidae*) in a neotropical stream from the Atlantic rainforest, southern Brazil. Neotrop Ichthyol 6(2): 211–222.

67. Barreto AP, Armiliato FC, Ribeiro VM, Albihna V (2013) On the diet of two endemic and rare species of *Trichomycterus* (Ostariophysi: Trichomycteridae) in the Jordão River, Içuaçu River basin, southern Brazil. Estudos de Biologia, 35(4): 17–23.

68. Wootton RJ (1990) Ecology of teleost fishes. London: Chapmann & Hall. 404 p.

69. Fedras SRN, Posey JLFOF (2003) Feeding of the silverside (*Menidia menidia*) in the Mirim and Mangueira lagoons, Rio Grande do Sul, Brazil. Ichthyologia Set Zool 95(2): 117–120.

70. Vitule JRS, Braga MR, Aranha JMR (2008) Ontogenetic, spatial and temporal variations in the feeding ecology of *Dentostomus langeri* Travassos, 1957 (*Teleostei: Characidae*) in a neotropical stream from the Atlantic rainforest, southern Brazil. Neotrop Ichthyol 6(2): 211–222.

71. Arim M, Abades SR, Laufer G, Loureiro M, Marquet PA (2010) Food web structure and body size: trophic position and resource acquisition. Oikos 119: 147–153.

72. Lima-Junior SE, Goitein R (2003) Ontogenetic diet shifts of a Neotropical catfish, *Pimelodus maculatus* (Siluriformes, Pimelodidae): An ecomorphological approach. Journ. Biol. Fishes 69: 68–79.

73. Mittelbach GG (1981) Foraging efficiency and body size: a study of optimal diet and habitat use by bluegills. Ecology 62: 1370–1386.

74. Brot U, Jonsson T, Berlow EL, Warren P, Banasek-Richter C et al. (2006) Consumer-resource body-size relationships in natural food webs. Ecology 87: 2411–2417.

75. Scott S, Pardo R, Vila I (2007) Trophic niche overlap between two Chillean endemic species of *Trichomycterus* (Teleostei: Siluriformes). Rev Chil Hat Nat 80: 431–457.

76. Albrecht M, Bohn T, Popova OA, Stakhvij F, Reshetnikov VS et al. (2003) Osteogenetic niche shifts and resource partitioning in a subtropical piscivore fish guild. Hydrobiologia 497: 109–119.

77. Albrecht M, Bohn T, Popova OA, Stakhvij F, Reshetnikov VS et al. (2003) Osteogenetic niche shifts and resource partitioning in a subtropical piscivore fish guild. Hydrobiologia 497: 109–119.

78. Albrecht M, Bohn T, Popova OA, Stakhvij F, Reshetnikov VS et al. (2003) Osteogenetic niche shifts and resource partitioning in a subtropical piscivore fish guild. Hydrobiologia 497: 109–119.