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Assessing the diet and trophic niche breadth of an omnivorous fish (*Glanidium ribeiroi*) in subtropical lotic environments: intraspecific and ontogenic responses to spatial variations

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Abstract. The diet of *Glanidium ribeiroi* was investigated in lotic stretches downstream from a cascade of reservoirs to determine how it responds to intraspecific and environmental variations. Monthly sampling was performed from 2013 to 2016 at sites including the main channel of the Iguaçu River and tributaries in preserved basins and agricultural land. The diet of individuals in the preserved tributaries was primarily associated with allochthonous resources, whereas in the non-preserved tributaries and main channel the diets were primarily associated with autochthonous resources. Trophic niche breadth and intraspecific variability differed significantly among sampling areas and size classes. Trophic niche overlap among size classes and sampling areas was low. Positive and negative relationships between the trophic niche breadth and the standard length of individuals were also found in different sampling areas. Intraspecific and ontogenic variations were strongly and consistently associated with forest cover. Individuals responded differently to local environmental variations due to differences in landscape gradients and life cycle changes. Therefore, the effects of spatial heterogeneity on diet composition and intraspecific variations therein appear to be crucial to the success of the populations evaluated. These results may help with the implementation of conservation measures for this and other endemic species.

Additional keywords: allochthonous resources, feeding, fish freshwater, preserved areas, trophic segregation.

Received 6 April 2018, accepted 18 January 2019, published online 11 April 2019

Introduction

Habitat, time and food, and how these are modulated by the intrinsic characteristics of species, are considered the pillars of population dynamics (Pianka 1969; Chase and Leibold 2003). Among these, food, including the manner by which a species makes use of food resources, is considered the most important because it modulates the basal activity level of each species (Schoener 1974; Ross 1986; Gerking 1994). In addition, food is a source of the energy that is invested in body growth and reproduction (Schoener 1974; Ross 1986; Gerking 1994). In turn, the nutritional requirements of each individual are interrelated with

time and habitat, because environmental variables strongly affect the availability of food resources (Chase and Leibold 2003; Winemiller and Kelso-Winemiller 2003; Leibold and McPeck 2006; da Silva *et al.* 2017), which leads to changes in trophic niche breadth (i.e. the variety of resources used by the population; Chase and Leibold 2003). Assessing trophic niche breadth provides indicators of how the population behaves under different environmental conditions.

Recognisably different environmental variables are observed in lotic environments that have natural gradients in ecological variables along their course (Neves *et al.* 2018), as well as

complex interactions with the surrounding area and consequent changes in resource availability (Lampert and Sommer 2007; Humphries *et al.* 2014; da Silva *et al.* 2017). In lower-order rivers, such as tributaries, the abundance and availability of allochthonous resources (i.e. those originating from the terrestrial environment) are negatively correlated with the size, depth and slope of the river (Berggren *et al.* 2015; da Silva *et al.* 2017; Neves *et al.* 2018). In addition, it is predicted that resources of autochthonous origin (originating from the aquatic environment) could dominate under certain conditions (Vannote *et al.* 1980; Lampert and Sommer 2007; Teresa and Casatti 2010; da Silva *et al.* 2017; Neves *et al.* 2018). In contrast, in downstream reaches, where the main channel dimensions increase, the river is susceptible to less direct physical influence from the surrounding vegetation, but receives greater inputs of nutrients, which leads to greater availability of autochthonous resources (Wolff *et al.* 2013; Humphries *et al.* 2014; Neves *et al.* 2018).

The feeding activity of a species can be influenced by both extrinsic factors (environment, competition, presence of predators and availability of prey) and intrinsic factors (innate species-specific behaviour; Gerking 1994; Ward *et al.* 2006). Changes in foraging ability and consequent food selectivity frequently occur during development, caused primarily by changes in the body's morphological characteristics (Keppeler *et al.* 2015). Therefore, individuals with similar body sizes will have feeding abilities and prey preferences that differ from those of individuals in other size classes (Santos-Filho 1997; Dias *et al.* 2017). Variations on foraging are then modulated by morphological features and spatial segregation, with consequent changes in dietary amplitude among conspecific individuals (Silva *et al.* 2007). From this perspective, the importance of environmental influences on the trophic niche of fishes may contribute additional elements into their intraspecific interactions (Ward *et al.* 2006; Wiens *et al.* 2010; Sá-Oliveira and Isaac 2013; Quirino *et al.* 2015; Wang *et al.* 2015; Mateus *et al.* 2016).

In tropical aquatic environments, there is high environmental heterogeneity resulting of the interactions between the seasonal variations in key climate factors and the geomorphological characteristics of the landscape that determines modifications in the interface of marginal–river areas (Lowe-McConnell 1999; Neves *et al.* 2018). The Iguazu River basin, in the subtropical Atlantic Forest region of Brazil, has physiognomies typical of a plateau river, with pronounced variations in slope (Baumgartner *et al.* 2012) and a variety of land uses, including preserved, agricultural and urban areas (Vitule and Abilhoa 2009; Baumgartner *et al.* 2012). The high slopes of this basin that extend to adjacent areas lead to particularly strong interactions between the characteristics of marginal areas and the trophic dynamics of aquatic ecosystems.

Riparian vegetation affects the illumination of river waters, directly affecting aquatic primary production (Alberts *et al.* 2017) and the amount of organic material input to the river from adjacent land areas (Roberts *et al.* 2007; Demars *et al.* 2011). However, a decrease in the permeable vegetative cover associated with human development drives disturbances in natural hydrological patterns, as well as changes in the biological communities (Paul and Meyer 2001; Snyder *et al.* 2003; Alberts *et al.* 2017) and trophic dynamics of the aquatic ecosystem.

In this sense, spatial heterogeneity is essential and can be used as a predictor to evaluate the responses of fish populations to these variations.

Studies of trophic ecology allow the processes that regulate population dynamics to be elucidated (Gerking 1994). This information is crucial for conservation actions in general, but becomes even more important for the conservation of species that have restricted areas of occurrence, such as endemic species. The Iguazu River basin is also characterised by its high endemism and low fish species richness compared with other tributaries of the Paraná River (Bifi *et al.* 2006; Baumgartner *et al.* 2012). Among the endemic species within this river basin, *Glanidium ribeiroi* Haseman, 1911 (Auchenipteridae) is among the most abundant (Baumgartner *et al.* 2012). This species is considered to be medium sized, has a short body, a slightly depressed, broad head and a broad and terminal or slightly prognathous mouth (Baumgartner *et al.* 2012). Only Hahn *et al.* (1997), Ortêncio Filho *et al.* (2001) and Delariva *et al.* (2013) have investigated the diet of this species previously, with results indicating that *G. ribeiroi* consumes insects and fish. High trophic plasticity was also detected, because dietary changes were observed as a result of changes in the environment caused by dams (Delariva *et al.* 2013).

In this context, the objectives of the present study were to evaluate the diet of *G. ribeiroi* and how it responds to environmental variations in downstream stretches, but not yet fragmented by hydroelectric plants. We hypothesised that the diet and trophic niche breadth of this species would be altered by spatial variations arising from different land use configurations in the lower Iguazu River and its tributaries. Based on this hypothesis we tested three predictions: (1) greater incorporation of allochthonous resources, as well as wider trophic niches, would occur in the diets of individuals sampled in preserved tributaries; (2) individuals of smaller size would have a greater trophic niche breadth; and (3) intraspecific and ontogenic variations in resource use would promote trophic segregation among different size classes. The expectation was that the high abundance of this species in the studied basin is associated with its omnivorous and opportunistic feeding habits, which change according to spatial and intraspecific variations. These characteristics allow the species to be successful in environments subject to both natural and anthropogenic variations.

Materials and methods

Study area

The study area comprised the Iguassu ecoregion (*sensu* Freshwater Ecoregions of the World (FEOW) code #346; Hales and Petry 2018), which includes the Iguazu River basin and all its tributaries in Brazil above Iguazu (Iguassu) Falls. The Iguazu River basin has been isolated from the Paraná for more than 22×10^6 years by Iguazu Falls and other cascades, resulting in speciation and high endemism (Baumgartner *et al.* 2012; Hales and Petry 2018).

The Iguazu River basin is divided into the high, medium, and low Iguazu. The Iguazu River's headwaters are located in the Serra do Mar, and it crosses the Paraná Plateau before falling from the plateau at Iguazu Falls, near its confluence with the Paraná River. Elevations range between 136 and 1350 m above

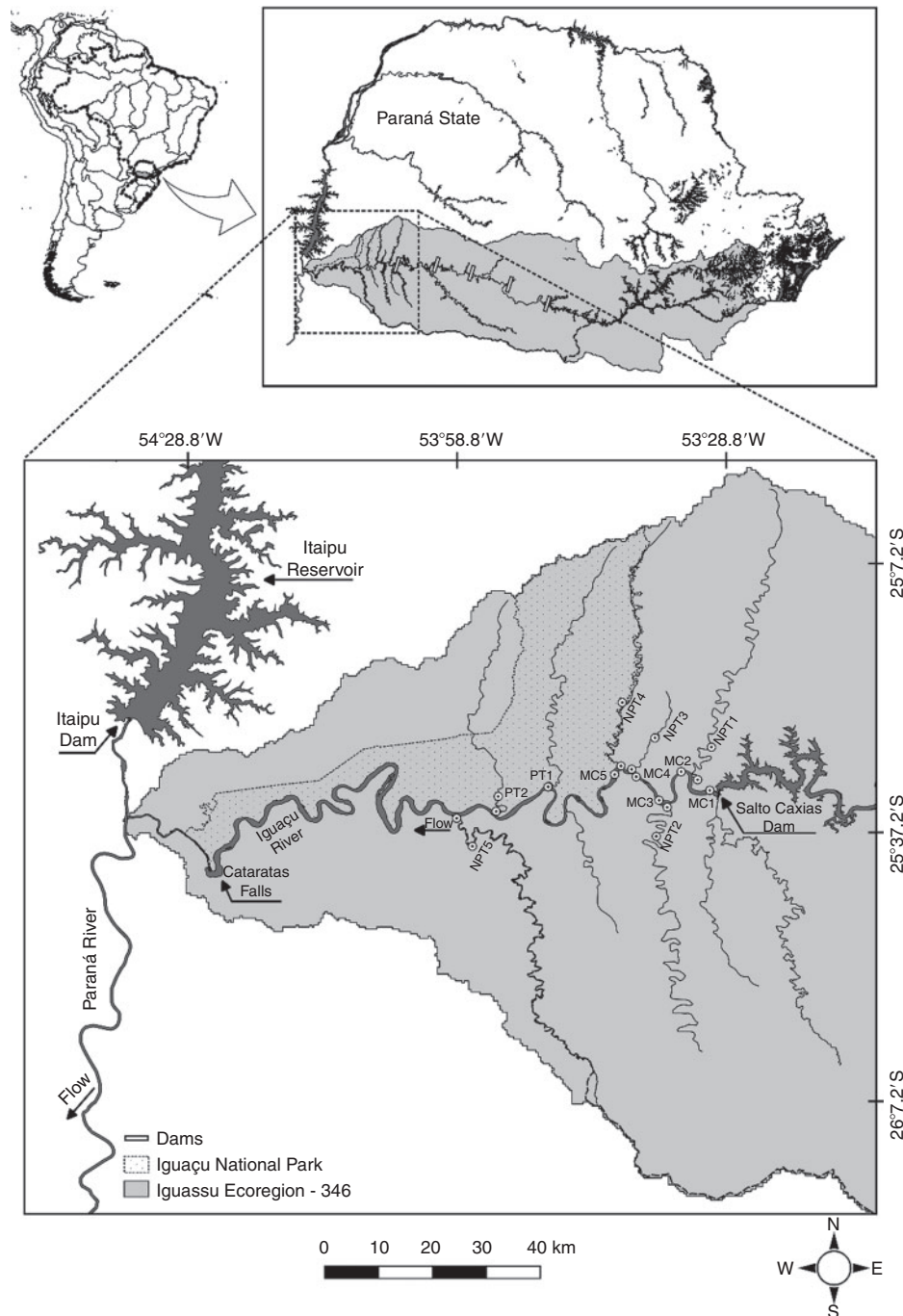


Fig. 1. Study area. Location of sampling sites in preserved tributaries (PT), non-preserved tributaries (NPT) and main channels (MC1–5) of the Iguazu River, Brazil. PT1, Floriano River; PT2, Silva Jardim; NPT1, Andradá; NPT2, Capanema; NPT3, Monteiro; NPT4, Gonçalves Dias; NPT5, Santo Antônio.

sea level, with an average of 800 m, and the river encounters numerous rapids and falls along its course before it abruptly falls at Iguazu Falls (Baumgartner *et al.* 2012). The steep slope of the Iguazu River basin on its third plateau was highly attractive for the development of hydroelectric plants, leading to the construction of five large reservoirs (flooding a total area of 656 km²) beginning in the 1970s.

The basin of the lower Iguazu River comprised the main study area. This area includes the main channel of the Iguazu River and tributaries in both non-preserved and preserved areas (Fig. 1). Among the preserved areas in the Iguazu River basin, Iguazu National Park (Fig. 1), a Federal Conservation Unit, comprises the largest remaining forest in western Paraná, Brazil. This reserve covers an area of 260 000 ha in a contact region

between Semideciduous Seasonal Forest and Mixed Ombrophilous Forest, two physiognomies of the Atlantic Forest *sensu lato* in the State of Paraná (Joly *et al.* 1999).

Sampling

Monthly sampling was conducted from 2013 to 2016 at 13 sites comprising the following: 2 tributaries whose basins drain areas within the Iguazu National Park and were considered to be preserved areas (Floriano (PT1) and Silva Jardim (PT2)); 5 tributaries under agricultural influence that were considered to be non-preserved areas (Andrada (NPT1); Capanema (NPT2); Monteiro (NPT3); Gonçalves Dias (NPT4); Santo Antônio (NPT5)); and 5 sites along the main channel of the Iguazu River located downstream of the Salto Caxias dam (the last of a sequence of 5 dams; Fig. 1). Sampling of each tributary except for the Floriano River included samples taken very near the mouth (150 m) and in the middle course section (Fig. 1). Fish sampling was conducted using gill nets of different sizes (mesh 2.5–14 cm between opposite knots; length 5 or 10 m) and longlines (20 hooks of 5/00), which were inspected every 8 h.

The fish caught were killed with 250 mg L⁻¹ benzocaine; this procedure was approved by the Ethics Committee on Animal Experimentation of the Universidade Estadual do Oeste do Paraná (Protocol 62/09). Specimens were identified in the laboratory and preserved in 70% alcohol. Voucher specimens were deposited in the fish collection of the Museu de Zoologia, Universidade Estadual de Londrina (MZUEL), Brazil, under the following voucher numbers: MZUEL13273, MZUEL16268, MZUEL16344, MZUEL16313, MZUEL16317, MZUEL17666, MZUEL17653, MZUEL17647 and MZUEL16243.

Stomach contents were examined under a stereomicroscope and optical microscope to identify food items. The contents were measured using a volumetric method (Hyslop 1980), in which the displacement of each food item or group of items sorted from the stomach contents is measured, usually in some type of graduated measuring device, and this displacement volume is considered to be equal to the volume of the food item in the stomach. In the present study, we used graduated test tubes and a glass counting plate (Hellawell and Abel 1971).

Data analyses

To verify the distribution of different fish size classes captured in the sampled areas, the catch per unit effort (CPUE) of each fishing apparatus was determined. These calculations considered the number of individuals caught and the effort needed to do so in terms of every 1000 m² for the net and 100 hooks for the longline over 24 h exposure.

To verify spatial variations in the CPUE for the different fish sizes classes, the fish caught were grouped based on length into 2.9-cm size classes between the minimum (6.0 cm) and maximum (25.0 cm) standard lengths (SLs) observed. To calculate the CPUE for each size class, all individuals of *G. ribeiroi* were grouped into the following size classes based on their SL and according to the aforementioned criteria: 6.0–9.0, 9.1–12.0, 12.1–15.0, 15.1–18.0 and >18.1 cm SL.

To report the diets of the sampled fish, individuals whose stomachs contained different food items were grouped into sizes

classes as described above for CPUE. In addition, food items were classified as allochthonous (originating from the terrestrial environment), autochthonous (originating from the aquatic environment; da Silva *et al.* 2017) or indeterminate for each sampling site. This was done to relate the diets of individuals to their surrounding areas.

A non-metric multidimensional scaling (nMDS; Kruskal 1964) analysis was performed to summarise the diet data of the different sampling areas (preserved tributaries, non-preserved tributaries and main channel sites) and sizes classes. To do this, values of the Bray–Curtis dissimilarity index were calculated based on a matrix of square root-transformed data for the volumetric abundances of the different food resources. A confidence index (stress) was obtained of the proximity of the graphical representation in the nMDS results to the real data. Stress values <0.20 indicate that a two-dimensional (2-D) nMDS can be used to represent the data (Clarke and Warwick 2001). Data were randomised 100 times, and the stability criterion was 0.005 standard deviations in the stress after 100 iterations. Using the same volumetric data matrix, similarity percentage analysis (SIMPER) was used to verify which food items were responsible for any spatial differences observed. All possible pairs of samples were compared using the Bray–Curtis index, as above (Clarke 1993).

In order to verify differences in the incorporation of allochthonous, autochthonous and indeterminate dietary resources among the sampling areas, and in this way to test the prediction that the greatest incorporation of allochthonous material in the diet occurs in the preserved tributaries, the non-parametric Kruskal–Wallis test was used.

A permutational analysis of multivariate dispersion (PERMDISP; Anderson 2004, 2006) was also conducted to test the prediction that spatial (among preserved tributaries, non-preserved tributaries and main channel sites) and ontogenic (among sizes class) variations occurred in the diets and niche breadth of individual *G. ribeiroi*. This analysis is based on the distance of the samples' data (diet) from the group (site) mean (Anderson 2006). This analysis has been increasingly used in recent years to assess the intraspecific variability in the niche breadth of individuals (Correa and Winemiller 2014; Quirino *et al.* 2015; da Silva *et al.* 2017). Using PERMDISP, the distance from the centroid of a group defined *a priori*, in this case the species, is calculated through a principal component analysis (PCoA). Calculation of the centroid of the group was performed using Bray–Curtis dissimilarity index values to allow the average dissimilarity among the *n* individual observations within the group to be compared. In this case, the distance from the centroid (*D*) corresponded to the niche breadth. To test the null hypothesis that the intraspecific variability and niche breadth did not differ among the groups, values of the *F*-statistic were calculated to compare the average distance of each sample from the centroid of the group. Subsequently, the *P*-value was obtained through 9999 permutations of the least-squares residuals (Anderson 2006). Post hoc pairwise comparisons were conducted using Tukey's honest significant difference (HSD) test. The assumption was that differences in the distance between sites indicated that fish in some sites had more restricted or broader diets than those of others (Correa and Winemiller 2014; da Silva *et al.* 2017).

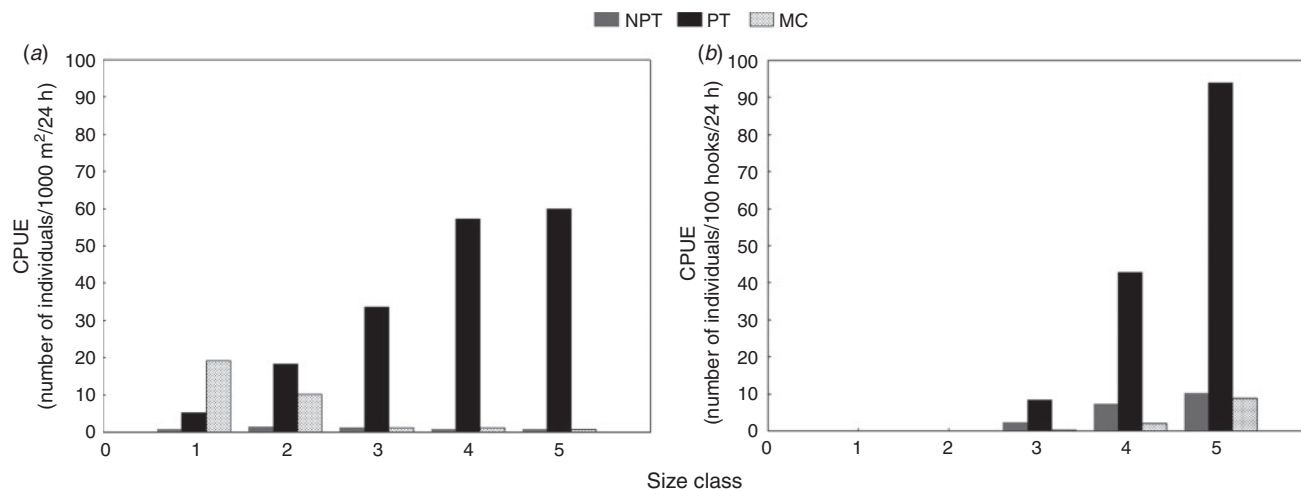


Fig. 2. Numerical abundance of *Glanidium ribeiroi* in different size classes led by the catch per unit effort (CPUE) for (a) gill nets and (b) longlines in sampling areas in preserved tributaries (PT; Floriano and Silva Jardim rivers), non-preserved tributaries (NPT; Andrada, Capanema, Monteiro, Gonçalves Dias and Santo Antonio rivers) and main channels (MC) of the Iguaçu River. The size classes were as follows: 1, 6.0–9.0-cm standard length (SL); 2, 9.1–12.0 cm SL; 3, 12.1–15.0 cm SL; 4, 15.1–18.0 cm SL; 5, ≥ 18.1 cm SL.

To test the last prediction that there is segregation of individuals in their use of resources, the overlap of the diet per each sample was calculated for each pair of individuals that co-occurred in time and space (month, site and size class) based on the matrix of volume data for the different food items using the Pianka (1973) food overlap index, which is described by the following equation:

$$O_{jk} = \sum_i^n P_{ij} \times P_{ik} \div \sqrt{\left(\sum_i^n P_{ij}^2 \times \sum_i^n P_{ik}^2\right)}$$

where O_{jk} is the Pianka measure of the niche overlap between species j and k , P_{ij} is the proportion of food item i in the diet of species j , P_{ik} is the proportion of food item i in the diet of species k and n is the total number of food items. The overlap values range from 0 (no overlap) to 1 (total overlap). In this study overlap values were divided into three levels, namely low (overlap values 0–0.39), intermediate (overlap values 0.4–0.6) and high (overlap values 0.61–1), as described by Grossman (1986) and modified by Corrêa *et al.* (2011). A null model (Harvey *et al.* 1983) was used to assess the significance of the Pianka index. In this procedure, the observed percentages of food represented by each category were randomised 10 000 times within each sample and, for each randomisation, the Pianka index was calculated again. For this analysis, we used the randomisation algorithm RA3, which retains the niche breadth of the observed species but allows for the use of any resource available in the diet matrix. The average dietary overlap based on real data was compared with the average calculated using these null models (Winemiller and Pianka 1990). Two-way analysis of variance (ANOVA) was then used to test for possible differences in dietary overlap values among sites and sizes classes.

The trophic niche breadth was calculated based on the volumetric data for the different food items using the standard Levin's Index (Ba). This index ranges from 0 (when a single species consumes only a single type of food item) to 1 (when one

species consumes all available food resources similarly). This index is calculated using the formula proposed by Hurlbert (1978), as follows:

$$Ba = \left(\left(\sum P_{ij}^2 \right)^{-1} - 1 \right) \div (n - 1)$$

To test the prediction that differences in the niche breadth of individuals are related to their SL, a non-parametric Spearman correlation test (Siegel and Castellan 2006) was performed between the niche breadth values and SL of the individuals at each site.

PERMDISP, permutational ANOVA, nMDS, trophic niche breadth and Spearman correlation were run using an R programming environment (ver. 3.2.3, R Foundation for Statistical Computing, Vienna, Austria), with the help of the Vegan package (J. Oksanen, F. G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, E. Szoecs, and H. Wagner, see <https://cran.r-project.org>; <https://github.com/vegandevs/vegan>, accessed 5 August 2018). SIMPER was run using PAST (ver. 2.08, Paleontological Statistics Software, see https://palaeo-electronica.org/2001_1/past/issue1_01.htm, accessed 19 February 2019; Hammer *et al.* 2001). ANOVA two-way and Kruskal–Wallis tests were performed using Statistica (ver. 7.0, Statsoft, see <http://www.statsoft.com>, accessed 19 February 2019). The diet overlap was calculated using EcoSim (ver. 7.0, N. J. Gotelli and G. L. Entsminger, see <http://www.garyentsminger.com/ecosim/>, accessed 19 February 2019). The level of statistical significance for all analyses was $P < 0.05$.

Results

The abundance (CPUE) and distribution of different sizes classes varied among the evaluated (Fig. 2). The number of individuals with SLs between 6 and 15 cm (Size Classes 1 and 2)

was higher in the main channel, whereas in the tributaries the sizes classes containing individual >15 cm SL were predominant (Sizes Classes 3–5). It should be emphasised that among the tributaries, the greatest abundance of fish in Sizes Classes 3–5 occurred in the preserved tributaries (Fig. 2).

In all, the contents of 242 stomachs were analysed (Table 1). Based on these analyses, *G. ribeiroi* had a broad diet containing food resources of both animal and plant origin, such as immature insects, terrestrial insects, seeds, crustaceans, fish and Rodentia (Table 1).

When the diet data were summarised through an nMDS analysis (two-axis solution; stress = 0.08), different food resources were found to be consumed by this species among the sampled sites and size classes, because these were separated along Axis 2 of the nMDS plot. The larger individuals (Size Classes 4 and 5) consumed a higher proportions of seeds, terrestrial insects, crustaceans and Rodentia in the preserved tributaries. Conversely, in the non-preserved tributaries, a more varied diet was observed, which included resources from all trophic levels, such as fish, terrestrial and aquatic insects and terrestrial vegetation. Individuals in Sizes Classes 1–3 were found to be more strongly associated with smaller food items, such as immature insects and algae, at all sites and especially those in the main channel (Fig. 3).

Fish, seeds and algae were the main food resources responsible for the observed differences among the sampling areas. Fish were preferentially consumed in the non-preserved tributaries and in the main channel, whereas seeds differentiated the diet of individuals in the preserved tributaries from those in other sites (Table 2).

In general, there was a predominance of allochthonous resources in the diets of individuals sampled from the preserved tributaries ($H = 41.53$, d.f. = 2, $n = 242$, $P < 0.05$), whereas in the non-preserved tributaries ($H = 6.15$, d.f. = 2, $n = 242$, $P < 0.05$) and in the main channel ($H = 6.15$, d.f. = 2, $n = 242$, $P < 0.05$) there was a greater contribution of autochthonous resources to the diet (Fig. 4).

Marked variations were observed in fish diet among size classes. In general, larger food items, such as fish, terrestrial vertebrates and aquatic invertebrates, were consumed primarily by individuals >15.1 cm SL, whereas aquatic and terrestrial plants and aquatic and terrestrial insects were preferentially consumed by individuals between 6 and 15 cm SL (Fig. 5).

There were significant differences in trophic niche breadth among sites and size classes (PERMDISP, d.f. = 14, $F = 2.30$, $P = 0.005$; Fig. 6; Table 3). In the preserved tributaries, the diet variability among individuals was higher in the smaller size classes, whereas the mean dietary breadth was greater for individuals in the larger size classes. In the non-preserved tributaries, the variability did not differ among the size classes, although the mean amplitude was higher for individuals of the lower size classes. In the main channel, the mean dietary breadth was also higher for the smaller individuals, but there was no clear pattern in this variability (Fig. 6).

Trophic niche overlap was low (0–0.40) for 62.1% of individuals. High overlap (0.61–1) was observed for only 30% of individuals and was more conspicuous in the diets of individuals in the non-preserved tributaries (16.6%), whereas intermediate overlap (0.40–0.60) was found for only 7% of the

individuals examined. However, no significant differences in diet overlap were observed ($H = 1.12$, $P = 0.5696$). According to the Pianka index, the maximum observed values (83%) were not significantly higher than those expected by chance, suggesting that there was high dietary segregation among individuals in different sites and size classes.

The correlation between the trophic niche breadth values (Levin's index) and SLs of individuals confirmed that differences in the variety of items consumed by the studied occur among different sizes and sampling sites. A positive correlation was found between body size and trophic niche breadth in individuals sampled in the preserved tributaries, but it was not significant ($r = 0.16$, $P = 0.11$, Fig. 7). At the sites sampled along the main channel and non-preserved tributaries, the correlation was negative, showing that larger individuals exhibited lower niche breadth in these sites ($r = -0.28$, $P = 0.005$; $r = -0.28$, $P = 0.03$ respectively; Fig. 7).

Discussion

The observed consumption of food items of different trophic levels and origins (aquatic and terrestrial) and the spatial variations in diet composition revealed the omnivorous habit of *G. ribeiroi*, as well as its generalist and opportunistic diet. These findings disagree with previous studies performed upstream of the study area, which described the species' habit as carnivorous (Ortêncio Filho *et al.* 2001; Delariva *et al.* 2013). The morphological characteristics of this species, such as its dorsoventrally compressed head and a wide terminal mouth (Baumgartner *et al.* 2012), favour the consumption of items of different sizes. This morphological peculiarity allows this species to extend the range of prey it can consume according to the availability of different food types, which is variable in time and space (Bernal *et al.* 2015).

There was a strong association between different land use types and the proportion of allochthonous resources ingested by the fish population sampled. Allochthonous resources were more dominant in the diets of individuals from the tributaries draining preserved areas, which run through areas of the Atlantic Forest where the physiognomies of the Semideciduous Seasonal and Mixed Ombrophilous Forest converge over more than 50% of the drainage basin's area (Joly *et al.* 1999; Tabarelli *et al.* 2005). Vegetation and the use of a surrounding area's resources for fish fauna have been established in the literature as crucial for the maintenance of lotic ecosystems, particularly because of the exchange of organic and inorganic material between the stream and terrestrial environments (Pusey and Arthington 2003; Lampert and Sommer 2007; Feld 2013; Molina *et al.* 2017). This transferred material of allochthonous origin directly and indirectly contributes food for fish (Schoener 1974; Trindade *et al.* 2013; Ceneviva-Bastos and Casatti 2014). In the same manner, in environments where the surrounding vegetation is degraded, there are changes in the supply and transport of terrestrial material, such as plants and insects, which thus interfere with the lotic food web.

The trophic plasticity of the evaluated species verified in this study has also been described for most other fish species in tropical regions (Gerking 1994; Abelha *et al.* 2001). The positive relationship between the presence of vegetation around river channels and the contribution of allochthonous resources

Table 1. Feed items consumed by *Glanidium ribeiroi* in the sampled areas in the Iguazu River basin, Brazil, according to size class

Values are percentage data of the volume of food items. PT, preserved tributary; NPT, non-preserved tributary; MC, main channel; autochthonous, the aquatic environment origin; allochthonous, origin outside the aquatic environment; SL, standard length

		Size class (cm SL)														
		6.0–9.0			9.1–12			12.1–15			15.1–18			>18		
		PT	NPT	MC	PT	NPT	MC	PT	NPT	MC	PT	NPT	MC	PT	NPT	MC
Number of stomachs		2	7	54	5	10	24	18	14	4	33	14	6	33	11	7
Autochthonous food items (percentage volume)																
Algae				0.01					1.67							
Aquatic plants			6.58	0.07		0.24	1.90				0.05	0.02		1.36		
Diptera – immature			28.20	0.13			4.93			1.36						
Others aquatic insect			1.31	0.41	0.16	0.92	9.10	0.01	0.33							
<i>Aegla</i> sp.			10.44	19.43	22.31			20.60	21.27		12.78	24.25	17.58	12.93	21.44	26.90
Aquatic invertebrates			6.79	0.73		0.07			8.31				17.58	6.53	0.82	0.50
Fish remains				30.42		0.55	0.08	3.48	2.33	34.10	8.77	26.93	64.83	4.23	27.82	6
Perciformes									21.60		0.80	21.27		6.81		35.90
Synbranchiiformes				2.92											3.27	7.50
Siluriformes									9.97					4.08		
Characiformes				14.58					26.59		17.52				16.37	17.90
Sum			53.32	68.69	22.47	1.78	16	24.09	92.06	35.46	39.92	72.48	100	35.95	69.72	94.70
Allochthonous food items (percentage volume)																
Terrestrial plants																
Seeds			25.38	0.28	2.15	75.33	0.82	0.06	0.55	13.31				0.44	0.13	
Hemiptera		3.77		6.15	18.02	7.84	4.84	62.11	4.98	49.90	39.97	10.64		29.81	6.91	
Coleoptera		81.13	6.01	3.52	1.54	2.73	51.68	0.66	0.83			6.38		0.27		5.20
Hymenoptera		15.09	4.18	0.40		0.03	5.45	4.05	1.58		3.19	3.83		0.63	3.28	
Orthoptera			0.31		12.87			6.45			0.80					
Others terrestrial insect			0.37	10.14	42.94	2.88	17.11				1.79	6.68		0.26	10.69	
Mammalia, Rodentia											7.56			23.52		
Sum	100		36.24	22.74	77.53	95.52	79.91	75.91	7.94	63.21	53.31	27.52		63.92	21	5.20
Indeterminate or detritus			10.44	1.24		2.70	4.09			0.20				0.13	1.09	

may also be relevant to explaining the significant differences in intraspecific spatial variability in the diet, as well as the positive correlation between body size and trophic niche breadth observed in preserved tributaries. In these environments, there is typically a relationship between water depth and the extent of the riparian vegetation area, and thus preserved tributaries are more susceptible to variations in the input and transportation of food resources into the aquatic environment (Vannote *et al.* 1980; Prejs and Prejs 1987; da Silva *et al.* 2017). Fish, in turn, increase their feeding spectra by taking advantage of these energetically favourable items, resulting in greater feeding efficiency (Schoener 1971; Gerking 1994). The characteristics of *G. ribeiroi* are particularly beneficial in this sense because this species exhibits surface swimming, a characteristic of the family Auchenipteridae (Ferraris 2003) that favours the consumption of resources like terrestrial insects and the leaves and seeds of plants.

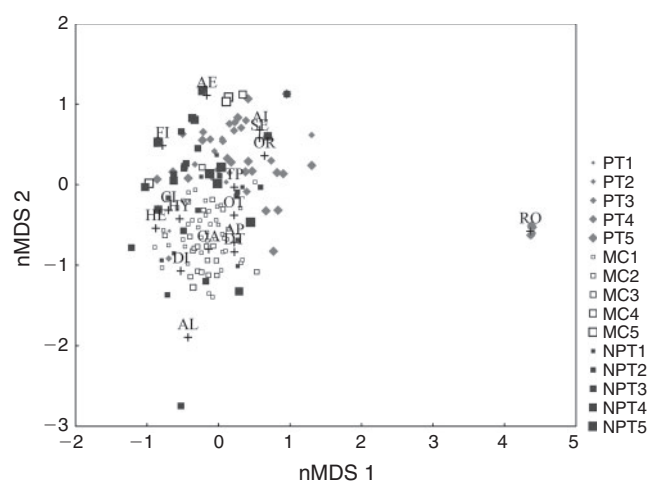


Fig. 3. Graphical representation of the first two axes of the non-metric multidimensional scaling (nMDS), demonstrating the food resources used by *Glanidium ribeiroi* between sampling areas in the Iguçu River basin, Brazil. PT, preserved tributary (Floriano and Silva Jardim rivers); NPT, non-preserved tributary (Andrada, Capanema, Monteiro, Gonçalves Dias and Santo Antonio rivers); MC, main channel of the Iguçu River. Numbers from 1 to 5 indicate size classes: 1, 6.0–9.0-cm standard length (SL); 2, 9.1–12.0 cm SL; 3, 12.1–15.0 cm SL; 4, 15.1–18.0 cm SL; 5, ≥ 18.1 cm SL. AE, *Aegla* sp.; AI, aquatic invertebrates; AL, algae; AP, aquatic plants; CI, Coleoptera – immature; DI, Diptera immature; DT, detritus; FI, fish remains; HE, Hemiptera; HY, Hymenoptera; OA, other aquatic insects; OR, Orthoptera; OT, other terrestrial insects; RO, Mammalia – Rodentia; SE, seed; TP, terrestrial plants.

The concept that many populations are composed of ecologically heterogeneous individuals that exhibit trade-offs in the manner in which they exploit their environments has been consolidated (Bolnick *et al.* 2003; Araújo *et al.* 2011; Bolnick *et al.* 2011). For example, food is ingested in a way that maximises the rate of energy gain (Pulliam 1974; Correa and Winemiller 2014; Coblenz *et al.* 2017), based on balancing the energetic values of different resources and the search and handling times involved in their capture, containment and digestion (Pires *et al.* 2011). However, this individual niche variation may also occur as a result of size-specific characteristics and ontogenic variations (Schoener 1986; Chase and Leibold 2003; Marsh *et al.* 2017). Previous studies reported differences in fish feeding throughout their life cycle that were primarily related to changes in morphological characteristics as well as body size (Neves *et al.* 2015; Dias *et al.* 2017; Schilling *et al.* 2017). In the present study, the populations of *G. ribeiroi* evaluated exhibited intraspecific differences in their feeding spectra among individuals of the same size class.

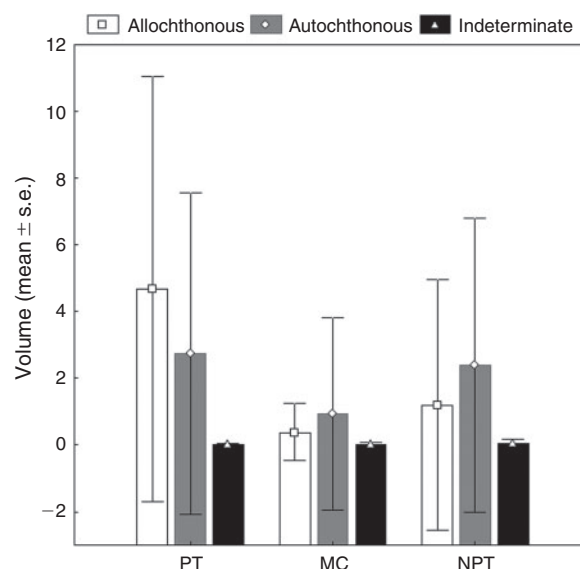


Fig. 4. Spatial variation in the origin of food items in the diet of *Glanidium ribeiroi* between sampling areas in the Iguçu River basin, Brazil. PT, preserved tributary (Floriano and Silva Jardim rivers); NPT, non-preserved tributary (Andrada, Capanema, Monteiro, Gonçalves Dias and Santo Antonio river); MC, main channel of the Iguçu River. Data are the mean \pm s.e.

Table 2. Results of similarity percentage analysis (SIMPER) of the proportion of food items consumed by *Glanidium ribeiroi* between sampling areas in the Iguçu River basin, Brazil

PT, preserved tributary; NPT, non-preserved tributary; MC, main channel

Food item	Overall average dissimilarity	Contribution (%)	Cumulative contribution (%)	Mean abundance		
				PT	NPT	MC
Seed	96.05	26.25	26.25	2.75	0.0316	0.217
Fish		19.01	45.26	1.38	0.614	1.58
<i>Aegla</i>		18.33	63.59	1.04	0.221	0.67

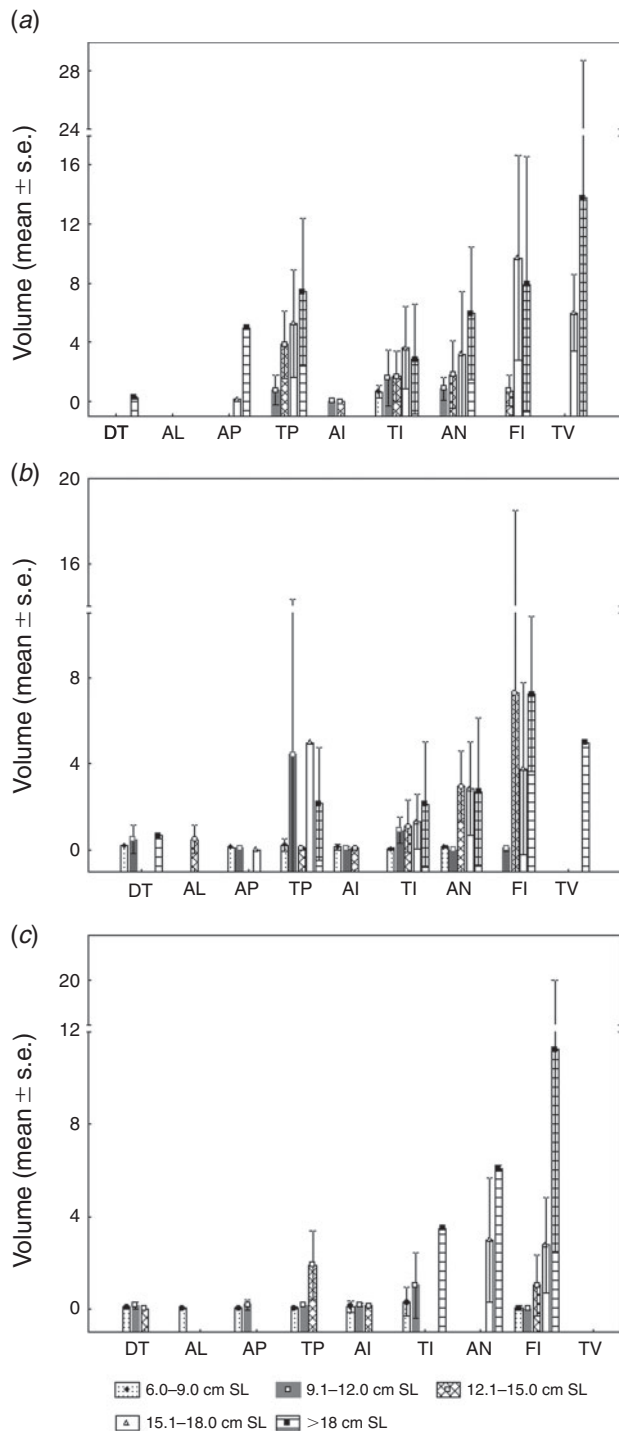


Fig. 5. Diet composition according to the standard length (SL) of *Glanidium ribeiroi* specimens between the sampling areas in the Iguaçu River basin, southern Brazil: (a) preserved tributary (Floriano and Silva Jardim rivers); (b) non-preserved tributary (Andrada, Capanema, Monteiro, Gonçalves Dias and Santo Antonio river); (c) MC, main channel of the Iguaçu River. Data are the mean \pm s.e. AI, aquatic insects; AL, algae; AN, aquatic invertebrates; AP, aquatic plants; DT, detritus; FI, fish; TI, terrestrial insects; TP, terrestrial plants; TV, terrestrial vertebrates.

Fish, aquatic invertebrates and terrestrial vertebrates were preferentially consumed by individuals longer than 15 cm, both in the main channel and in the tributaries. The larger mouth sizes of larger individuals favoured the consumption of the largest and most energy-efficient resources (Chase and Leibold 2003; Tupinambás *et al.* 2015; Marsh *et al.* 2017), such as fish and terrestrial vertebrates. In contrast, in the case of individuals <15 cm SL, a predominance of smaller food items, such as insects and plants, was observed in their diets. It is known that energy demands increase as the fish grows, and thus there is a change or extension in the optimal range of resources captured by their foraging behaviour (Werner and Gilliam 1984; Scharf *et al.* 2000; Marsh *et al.* 2017). It has been suggested that small fish may be more generalist in the ways in which they meet their energy demands with food (Ward *et al.* 2006; Neves *et al.* 2015; Dias *et al.* 2017; Schilling *et al.* 2017). These differences between larger and smaller individuals, particularly in terms of swimming ability (Weihs 1977; Schilling *et al.* 2017) and mouth and maxillary size, permit the exploitation of a greater variety of habitats and larger sizes of prey as the fish grows (Chase and Leibold 2003; Ward *et al.* 2006; Tupinambás *et al.* 2015; Schilling *et al.* 2017).

The average diet breadth observed in PERMDISP shows that individuals with a larger body size in preserved environments consumed a greater variety of food items, whereas in the main channel and in non-preserved tributaries smaller individuals consumed a greater variety of items. Studies have shown that ontogenetic differences may reduce intraspecific competition for food items through diet segregation (Canavero *et al.* 2014; Ortiz and Arim 2016). Further, direct interactions may be reduced through spatial segregation, because competitive interactions are stronger among individuals of similar sizes (Canavero *et al.* 2014; Ortiz and Arim 2016). Corroborating PERMDISP results,

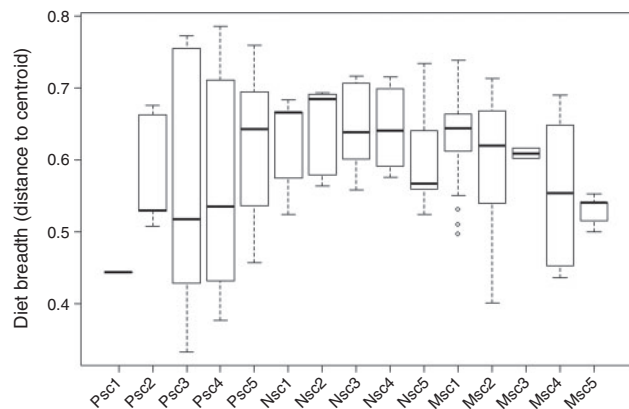
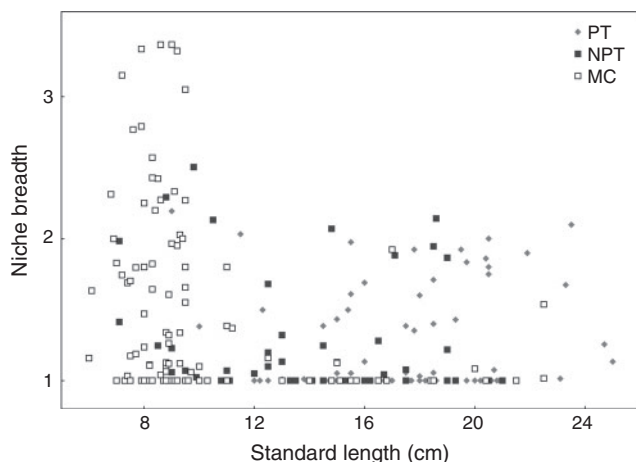


Fig. 6. Variation in the diet breadth of *Glanidium ribeiroi* using permutational analysis of multivariate dispersion (PERMDISP) for sampling areas in the Iguaçu River basin, southern Brazil. Psc, size class of preserved tributary; Nsc, size class of non-preserved tributary; Msc, size class of main channel. Numbers from 1 to 5 indicate size classes: 1, 6.0–9.0-cm standard length (SL); 2, 9.1–12.0 cm SL; 3, 12.1–15.0 cm SL; 4, 15.1–18.0 cm SL; 5, ≥ 18.1 cm SL. Boxes represent the 25th and 75th quartiles and demonstrate the individual variability of the diet. The horizontal bars in each box represent mean diet breadth. Whiskers indicate the range and individual symbols indicate outliers.

Table 3. Summary of permutational analysis of multivariate dispersion (PERMDISP) showing *P*-values of diet breadth comparisons of *Glanidium ribeiroi* for the sampling areas and size classes in the Iguaçu River basin, Brazil

PT, preserved tributary; NPT, non-preserved tributary; MC, main channel. Numbers from 1 to 5 indicate size classes: 1, 6.0–9.0-cm standard length (SL); 2, 9.1–12.0 cm SL; 3, 12.1–15.0 cm SL; 4, 15.1–18.0 cm SL; 5, ≥18.1 cm SL

	PT1	PT2	PT3	PT4	PT5	NPT1	NPT2	NPT3	NPT4	NPT5	MC1	MC2	MC3	MC4	MC5
PT1		0.071	0.261	0.198	0.006	0.007	0.002	0.001	0.001	0.01	0.001	0.011	0.001	0.237	0.001
PT2			0.886	0.949	0.378	0.355	0.095	0.088	0.076	0.592	0.034	0.51	0.525	0.654	0.133
PT3				0.89	0.142	0.421	0.149	0.103	0.109	0.496	0.011	0.365	0.629	0.833	0.494
PT4					0.148	0.417	0.135	0.098	0.088	0.558	0.004	0.366	0.632	0.727	0.389
PT5						0.979	0.415	0.449	0.399	0.577	0.358	0.533	0.778	0.11	0.013
NPT1							0.465	0.519	0.413	0.576	0.52	0.653	0.678	0.206	0.004
NPT2								0.891	0.934	0.167	0.603	0.185	0.238	0.057	0.001
NPT3									0.932	0.172	0.709	0.168	0.299	0.043	0.001
NPT4										0.13	0.656	0.158	0.252	0.033	0.001
NPT5											0.084	0.904	0.891	0.295	0.024
MC1												0.058	0.316	0.005	0.001
MC2													0.96	0.198	0.019
MC3														0.391	0.001
MC4															0.58
MC5															

**Fig. 7.** Graphic representation of the relationship between variables the trophic niche breadth and the standard length of *Glanidium ribeiroi* for sampling areas in the Iguaçu River basin, Brazil. PT, preserved tributary (Floriano and Silva Jardim rivers); NPT, non-preserved tributary (Andrada, Capanema, Monteiro, Gonçalves Dias and Santo Antonio river); MC, main channel of the Iguaçu River.

the observed low niche overlap was not significantly higher than expected by chance, suggesting that there was high dietary segregation between individuals at different sites and in different size classes. Furthermore, the observed correlation between breadth niche and the SL of individuals confirms the trophic segregation between individuals due to morphological changes and an increase in size throughout the life cycle.

In summary, the diet of *G. ribeiroi* was found to contain diverse items of both animal and vegetable origin, demonstrating the omnivory of this species. In addition, the occurrence of dietary changes associated with spatial variations was verified, as well as the high trophic plasticity and opportunism of this

species. Furthermore, intraspecific and ontogenic variations were strongly and consistently associated with forest cover and the local environmental conditions linked to landscape gradients. The results of this study demonstrate that individuals respond differently to environmental variation and life cycle changes, supporting our initial predictions. Evaluating the consequences of environmental fluctuations (spatial heterogeneity), diet composition and intraspecific variations that favour the success of a population may help in the implementation of conservation measures for the species. This is relevant considering that the natural dynamics of the Iguaçu River basin are under constant threat, particularly by hydroelectric reservoirs and agricultural use. Both situations strongly alter the exchange of materials between tributaries and their surrounding environments, as well as the input of allochthonous resources, with the latter being important in the diet of the endemic species evaluated herein.

Conflicts of interest

The authors declare that they have no conflicts of interest.

Declaration of funding

This project was funded by the Consórcio Empreendedor Baixo Iguaçu (CEBI).

Acknowledgements

The authors thank CEBI for financial support, GETECH for providing logistical support for sampling and the analysis of materials and the Meteorological Institute of Paraná (SIMEPAR) for providing precipitation and temperature data.

References

- Abelha, M. C. F., Agostinho, A. A., and Goulart, E. (2001). Plasticidade trófica em peixes de água doce. *Acta Scientiarum* **23**, 425–434.
- Alberts, J. M., Beaulieu, J. J., and Buffam, I. (2017). Watershed land use and seasonal variation constrain the influence of riparian canopy cover on

- stream ecosystem metabolism. *Ecosystems* **20**, 553–567. doi:10.1007/S10021-016-0040-9
- Anderson, M. J. (2004). 'PERMDISP: a FORTRAN Computer Program for Permutational Analysis of Multivariate Dispersions (for any Two-Factor ANOVA Design) using Permutation Tests.' (Department of Statistics, University of Auckland: Auckland, New Zealand).
- Anderson, M. J. (2006). Distance-based tests for homogeneity of multivariate dispersions. *Biometrics* **62**, 245–253. doi:10.1111/J.1541-0420.2005.00440.X
- Araújo, M. S., Bolnick, D. I., and Layman, C. A. (2011). The ecological causes of individual specialization. *Ecology Letters* **14**, 948–958. doi:10.1111/J.1461-0248.2011.01662.X
- Baumgartner, G. C. S., Pavanelli, C. S., Baumgartner, D., Bifi, A. G., Debona, T., and Frana, V. A. (2012). 'Peixes do baixo Rio Iguaçu.' (EDUEM: Maringá, Brazil.)
- Berggren, M., Bergström, A. K., and Karlsson, J. (2015). Intraspecific autochthonous and allochthonous resource use by zooplankton in a humic lake during the transitions between winter, summer and fall. *PLoS One* **10**, e0120575. doi:10.1371/JOURNAL.PONE.0120575
- Bernal, A., Olivar, M. P., Maynou, F., and de Puellas, M. L. F. (2015). Diet and feeding strategies of mesopelagic fishes in the western Mediterranean. *Progress in Oceanography* **135**, 1–17. doi:10.1016/J.POCEAN.2015.03.005
- Bifi, A. G., Baumgartner, D., Baumgartner, G., Frana, V. A., and Debona, T. (2006). Composição específica e abundância da ictiofauna do rio dos Padres, bacia do rio Iguaçu, Brasil. *Acta Scientiarum. Biological Sciences* **28**, 203–211.
- Bolnick, D. I., Svanback, R., Fordyce, J. A., Yang, L. H., Davis, J. M., Hulsey, C. D., and Forister, M. L. (2003). The ecology of individuals: incidence and implications of individual specialization. *American Naturalist* **161**, 1–28. doi:10.1086/343878
- Bolnick, D. I., Amarasekare, P., Araújo, M. S., Burger, R., Levine, J. M., Novak, M., Rudolf, V. H. W., Schreiber, S. J., Urban, M. C., and Vasseur, D. (2011). Why intraspecific trait variation matters in community ecology. *Trends in Ecology & Evolution* **26**, 183–192. doi:10.1016/J.TREE.2011.01.009
- Canavero, A., Hernández, D., Zarucki, M., and Arim, M. (2014). Patterns of co-occurrences in a killifish metacommunity are more related with body size than with species identity. *Austral Ecology* **39**, 455–461. doi:10.1111/AEC.12103
- Ceneviva-Bastos, M., and Casatti, L. (2014). Shading effects on community composition and food web structure of a deforested pasture stream: evidences from a field experiment in Brazil. *Limnology* **46**, 9–21. doi:10.1016/J.LIMNO.2013.11.005
- Chase, J. M., and Leibold, M. A. (2003). 'Ecological Niches: Linking Classical and Contemporary Approaches.' (University of Chicago Press: Chicago, IL, USA.)
- Clarke, K. R. (1993). Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* **18**, 117–143. doi:10.1111/J.1442-9993.1993.TB00438.X
- Clarke, K. R., and Warwick, R. M. (2001). A further biodiversity index applicable to species lists: variation in taxonomic distinctness. *Marine Ecology Progress Series* **216**, 265–278. doi:10.3354/MEPS216265
- Coblentz, K. E., Rosenblatt, A. E., and Novak, M. (2017). The application of Bayesian hierarchical models to quantify individual diet specialization. *Ecology* **98**, 1535–1547. doi:10.1002/ECY.1802
- Correa, S. B., and Winemiller, K. O. (2014). Niche partitioning among frugivorous fishes in response to fluctuating resources in the Amazonian floodplain forest. *Ecology* **95**, 210–224. doi:10.1890/13-0393.1
- Corrêa, C. E., Albrecht, M. P., and Hahn, N. S. (2011). Patterns of niche breadth and feeding overlap of the fish fauna in the seasonal Brazilian Pantanal, Cuiabá River basin. *Neotropical Ichthyology* **9**, 637–646. doi:10.1590/S1679-62252011000300017
- da Silva, J. C., Gubiani, É. A., Neves, M. P., and Delariva, R. L. (2017). Coexisting small fish species in lotic neotropical environments: evidence of trophic niche differentiation. *Aquatic Ecology* **51**, 275–288. doi:10.1007/S10452-017-9616-5
- Delariva, R. L., Hahn, N. S., and Kashiwaqui, E. A. L. (2013). Diet and trophic structure of the fish fauna in a subtropical ecosystem: impoundment effects. *Neotropical Ichthyology* **11**, 891–904. doi:10.1590/S1679-62252013000400017
- Demars, B. O. L., Manson, J. R., Olafsson, J. S., Gislason, G. M., Gudmundsdottir, R., Woodward, G., Reiss, J., Pichler, D. E., Rasmussen, J. J., and Friberg, N. (2011). Temperature and the metabolic balance of streams. *Freshwater Biology* **56**, 1106–1121. doi:10.1111/J.1365-2427.2010.02554.X
- Dias, T. S., Stein, R. J., and Fialho, C. B. (2017). Ontogenetic variations and feeding habits of a Neotropical annual fish from southern Brazil. *Iheringia. Série Zoologia* **107**, 1–15. doi:10.1590/1678-4766E2017020
- Feld, C. K. (2013). Response of three lotic assemblages to riparian and catchment-scale land use: implications for designing catchment monitoring programmes. *Freshwater Biology* **58**, 715–729. doi:10.1111/FWB.12077
- Ferraris, C. (2003). Family Auchenipteridae (Driftwood catfishes). In 'Checklist of the Freshwater Fishes of South and Central America'. (Eds R. E. Reis, S. O. Kullander, and C. J. Ferraris Jr.) pp. 471–483. (Editora da Pontifícia Universidade Católica do Rio Grande do Sul (EDIPUCRS): Porto Alegre, Brazil.)
- Gerking, S. D. (1994). Larval feeding. In 'Feeding Ecology of Fish'. (Ed. S. D. Gerking.) pp. 139–170. (Academic Press: San Diego, CA, USA.)
- Grossman, G. D. (1986). Food resources partitioning in a rocky intertidal fish assemblage. *Journal of Zoology* **2**, 317–355.
- Hahn, N. S., Adrian, I. F., Fugli, R., and Almeida, V. L. L. (1997). Ecologia trófica. In 'A planície de inundação do alto rio Paraná: aspectos físicos, biológicos e socioeconômicos'. (Eds A. E. A. M. Vazzoler, A. A. Agostinho, and N. S. Hahn.) pp. 209–228. (EDUEM: Maringá, Brazil.)
- Hales, J., and Petry, P. (2018). Freshwater ecoregions of the world – 346: Iguassu. Available at <http://www.feow.org/ecoregions/details/346> [Verified 2 August 2018].
- Hammer, Ø., Harper, D. A. T., and Ryan, P. D. (2001). Paleontological statistics software: package for education and data analysis. *Palaeontologia Electronica* **4**, 1–259.
- Harvey, P. H., Colwell, R. K., Silvertown, J. W., and May, R. M. (1983). Null models in ecology. *Annual Review of Ecology Evolution and Systematics* **14**, 189–211. doi:10.1146/ANNUREV.ES.14.110183.001201
- Hellawell, J. M., and Abel, R. A. (1971). Rapid volumetric method for the analysis of the food of fishes. *Journal of Fish Biology* **3**, 29–37. doi:10.1111/J.1095-8649.1971.TB05903.X
- Humphries, P., Keckeis, H., and Finlayson, B. (2014). The river wave concept: integrating river ecosystem models. *Bioscience* **64**, 870–882. doi:10.1093/BIOSCI/BIU130
- Hurlbert, S. H. (1978). The measurement of niche overlap and some relatives. *Ecology* **59**, 67–77. doi:10.2307/1936632
- Hyslop, E. J. (1980). Stomach contents analysis: a review of methods and their application. *Journal of Fish Biology* **17**, 411–429. doi:10.1111/J.1095-8649.1980.TB02775.X
- Joly, C. A., Aidar, M. P. M., Klink, C. A., McGrath, D. G., Moreira, A. G., Moutinho, P., Nepstad, D. C., Oliveira, A. A., Pott, A., Rodal, M. J. N., and Sampaio, E. V. S. B. (1999). Evolution of the Brazilian phytogeography classification systems: implications for biodiversity conservation. *Ciência e Cultura* **51**, 331–348.
- Keppeler, F. W., Lanés, L. E. K., Rolon, A. S., Stenert, C., Lehmann, P., Reichard, M., and Maltchik, L. (2015). The morphology–diet relationship and its role in the coexistence of two species of annual fishes. *Ecology Freshwater Fish* **24**, 77–90. doi:10.1111/EF.12127
- Kruskal, J. B. (1964). Nonmetric multidimensional scaling: a numerical method. *Psychometrika* **29**, 115–129. doi:10.1007/BF02289694
- Lampert, W., and Sommer, U. (2007). 'Limnology: the Ecology of Lakes and Streams.' (Oxford University Press: Oxford, UK.)

- Leibold, M. A., and McPeck, M. A. (2006). Coexistence of the niche and neutral perspectives in community ecology. *Ecology* **87**, 1399–1410. doi:10.1890/0012-9658(2006)87[1399:COTNAN]2.0.CO;2
- Lowe-McConnell, R. H. (1999). 'Estudos ecológicos de comunidades de peixes tropicais.' (Editora da Universidade de São Paulo: São Paulo, Brazil.)
- Marsh, J. M., Mueter, F. J., Iken, K., and Danielson, S. (2017). Ontogenetic, spatial and temporal variation in trophic level and diet of Chukchi Sea fishes. *Deep-sea Research – II. Topical Studies in Oceanography* **135**, 78–94. doi:10.1016/j.dsr2.2016.07.010
- Mateus, L., Ortega, J., Mendes, A., and Penha, J. (2016). Nonlinear effect of density on trophic niche width and between-individual variation in diet in a neotropical cichlid. *Austral Ecology* **41**, 492–500. doi:10.1111/AEC.12335
- Molina, M. C., Roa-Fuentes, C. A., Zeni, J. O., and Casatti, L. (2017). The effects of land use at different spatial scales on instream features in agricultural streams. *Limnologia* **65**, 14–21. doi:10.1016/j.limnol.2017.06.001
- Neves, M. P., Delariva, R. L., Guimarães, A. T. B., and Sanches, P. V. (2015). Carnivory during ontogeny of the *Plagioscion squamosissimus*: a successful nonnative fish in a lentic environment of the upper Paraná river basin. *PLoS One* **10**(11), e0141651. doi:10.1371/JOURNAL.PONE.0141651
- Neves, M. P., Baumgartner, D., Baumgartner, G., and Delariva, R. L. (2018). Do environmental variables predict the trophic structure of fish fauna in a subtropical river (Uruguay River Ecoregion)? *Journal of Limnology* **77**(2), 285–299. doi:10.4081/JLIMNOL.2018.1738
- Ortêncio Filho, H., Hahn, N. S., Fugui, R., and Russo, M. R. (2001). Aspectos da alimentação de *Glanidium ribeiroi* (Haseman, 1911) (Teleostei, Auchenipteridae), espécie endêmica do rio Iguaçu, PR. *Acta Limnologia Brasiliensis* **13**, 85–92.
- Ortiz, E., and Arim, M. (2016). Hypotheses and trends on how body size affects trophic interactions in a guild of South American killifishes. *Austral Ecology* **41**, 976–982. doi:10.1111/AEC.12389
- Paul, M. J., and Meyer, J. L. (2001). Streams in the urban landscape. *Annual Review of Ecology and Systematics* **32**, 333–365. doi:10.1146/ANNUREV.ECOLSYS.32.081501.114040
- Pianka, E. R. (1969). Sympatry of desert lizards (Ctenotus) in Western Australia. *Ecology* **50**, 1012–1030. doi:10.2307/1936893
- Pianka, E. R. (1973). The structure of lizard communities. *Annual Review of Ecology Evolution and Systematics* **4**, 53–74. doi:10.1146/ANNUREV.ES.04.110173.000413
- Pires, M. M., Guimarães, P. R., Araújo, M. S., Giaretta, A. A., Costa, J. C. L., and Dos Reis, S. F. (2011). The nested assembly of individual–resource networks. *Journal of Animal Ecology* **80**(4), 896–903. doi:10.1111/J.1365-2656.2011.01818.X
- Prejs, A., and Prejs, K. (1987). Feeding of tropical freshwater fishes: seasonality in resource availability and resource use. *Oecologia* **71**, 397–404. doi:10.1007/BF00378713
- Pulliam, H. R. (1974). On the theory of optimal diets. *American Naturalist* **108**, 59–74. doi:10.1086/282885
- Pusey, B. J., and Arthington, A. H. (2003). Importance of the riparian zone to the conservation and management of freshwater fish: a review. *Marine and Freshwater Research* **54**, 1–16. doi:10.1071/MF02041
- Quirino, B. A., Carniatio, N., Gaiotto, J. V., and Fugui, R. (2015). Seasonal variation in the use of food resources by small fishes inhabiting the littoral zone in a neotropical floodplain lake. *Aquatic Ecology* **49**, 431–440. doi:10.1007/S10452-015-9535-2
- Roberts, B. J., Mulholland, P. J., and Hill, W. R. (2007). Multiple scales of temporal variability in ecosystem metabolism rates: results from 2 years of continuous monitoring in a forested headwater stream. *Ecosystems* **10**, 588–606. doi:10.1007/S10021-007-9059-2
- Ross, S. T. (1986). Resource partitioning in fish assemblages: a review of field studies. *Copeia* **352**–388. doi:10.2307/1444996
- Sá-Oliveira, J. C., and Isaac, V. J. (2013). Diet breadth and niche overlap between *Hypostomus plecostomus* (Linnaeus, 1758) and *Hypostomus emarginatus* (Valenciennes, 1840) (Siluriformes) in the Coaracy Nunes hydroelectric reservoir, Ferreira Gomes, Amapá-Brazil. *Biota Amazônia* **3**, 116–125. doi:10.18561/2179-5746/BIOTAAMAZONIA.V3N2P116-125
- Santos-Filho, P. S. (1997). The effect of body size on prey choice by *Rivulus muelingi* Seegers 1984 (Aplocheiloidei: Rivulidae). *Revista Brasileira de Biologia* **57**, 551–562.
- Scharf, F. S., Juanes, F., and Rountree, R. A. (2000). Predator size–prey size relationships of marine fish predators: interspecific variation and effects of ontogeny and body size on trophic-niche breadth. *Marine Ecology Progress Series* **208**, 229–248. doi:10.3354/MEPS208229
- Schilling, H. T., Hughes, J. M., Smith, J. A., Everett, J. D., Stewart, J., and Suthers, I. M. (2017). Latitudinal and ontogenetic variation in the diet of a pelagic mesopredator (*Pomatomus saltatrix*), assessed with a classification tree analysis. *Marine Biology* **164**, 75. doi:10.1007/S00227-017-3105-1
- Schoener, T. W. (1971). Theory of feeding strategies. *Annual Review of Ecology Evolution and Systematics* **2**, 369–404. doi:10.1146/ANNUREV.ES.02.110171.002101
- Schoener, T. W. (1974). Resource partitioning in ecological communities. *Science* **185**, 27–39. doi:10.1126/SCIENCE.185.4145.27
- Schoener, T. W. (1986). Resource partitioning. In 'Community Ecology: Pattern and Process'. (Eds J. Kikkawa and D. J. Anderson.) pp. 91–126. (Blackwell Scientific Publications: Oxford, UK.)
- Siegel, S., and Castellan, N. J. Jr (2006). 'Estatística não-paramétrica para ciências do comportamento.' 2nd edn. (Artmed: Porto Alegre, Brazil.)
- Silva, E. L., Fugui, R., and Hahn, N. S. (2007). Variações temporais e ontogenéticas na dieta de um peixe onívoro em ambiente impactado (reservatório) e em ambiente natural (baía) da bacia do rio Cuiabá. *Acta Scientiarum. Biological Sciences* **29**, 387–394.
- Snyder, C. D., Young, J. A., Villella, R., and Lemarie, D. P. (2003). Influences of upland and riparian land use patterns on stream biotic integrity. *Landscape Ecology* **18**, 647–664. doi:10.1023/B:LAND.0000004178.41511.DA
- Tabarelli, M., Pinto, L. P., Silva, J. M. C., Hirota, M. M., and Bedê, L. C. (2005). Desafios e oportunidades para a conservação da biodiversidade na Mata Atlântica brasileira. *Megadiversidade* **1**, 132–138.
- Teresa, F. B., and Casatti, L. (2010). Importância da vegetação ripária em região intensamente desmatada no sudeste do Brasil: um estudo com peixes de riacho. *Pan-American Journal of Aquatic Sciences* **5**, 444–453.
- Trindade, M. E. D. J., Peressin, A., Cetra, M., and Jucá-Chagas, R. (2013). Variation in the diet of a small characin according to the riparian zone coverage in an Atlantic Forest stream, northeastern Brazil. *Acta Limnologia Brasiliensis* **25**, 34–41. doi:10.1590/S2179-975X2013000100005
- Tupinambás, T. H., Pompeu, P. S., Gandini, C. V., Hughes, R. M., and Callisto, M. (2015). Fish stomach contents in benthic macroinvertebrate assemblage assessments. *Brazilian Journal of Biology* **75**, 157–164. doi:10.1590/1519-6984.09913
- Vannote, R. L., Minshall, G. W., Cummins, K. W., Sedell, J. R., and Cushing, C. E. (1980). The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences* **37**, 130–137. doi:10.1139/F80-017
- Vitule, J. R. S., and Abilhoa, V. (2009). Plano de Conservação para Peixes do Rio Iguaçu. In 'Plano de Conservação para Espécies da Ictiofauna ameaçada no Paraná Instituto Ambiental do Paraná'. (Eds G. P. Vidolin, M. G. P. Tossulino, and M. M. Britto.) pp. 26–37. (Instituto Ambiental do Paraná: Curitiba, Brazil.)
- Wang, M., Liu, F., Lin, P., Yang, S., and Liu, H. (2015). Evolutionary dynamics of ecological niche in three Rhinogobio fishes from the upper Yangtze River inferred from morphological traits. *Ecology and Evolution* **5**, 567–577. doi:10.1002/ECE3.1386
- Ward, A. J. W., Webster, M. M., and Hart, P. J. B. (2006). Intraspecific food competition in fishes. *Fish and Fisheries* **7**, 231–261. doi:10.1111/J.1467-2979.2006.00224.X

- Weihls, D. (1977). Periodic jet propulsion of aquatic creatures. *Fortschritte der Zoologie* **24**, 171–175.
- Werner, E. E., and Gilliam, J. F. (1984). The ontogenetic niche and species interactions in size structured populations. *Annual Review of Ecology Evolution and Systematics* **15**, 393–425. doi:10.1146/ANNUREV.ES.15.110184.002141
- Wiens, J. J., Ackerly, D. D., Allen, A. P., Anacker, B. L., Buckley, L. B., Cornell, H. V., Wiens, J. J., Damschen, E. I., Davies, T. J., Grytne, J. A., Harrison, S. P., Hawkins, B. A., Holt, R. D., McCain, C. M., and Stephens, P. R. (2010). Niche conservatism as an emerging principle in ecology and conservation biology. *Ecology Letters* **13**, 1310–1324. doi:10.1111/J.1461-0248.2010.01515.X
- Winemiller, K. O., and Kelso-Winemiller, L. C. (2003). Food habits of tilapiine cichlids of the Upper Zambezi River and floodplains during the descending phase of the hydrological cycle. *Journal of Fish Biology* **63**, 120–128. doi:10.1046/J.1095-8649.2003.00134.X
- Winemiller, K. O., and Pianka, E. R. (1990). Organization in natural assemblages of desert lizards and tropical fishes. *Ecological Monographs* **60**, 27–55. doi:10.2307/1943025
- Wolff, L. L., Carniatto, N., and Hahn, N. S. (2013). Longitudinal use of feeding resources and distribution of fish trophic guilds in a coastal Atlantic stream, southern Brazil. *Neotropical Ichthyology* **11**, 375–386. doi:10.1590/S1679-62252013005000005

Handling Editor: Michael Joy