

An Acad Bras Cienc (2021) 93(Suppl.3): e20200438 DOI 10.1590/0001-3765202120200438 Anais da Academia Brasileira de Ciências | *Annals of the Brazilian Academy of Sciences* Printed ISSN 0001-3765 I Online ISSN 1678-2690 www.scielo.br/aabc | www.fb.com/aabcjournal

ECOSYSTEM

Trophic ecology of *Loricariichthys anus* (Valenciennes, 1835), (Loricariidae: Loricariinae) in a subtropical reservoir, Rio Grande do Sul, Brazil

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Abstract. The paper describes the trophic ecology of the *Loricariichthys anus* in a subtropical reservoir. The specimens were collected in the reservoir of the Chasqueiro stream, in Rio Grande do Sul, Brazil. The digestive tract of each specimen was removed for the analysis of the contents and definition of the diet. The Index of Relative Importance (IRI) was used to estimate which types of prey were most important. The diet of the *L. anus* population was compared among different water levels, seasons, ontogenetic classes, feeding strategy and fractional trophic level. There was a significant difference between hydrological levels, although no significant variation was found in the composition of the *L. anus* is a specialist species, with a diet composed predominantly of fine particulate material. At the trophic level, the diet of the species was based on detritus, which reflects the morphology of its body and digestive tract. Considering these findings, *L. anus* may be a keystone species in the Chasqueiro reservoir and its conservation, in both natural and artificial environments, is necessary for the bottom-up management of this and other Neotropical ecosystems.

Key words: Diet, Neotropical region, Lagoa Mirim system, Siluriformes.

INTRODUCTION

In the aquatic environments of the Neotropical region, the hydrological cycle is one of the principal environmental forces that influence the availability of feeding resources, leading to changes in the trophic level of the fish, and modifying the structure of the local food web (Junk 1980, Garcia et al. 2017, Quirino et al. 2017). The construction of reservoirs is one of the principal types of anthropogenic modification that can alter the hydrological cycle of a river basin (Bailly et al. 2016), modifies primary productivity and changes both abiotic (e.g., dissolved oxygen, luminosity) and biotic variables (e.g., predation, reproduction), as well as fish feeding patterns and these impacts cause disturbances throughout the aquatic ecosystem (Winemiller 1989, Ferreira et al. 2014, Corrêa et al. 2015, Winemiller et al. 2016).

In addition to measuring intraspecific trophic interactions, studies of trophic ecology provide an important systemic perspective on the processes associated with feeding patterns (Winemiller 1990, Roach et al. 2014, Peralta-Maraver et al. 2017). Quirino et al. (2017) concluded that changes in the composition of the diet of a fish population are associated with seasonal and spatial shifts in the distribution of resources, which reinforces the need to segregate feeding strategies, ontogenetic variations in the diet, and the trophic position of each species. Gerking (1994) notes that, while most species adopt a specific type of feeding strategy (e.g., specialist or generalist), environmental factors may force them to feed on resources outside the normal range of their trophic level.

One other major feature of trophic ecology is that many fish species exhibit marked ontogenetic variation in feeding behavior, which is driven, in particular, by shifts in morphological characteristics, such as the buccal apparatus, and body shape and structure, as well as the anatomy of the digestive system (Youson & Al-Mahrouki 1999, Hahn et al. 2000, Giora et al. 2005, Vital-Rodriguéz et al. 2017). The ontogenetic variation found in some fish species results in shifts in trophic level and the position of the species in the local food web over the course of its life cycle. The fractional trophic level of the organisms in a food web is an important metric that reveals how changes in the system affect its energy flow patterns and, in turn, the availability of food, which allows fish to migrate between distinct trophic levels (Pauly & Christensen 2000, Stergiou & Karpouzi 2002, Wesner & Belk 2015).

Basal groups such as the species of the family Loricariidae that have iliophagous or detritivorous feeding habits, are prominent regulators of the energy flow in aquatic systems, participating directly in the nutrient cycling through their consumption of fine particulate matter (Bowen 1983, Silva et al. 1997, Peretti & Andrian 2004, Corrêa & Piedras 2008, Delariva et al. 2013). When these detrivorous fishes are preyed on by piscivores this material ends up being transferred to higher trophic levels (Garcia et al. 2007, 2017, Corrêa et al. 2012, Oliveira et al. 2014), favoring the energetic increment of the predators at the top of the food chain. Loricarrids thus constitute an important trophic link that promotes the recycling of nutrients, in

addition to linking the different trophic levels in the food web (Fugi et al. 2001, Peretti & Andrian 2004, Garcia et al. 2007, Souto et al. 2011).

The Loricariidae is a highly diverse catfish family endemic to Central and South America (Lujan et al. 2012, Zawadzki et al. 2015, 2018, Reis et al. 2016). The locariid species Loricariichthys anus (Valenciennes, 1835) is widely distributed in the Neotropical region, occurring in Argentina, Uruguay, and Brazil (Reis & Pereira 2000, Malabarba et al. 2013). This species is an important resource for subsistence and smallscale fisheries operating on the coastal lagoons of southern Brazil (Petry & Schulz 2000, Corrêa et al. 2015, Fontoura et al. 2016). This fishery resource has been exploited in an increasingly systematic manner in recent years due to its high value and the growing demand for its meat. Despite the widespread distribution of *L. anus*. and its considerable ecological and economic importance for the aquatic ecosystems of the Austral region of Brazil, few trophic data are available for this species. In the present study, the trophic ecology of L. anus was investigated in a reservoir to evaluate fundamental ecological features, such as the influence of the water level, seasonal variation, ontogenetic development on the species' diet, in addition to estimating the feeding strategy and estimating its fractional trophic level. The data compiled in the study provide important insights for the development of effective conservation and management strategies for this species in the coastal lagoon systems of the southern extreme of Brazil.

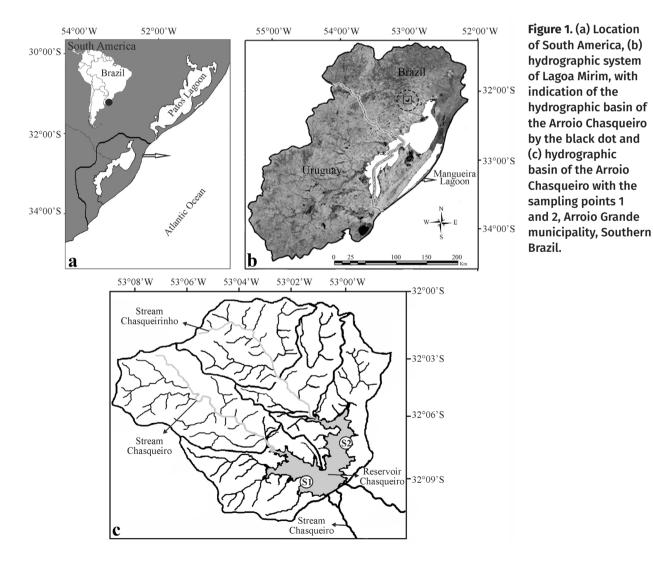
MATERIALS AND METHODS

Study area

The hydrographic basin of the Chasqueiro stream (Arroio Chasqueiro) is located at the western extreme of the Lagoa Mirim lagoon system, in the municipality of Arroio Grande, southern Brazil (31°6′51″ S, 50°5′17″ W; Figure 1). This basin is formed by two principal streams (Chasqueiro and Chasqueirinho) and a reservoir. The area upstream from the reservoir is 248.4 km², being formed by both the Chasqueiro (114.84 km²) and Chasqueirinho (133.58 km²) basins. The Chasqueiro reservoir has an area of 1,800 ha, which is used mainly to support the irrigated cultivation of rice (Sondotécnica 1976). At sampling site 1, the margins of the reservoir are dominated by planted pasture, used for grazing, and some large boulders, with a mainly sandy substrate (73.6%), followed by clay (14.0%) and silt (12.4%), with some large stones. The margin at site 2 is also dominated by pasture, with a sandy substrate (73.5%), clay (14.0%) and silt (12.2%), for a detailed description of the characteristics of the study areas, see Corrêa et al. (2014, 2015).

Fish sampling and dietary analysis

The fish specimens were collected monthly between August 2012 and July 2013 (SISBIO license no. 34389-1) at the two sampling points in the Chasqueiro reservoir, using: (a) a gillnet, 75 m in length with 10, 20, 30, 40, and 50 mm meshes, which was set for 24h and checked for fish every 12h, and (b) a 5-m seine net, 5 m in length and 2.25 high, with a 5 mm mesh. The gillnet was used to sample the deeper parts



of the reservoir (depths of 1.0–2.5 m) in order to capture larger individuals (> 200 mm), while the seine net was used at the margins of the reservoir, with the net being deployed five times per point. The specimens collected were placed in plastic bags, anesthetized with a Eugenol solution (Keene et al. 1998), tagged, and then fixed in 5% formaldehyde for 24h before being transferred to 70% alcohol for storage. Voucher specimens were deposited in the ichthyological collection of the Universidade Federal do Rio Grande (ICFURG #0045).

For the dietary study, the individuals were eviscerated and the anterior third of the intestine was examined following Fugi et al. (1996). The intestine was analyzed because, in the loricariids, the stomach is typically an accessory organ for respiration (Silva et al. 1997). The specimens were subsequently identified to the lowest possible taxonomic level based on the available literature, for example, algae (Menezes & Bicudo 2006), insects (Costa et al. 2006), and macroinvertebrates (Mugnai et al. 2010). The sediment or detritus was classified as Fine Particulate Matter (FPM). The different dietary items were evaluated according to the following metrics, proposed by Hyslop (1980): (a) frequency of occurrence (% F), percentage of individuals in which a given food item was found, (b) numerical frequency (%N), that is, the percentage of the item in relation to the total abundance of all items found in the digestive tract, and (c) the area of the item (% A), that is, the percentage area of the food item in relation to the total area of all the food items found, where the food item was spread evenly on a millimeter-grid plate. These metrics were combined to calculate the Index of Relative Importance of Pinkas et al. (1971) using the formula: IRI=%F * (%N + %A), the result of which is transformed into a percentage (Cortés 1997).

Effects of water level, seasonal variation, and ontogenetic development on the *L. anus* diet

For analysis, the reservoir level was classified as low or high, with the water level data being obtained from the meteorological station of the COODIC (Cooperative of the Landowners of the Chasqueiro Reservoir Irrigation District), in the southern extreme of Brazil (Figure 2). The diet was analyzed in relation to the low or high water level, the seasons (Winter, Spring, Summer, and

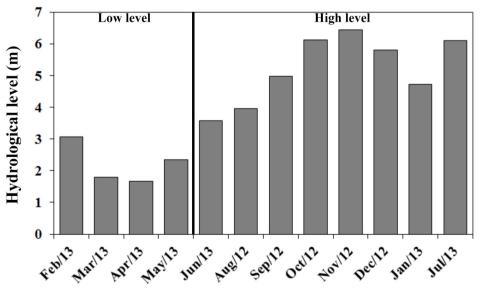


Figure 2. Hydrological level among the studied period, the left the low level and the right the high level, in the Chasqueiro reservoir, southern Brazil.

Study of period

Autumn), which are well defined in subtropical regions (Garcia et al. 2001), and for four size classes (Total Length or TL) were established for the ontogenetic analysis (Martins et al. 2017) class 1 (TL = 0-100 mm), class 2 (101-200 mm), class 3 (201–300 mm), and class 4 (301–400 mm). A semi-parametric permutational multivariate analysis of variance (PERMANOVA) was used to verify the significance of the variation in the L. anus diet between low and high water levels, and among seasons and ontogenetic classes, using the Bray-Curtis similarity index with 9999 permutations (Anderson 2005), with pairwise a posteriori comparisons between factors that had significant differences (p < 0.05). An analysis of the minimum percentage similarity (SIMPER) was also used to evaluate which dietary item contributed most to the dissimilarity among the seasons given that this variable presented significant variation (Clarke 1993). These analyses were run in the PRIMER statistical package (version 6; PRIMER-E, Plymouth, UK).

Feeding strategy and trophic position

The graphic method of Amundsen et al. (1996) was used to evaluate the feeding strategy of *L. anus*, with the frequency of occurrence on the abscissa and the prey abundance (Pi) on the ordinate axis. The value of Pi is defined as the relative abundance of an item in comparison with the total number of items, considering only the guts that contained item *i*, and is calculated by the formula: Pi = $(\Sigma Si / \Sigma St) \times 100$, where Si = the sum of item *i*, and St = the total number of items in the guts containing item *i*.

The fractional trophic levels were estimated from the IRI% values for the feeding categories (trophic level) recorded in the different seasons, using the TrophLab software (Pauly et al. 2000). Data available in the TrophLab software were used to determine the trophic position of the prey species (Pauly et al. 2000), where the estimate expresses the position of the organism in the food chain (Stergiou & Karpouzi 2002, Pauly & Christensen 2000, Pauly & Palomares 2000) based on the formula:

G

j=1

where: TROPHi = fractional trophic level of species *i*, TROPHj = fractional trophic level of prey *j*, DCij = % relative importance of *j* in the diet of *i*, and G = relative importance (IRI%) of the prey.

In this method (Pauly & Palomares 2000), the trophic levels of the prey species are considered to be measurable entities with values of 1.0 (primary producers and detritus/sediment). 2.0 (herbivores), 3.0 (omnivores), and 4.0-5.0 (carnivores/piscivores). A parametric one-way ANOVA was used to evaluate whether there was significant variation in the trophic level of the species by season, based on the assumptions of normality of the Jarque-Bera test (Jarque & Bera 1987, Zar 1996), with a significance level of 0.05%. To check for univariate trophic interactions of the species in relation to the water level. season, and size classes, bipartite graphs were plotted and adjusted to the highest degree of feeding importance, using the matrix of the IRI% values for the feeding categories. This procedure used the BIPARTITE algorithm of the R software, version 3.2.3 (Dormann et al. 2009, Dormann & Strauss 2014).

RESULTS

Effects of the water level on the L. anus diet

A total of 62 *L. anus* specimens were analyzed. These specimens had a mean Total Length (TL) of 319.4±10.2 mm and Total Weight (TW) of 225.4±14.9 g. Most (41) of the specimens were collected at low water, with a mean length of 315±13.7 mm and weight of 213.9±18.2 g, while 21 specimens were collected at high water (mean TL = 327.5±14.1; TW = 247.7±26.1 g). The PERMANOVA did not indicate any significant variation in the composition of the diet related to the level of the water (df = 1; pseudo-F = 1.91; p = 0.11). It is important to note, however, that the highest number of trophic links (15) was recorded during low water, when L. anus fed primarily on FPM (IRI% = 49.5) and plant matter (30.9%), with some insects of the order Ephemeroptera (5.7%). A total of 13 trophic links were recorded at high water, when FPM (IRI% = 53.3) and plant matter (29.5%) also contributed most to the diet *L. anus*, followed by the Nematoda, with 1.1% (Table I).

Effects of seasonal variation on the *L. anus* diet

The results of the PERMANOVA indicate significant variation among the seasons (df = 3, pseudo-F = 4.15; p = 0.001). The smallest number of food items were consumed during the winter, when FPM was the most important item (IRI% = 89.2), followed by plant matter (4.76). In the spring, the importance of FPM declined (IRI% = 38.3) while the insects of the order Ephemeroptera became a prominent component of the diet (IRI% = 26.9). In the summer, organic matter (IRI% = 40.3) and plant matter (40.1), while in the autumn. FPM increased (IRI% = 52.4), and plant matter (36.3) was still prominent, but decreased slightly (Table II), and the *pairwise* test among seasons are shown in Table III. The variation among the seasons was confirmed by the SIMPER analysis, in which FPM was the principal item contributing to the general dissimilarity. The highest mean global similarity was recorded between the autumn and the spring (72.2), while the lowest mean global dissimilarity (50.3) was recorded between the summer and winter (Table IV).

Effects of ontogenetic variation on the *L. anus* diet

The PERMANOVA did not indicate any significant variation among ontogenic classes (df = 3, pseudo-F = 0.52; p = 0.95), although certain shifts in the diet were observed, with body size class 2 having the smallest number of trophic links (seven), while class 3 had the largest number of links (17), including the consumption of Acari, Ephemeroptera, Nematoda, and seeds (Table V). Fine particulate matter was the most important item for all body size classes, varying from an IRI% of 60.3 for the smallest individuals to 34.0 in the largest ones. It is important to note. however, that the largest individuals consumed Thecamoeba (IRI% = 26.6), a resource used exclusively by size class 4 (Table V). The bipartite plots of the variation in water levels, seasons, and ontogenetic classes are shown in Figure 3.

Feeding strategy and trophic position

The graphic method of Amundsen indicates that the L. anus population followed a specialist feeding strategy, consuming a large proportion of fine particulate matter, which was consumed by more than half of the specimens analyzed, despite the reduced abundance of species, which indicates a relatively high phenotypic component. Smaller proportions of other items, such as Chelicerata, Nematoda, and Protozoa, were also included eventually in the L. anus diet (Figure 4). No significant variation was observed in the trophic position of the species among seasons (ANOVA: F = 0.14; p = 0.94). The lowest mean trophic levels were recorded in the winter (2.09±0.10) and spring (2.03±0.60), while the highest mean trophic level was recorded in the summer (2.72±0.30).

Table I. Frequency of occurrence (%F), numeric frequency (%N), area (%A) and index of relative importance (%IRI) for food items consumed by *L. anus* collected during the low and high hydrological level in the Chasqueiro reservoir, southern Brazil.

| Food items | | Low lev | el (n=21) | High level (n=41) | | | | | | |
|--------------------------------|------|---------|-----------|-------------------|------|------|------|-------|--|--|
| | %F | %N | %A | %IRI | %F | %N | %A | %IRI | | |
| Acari | 4.9 | 0.3 | 0.1 | <0.1 | | | | | | |
| Algae filamentous | 4.9 | 13.5 | 1.2 | 0.9 | 9.5 | 6.4 | 0.6 | 0.8 | | |
| Sand | 26.8 | 0.9 | 6.4 | 2.6 | 14.3 | 0.7 | 1.2 | 0.3 | | |
| Cladocera | 2.4 | 0.9 | 0.2 | <0.1 | | | | | | |
| Copepoda | 2.4 | 0.8 | 0.2 | <0.1 | | | | | | |
| Diptera (adult) | | | | | 4.8 | 0.5 | 0.0 | <0.1 | | |
| Ephemeroptera (adult) | 24.4 | 3.6 | 14.1 | 5.7 | | | | | | |
| Hemiptera (adult) | | | | | 4.8 | 0.2 | 0.0 | <0.1 | | |
| Coleoptera (larva) | 22.0 | 7.4 | 2.0 | 2.7 | 4.8 | 3.0 | 0.2 | 0.2 | | |
| Diptera (larva) | | | | | 9.5 | 0.5 | 0.5 | 0.1 | | |
| Fine particulate matter | 75.6 | 2.4 | 47.2 | 49.5* | 76.2 | 3.7 | 51.9 | 53.3* | | |
| Organic matter | 14.6 | 9.6 | 5.9 | 3.0 | 28.6 | 19.7 | 19.8 | 14.2 | | |
| Vegetable matter | 43.9 | 40.6 | 12.8 | 30.9* | 28.6 | 59.2 | 22.7 | 29.5* | | |
| Nemotoda | | | | | 19.0 | 2.5 | 2.0 | 1.1 | | |
| Ostracoda | 4.9 | 0.3 | 0.1 | <0.1 | | | | | | |
| Palaemonetes argentinus | 2.4 | 0.1 | 0.4 | <0.1 | | | | | | |
| Crustcean remains | 4.9 | 2.0 | 2.8 | 0.3 | 4.8 | 1.1 | 0.4 | 0.1 | | |
| Insect remains | | | | | 4.8 | 0.2 | 0.4 | <0.1 | | |
| Seed | 14.6 | 11.8 | 5.5 | 3.4 | 4.8 | 2.3 | 0.2 | 0.1 | | |
| Tecameba | 9.8 | 5.9 | 1.1 | 0.9 | | | | | | |
| * Food items larger importance | | | | | | | | | | |

Table II. Frequency of occurrence (%F), numeric frequency (%N), area (%A) and index of relative importance (%IRI) for food items consumed by *L. anus* collected during the low and high hydrological level in the Chasqueiro reservoir, southern Brazil.

| | | Winter | r (n=8) | | Spring (n=10) | | | | 9 | Summe | r (n=24 |) | Autumn (n=20) | | | |
|--------------------------------------|-------|--------|---------|-------|---------------|------|------|-------|------|-------|---------|-------|---------------|------|------|-------|
| | %F | %N | %A | %IRI | %F | %N | %A | %IRI | %F | %N | %A | %IRI | %F | %N | %A | %IRI |
| Acari | | | | | | | | | | | | | 8.3 | 0.5 | 0.1 | <0.1 |
| Algae filamentous | | | | | 10.0 | 32.2 | 2.8 | 4.7 | 10.0 | 3.2 | 0.3 | 0.4 | 4.2 | 2.2 | 0.5 | 0.1 |
| Sand | 12.5 | 2.1 | 2.9 | 0.5 | 35.0 | 1.3 | 8.2 | 4.5 | 20.0 | 0.7 | 1.2 | 0.4 | 16.7 | 0.5 | 3.6 | 0.7 |
| Cladocera | | | | | | | | | | | | | 4.2 | 1.3 | 0.2 | 0.1 |
| Copepoda | | | | | | | | | | | | | 4.2 | 1.2 | 0.2 | 0.1 |
| Diptera (adult) | | | | | | | | | 10.0 | 0.7 | 0.1 | 0.1 | | | | |
| Ephemeroptera (adult) | | | | | 50.0 | 8.6 | 31.5 | 26.9* | | | | | | | | |
| Hemiptera (adult) | 12.5 | 2.1 | 0.2 | 0.2 | | | | | | | | | | | | |
| Coleoptera (larva) | 12.5 | 27.1 | 1.1 | 2.9 | 15.0 | 1.1 | 0.2 | 0.3 | | | | | 25.0 | 10.5 | 2.5 | 3.3 |
| Diptera (larva) | | | | | | | | | 20.0 | 0.7 | 0.8 | 0.3 | | | | |
| Fine particulate matter | 100.0 | 16.7 | 90.8 | 89.2* | 80.0 | 3.0 | 32.7 | 38.3* | 50.0 | 1.8 | 29.2 | 16.9 | 75.0 | 2.1 | 67.5 | 52.4* |
| Organic matter | | | | | 25.0 | 22.7 | 9.0 | 10.6 | 60.0 | 30.2 | 31.3 | 40.3* | 4.2 | 0.1 | 2.5 | 0.1 |
| Vegetable matter | 12.5 | 43.8 | 2.1 | 4.8 | 35.0 | 18.8 | 7.1 | 12.1 | 40.0 | 58.2 | 33.3 | 40.1* | 50.0 | 57.8 | 14.4 | 36.3* |
| Nemotoda | 25.0 | 8.3 | 3.0 | 2.3 | | | | | 20.0 | 2.5 | 2.5 | 1.1 | | | | |
| Ostracoda | | | 1 | | 5.0 | 0.2 | 0.0 | <0.1 | | | | | 4.2 | 0.4 | 0.1 | 0.1 |
| Palaemonetes argentinus | | | | | 5.0 | 0.2 | 1.0 | 0.1 | | | | | | | | |
| Crustcean remains | | | | | 10.0 | 4.8 | 6.2 | 1.5 | 10.0 | 1.8 | 0.7 | 0.3 | | | | |
| Insect remains | | | | | | | | | 10.0 | 0.4 | 0.7 | 0.1 | | | | |
| Seed | | | | | 5.0 | 1.9 | 0.3 | 0.1 | | | | | 25.0 | 17.9 | 7.4 | 6.4 |
| Tecameba | | | | | 10.0 | 5.4 | 1.0 | 0.9 | | | | | 8.3 | 5.5 | 0.9 | 0.5 |
| * Food items larger importance | | | | | | | | | | | | | | | | |

Table III. The *pairwise* test among the seasons of *L. anus* diet, collected in the Chasqueiro reservoir, southern Brazil.

| Grups | t | p |
|-----------------|-------|-------|
| Summer x Autumn | 1.701 | 0.035 |
| Summer x Winter | 2.256 | 0.009 |
| Summer x Spring | 2.426 | 0.004 |
| Autumn x Winter | 1.884 | 0.016 |
| Autumn x Spring | 1.603 | 0.067 |
| Winter x Spring | 2.857 | 0.004 |

| | Overall average dissimilarity | Average dissimilarity | Contribution % |
|-------------------------|-------------------------------|-----------------------|----------------|
| Summer x Autumn | 61.9 | | |
| Fine particulate matter | | 22.6 | 36.5 |
| Vegetable matter | | 15.3 | 24.7 |
| Summer x Winter | 50.3 | | |
| Fine particulate matter | | 21.5 | 42.7 |
| Vegetable matter | | 17.6 | 35.1 |
| Summer x Spring | 68.9 | | |
| Fine particulate matter | | 21.7 | 31.5 |
| Organic matter | | 20.2 | 29.2 |
| Autumn x Winter | 58.5 | | |
| Fine particulate matter | | 21.7 | 37.2 |
| Insects | | 14.5 | 24.8 |
| Autumn x Spring | 72.2 | | |
| Organic matter | | 21.6 | 29.9 |
| Fine particulate matter | | 16.8 | 23.3 |
| Winter x Spring | 70.9 | | |
| Organic matter | | 24.7 | 34.7 |
| Fine particulate matter | | 21.3 | 30.0 |

Table IV. Similarity percentages (SIMPER) using for avalue the dissimilarity among the seasons of the year in the feeding of *L. anus* in the Chasqueiro reservoir, southern Brazil.

DISCUSSION

Effects of changes in the water level on the *L*. *anus* diet

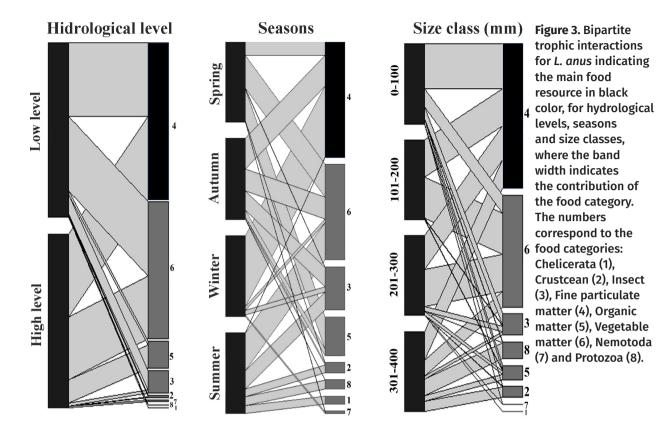
In the present study, no significant variation was found in the feeding behavior of *L. anus* between water levels, although a greater diversity of food items was recorded at low water, when the consumption of FPM increased, being associated with the reduction of the feeding area during the dry season, and the morphology and foraging strategies of the species (Oliveira et al. 2005, Lujan et al. 2012), another potentially important factor is that the fact that the lack of variation among the seasons may be associated with the constant presence of detritus in the environment. That is, although it may increase its availability in certain periods, detritus is a nonlimiting resource. The construction of reservoirs results in a series of impacts on aquatic ecosystems, which affect the connectivity of habitats, community structure, energy flow, and trophic patterns of the species (Corrêa et al. 2015, Winemiller et al. 2014, 2016). The results of the present study indicate that there was a greater abundance of individuals when the water level was low, reflecting the reduction in the area of the reservoir, as observed in previous studies (Agostinho et al. 1997, Bailly et al. 2008, Corrêa

| | | Class ² | 1 (n=6) | | | Class | 2 (n=7) | | | Class 3 | s (n=44 |) | Class 4 (n=4) | | | |
|-----------------------------------|-------|--------------------|---------|-------|------|-------|---------|-------|------|---------|---------|-------|---------------|------|------|-------|
| Food items | %F | %N | %A | %IRI | %F | %N | %A | %IRI | %F | %N | %A | %IRI | %F | %N | %A | %IRI |
| Acari | | | | | | | | | 4.5 | 0.4 | <0.1 | < 0.1 | | | | |
| Algae filamentous | 16.7 | 44.3 | 5.8 | 9.9 | 14.3 | 12.8 | 2.9 | 1.9 | 4.5 | 1.1 | 0.2 | 0.1 | | | | |
| Sand | 33.3 | 0.5 | 8.3 | 3.5 | 42.9 | 2.0 | 8.4 | 3.7 | 15.9 | 0.7 | 1.9 | 0.5 | 25.0 | 0.7 | 12.8 | 4.3 |
| Cladocera | | | | | | | | | | | | | 25.0 | 8.0 | 1.9 | 3.2 |
| Copepoda | | | | | | | | | | | | | 25.0 | 7.3 | 1.7 | 2.9 |
| Diptera (adult) | | | | | | | | | 2.3 | 0.2 | <0,1 | < 0.1 | | | | |
| Ephemeroptera (adult) | 33.3 | 3.1 | 18.2 | 8.4 | 14.3 | 1.4 | 3.5 | 0.6 | 13.6 | 2.8 | 6.2 | 1.6 | | | | |
| Hemiptera (adult) | 16.7 | 0.3 | 0.1 | 0.1 | | | | | | | | | | | | |
| Coleoptera (larva) | 33.3 | 0.8 | 0.2 | 0.4 | | | | | 15.9 | 8.5 | 1.1 | 2.0 | 25.0 | 11.7 | 4.3 | 5.1 |
| Diptera (larva) | | | | | 14.3 | 0.7 | 0.3 | 0.1 | 2.3 | 0.1 | 0.3 | <0.1 | | | | |
| Fine particulate matter | 100.0 | 1.6 | 49.4 | 60.3* | 85.7 | 4.1 | 56.8 | 43.7* | 70.5 | 3.0 | 50.1 | 48.9* | 75.0 | 2.2 | 33.2 | 34.0* |
| Organic matter | 16.7 | 30.6 | 5.8 | 7.2 | 28.6 | 1.4 | 3.6 | 1.2 | 18.2 | 8.4 | 13.7 | 5.2 | 25.0 | 0.7 | 25.6 | 8.4 |
| Vegetable matter | 33.3 | 10.9 | 9.8 | 8.2 | 57.1 | 77.7 | 24.5 | 48.9* | 38.6 | 57.8 | 19.0 | 38.8* | 25.0 | 13.9 | 4.8 | 6.0 |
| Nemotoda | 16.7 | 0.3 | | 0.1 | | | | | 6.8 | 1.0 | 1.2 | 0.2 | | | | |
| Ostracoda | 16.7 | 0.3 | 0.1 | 0.1 | | | | | 2.3 | 0.3 | <0.1 | <0.1 | | | | |
| Palaemonetes argentinus | | | | | | | | | 2.3 | 0.1 | 0.3 | <0.1 | | | | |
| Crustcean remains | | | | | | | | | 4.5 | 2.5 | 1.9 | 0.3 | 25.0 | 3.6 | 4.3 | 2.5 |
| Insect remains | | | | | | | | | 2.3 | 0.1 | 0.3 | <0.1 | | | | |
| Seed | 16.7 | 2.6 | 0.7 | 0.6 | | | | | 11.4 | 12.3 | 3.5 | 2.3 | 25.0 | 17.5 | 4.3 | 7.0 |
| Tecameba | 16.7 | 4.9 | 1.6 | 1.3 | | | | | 2.3 | 1.0 | 0.1 | <0.1 | 50.0 | 34.3 | 7.3 | 26.6* |
| * Food items larger importance | | | | | | | | | | | | | | | | |

| Table V. Frequency of occurrence (%F), numeric frequency (%N), area (%A) and index of relative importance (%IRI) |
|---|
| for food items consumed by <i>L. anus</i> in different size classes collected in the Chasqueiro reservoir, southern Brazil. |

et al. 2009). As a bottom feeder, *L. anus* inhabits the benthic zone (Petry & Schulz 2000) which, together with the low level of the reservoir, facilitated the collection of the specimens.

The composition of the *L. anus* diet recorded in the present study is broadly consistent with the findings of previous studies of the species' diet in the austral region, such as Petry & Schulz (2000), who described a preference for insect larvae, plant matter, and zooplankton. The ingestion of fine particulate matter, in particular, is a fundamentally important process for the efficient incorporation of nutrients into the trophic chain, through its assimilation by primary consumers (i.e., detritivorous fishes), which are, in turn, consumed by predators (Corrêa et al. 2009, 2012). The fine particulate matter is composed of a range of organisms of autochthonous and allochthonous origin (Jackson et al. 2013), which supports the microbial biota and provides an important resource for the food chain in Neotropical aquatic ecosystems.



Effects of seasonal variation on the *L. anus* diet

The L. anus diet varied considerably among the seasons, which may have been related to the hydrological dynamics of the Chasqueiro basin. In the dry season, the reduced flow into the reservoir resulted in a lower input of food items. The reservoir is supplied by two streams, the Chasqueiro and the Chasqueirinho (Corrêa et al. 2015), which transport allochthonous items to the reservoir, especially during the colder months, when rainfall levels increase, leads to an increase in the availability of food items for L. anus. Despite this, L. anus presented a diet consisting basically of fine particulate matter, which is consistent with the findings of Albrecht & Silveira (2001). During the flood season, plant matter may become more available through the vertical and lateral expansion of the reservoir. In a study of the coastal region of southernmost Brazil, Abreu et al. (2016) recorded a higher input of plant matter during an ENSO (El Niño South Oscillation) event, which triggered an excess of rainfall in the region. It is worth mentioning that the increase in the consumption of insects, in particular those of the order Ephemeroptera, during the spring, may be associated with the increase in temperature during this period, and also the occurrence of the breeding season. Rolla et al. (2009) emphasize that insects are important sources of nutrients, although this resource may vary considerably among seasons, shifting gradually over time.

Effects of ontogenetic variation on the *L. anus* diet

No variation in the *L. anus* diet was observed among the different ontogenetic classes, however, with similar feeding patterns being observed in immature and adult specimens. This was related in particular to the feeding specialization of the species, as observed in

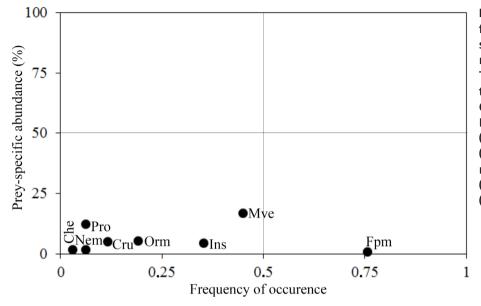


Figure 4. Feeding strategy for population of *L. anus* studied in the Chasqueiro reservoir, southern Brazil. The codes correspond to the food categories: Che (Chelicerata), Pro (Protozoan), Nem (Nematodea), Cru (Crustacean), Orm (Organic matter), Ins (Insecta), Mve (Vegetable matter) and Fpm (Fine particulate matter).

several other fish species from the Neotropical region (Winemiller 1989, Silva 2010, Corrêa et al. 2012). Even so, one important difference is that larger individuals consumed tecameba, which was probably related to the detritivorous diet of the species. As tecamebas are found in the biofilm on the substrate and vegetation of the margins of bodies of water (Souza 2005), the fish may ingest this item accidentally when foraging on these substrates. As L. anus is a widelyexploited fishery resource in the Austral region. laboratory studies based on feeding experiments may provide more conclusive insights into the ontogenetic variation in the diet of this species. Significant ontogenetic variation has been found in the diets of some siluriform species, such as the granulated catfish, Pterodoras granulosus, which was also studied in a Neotropical reservoir (Agostinho et al. 2009). This species undergoes a gradual change in its diet, with the juveniles feeding on allochthonous material derived from the adjacent terrestrial ecosystem, given that they tend to inhabit shallow areas, whereas the adults migrate to deeper areas

Feeding strategy and trophic position

The feeding strategy of *L. anus* in the study reservoir was based on a high degree of specialization for the exploitation of fine particulate matter, with the high frequency of this item in the digestive tract of the fish specimens supporting the classification of the species as a detritivorous. *Loricariichthys* anus has a dorsoventrally flattened body and occurs in the benthic zone of lentic aquatic ecosystems, and, occasionally, in the rapids of some lotic environments (Corrêa et al. 2015). Its buccal apparatus is shaped like a suction cup, located on the inferior surface of the head, which is used to suck or scrape food from substrates, facilitating the ingestion of fine particulate matter (Bowen 1983, Fugi et al. 2001, German & Miles 2010). Loricariichthys anus also has a long, narrow, and highly sinuous digestive tract, a common morphological feature of many Neotropical detritivorous fish (Bowen, 1983, Corrêa & Piedras 2008, Pouilly et al. 2003, German & Miles 2010). Fish species that feed on inorganic particles absorb many nutrientrich items, such as algae and microorganisms

(Bowen 1983, Garcia et al. 2007, Corrêa & Piedras 2008, Corrêa et al. 2009).

The Loricariichthys anus is classified in the second trophic level of the food chain due to its consumption of basal food items, with little variation in its trophic position being observed among seasons. Winter and spring were the seasons with the lowest trophic levels, while the summer had the highest level, which was associated with the consumption of insects. Garcia et al. (2006) examined the structure of the food web of Lake Nicola, in southern Brazil, and identified *L. anus* as a secondary consumer that plays an important role in the recycling of nutrients and the transfer of energy to higher trophic levels. Models of trophic position provide valuable insights into the feeding behavior of a species, and how it responds to the seasonal dynamics of the food chain (Zanden & Rasmussen 1996). In the summer, for example, L. anus presented the highest intake of insects, possibly because this is the period in which most species disperse and reproduce. In particular, dipteran larvae were preyed on only during the summer, which resulted in a singlestep increase in the trophic level of *L. anus* in the food chain. Rolla et al. (2009) concluded that insects are an important nutritional resource for fish, and represent one of the principal trophic links between terrestrial and aquatic environments. The availability and diversity of this resource may vary seasonally, and also in response to anthropogenic impacts and climate change. In general, few fish species are adapted morphologically for the exploitation of the fine particulate matter as a feeding resource, and in the Chasqueiro basin, this niche is almost exclusive to L. anus, which means that this catfish may be a keystone species in this reservoir, acting as an important link in the cycling of nutrients and transfer of energy to higher trophic levels. These findings emphasize

the importance of this type of study for the understanding of the ecological relationships of the detritivorous fish species found in southern Brazil.

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How to cite

CORRÊA F, TUCHTENHAGEN TS, POUEY J, PIEDRAS SRN & OLIVEIRA EF. 2021. Trophic ecology of *Loricariichthys anus* (Valenciennes, 1835), (Loricariidae: Loricariinae) in a subtropical reservoir, Rio Grande do Sul, Brazil. An Acad Bras Cienc 93: e20200438. DOI 10.1590/0001-3765202120200438.

Manuscript received on March 30, 2020; accepted for publication on August 3, 2020

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