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ZOOLOGY

Seasonal and ontogenetic diet patterns of the freshwater pufferfish *Colomesus asellus* (Müller & Troschel, 1849) in the upper-middle Tocantins River

Renata Bartolette[1*], Daniela Cristina Oliveira Rosa[2], Danielle Antunes Beserra[2], Bruno Eleres Soares[2], Miriam Pilz Albrecht[2] and Marcelo Fulgêncio Guedes Brito[1]

*[1]Departamento de Biologia, Laboratório de Ictiologia, Universidade Federal de Sergipe, Avenida Marechal Rondon, s/n., 49100-000, São Cristóvão, Sergipe, Brazil. [2]Departamento de Ecologia, Laboratório de Ecologia de Peixes, Centro de Ciências da Saúde, Instituto de Biologia, Universidade Federal do Rio de Janeiro, Ilha do Fundão, Rio de Janeiro, Brazil. *Author for correspondence. E-mail: rbartolette@gmail.com*

ABSTRACT. We described the feeding habits of *Colomesus asellus* from riverbanks of the upper-middle Tocantins River, Central Brazil. Two sampling expeditions were carried out in August (dry season) and in October (rainy season) of 2013, downstream from the Lajeado Hydroelectric Power Plant, Tocantins state. The diet of *C. asellus* was characterized and compared between juveniles and adults and between individuals captured in the dry season and in the rainy season. Individuals exhibited marked temporal segregation, with a predominance of adults on the riverbanks during the dry season and the predominance of juveniles in the rainy season. The diet of this species was based on diverse benthic prey, mostly Ephemeroptera nymphs (Insecta). Contrary to our expectations, the diet composition of *C. asellus* was not influenced by seasonal changes or ontogenetic factors, but the size of individuals determined the number of prey consumed. Thus, *C. asellus* can be classified in its trophic ecology as an insectivore without relation with fish size and seasonality.

Keywords: trophic ecology; benthic prey; insectivore.

Padrões sazonais e ontogenéticos da dieta do baiacu de água doce *Colomesus asellus* (Müller & Troschel, 1849) no alto-médio rio Tocantins

RESUMO. Descrevemos os hábitos alimentares de *Colomesus asellus* capturados nas margens do rio Tocantins, Brasil Central. Duas expedições de coleta foram realizadas em agosto (estação seca) e em outubro (estação chuvosa) de 2013, a jusante da Usina Hidrelétrica de Lajeado, Estado do Tocantins. A dieta de *C. asellus* foi caracterizada e comparada entre juvenis e adultos e entre indivíduos capturados na estação seca e na estação chuvosa. Os indivíduos apresentaram marcada segregação temporal, com predominância de adultos nas margens do rio durante a estação seca e predominância de juvenis na estação chuvosa. A dieta desta espécie foi baseada em diversas presas bentônicas, principalmente ninfas de Ephemeroptera (Insecta). Contrariamente às nossas expectativas, a composição da dieta de *C. asellus* não foi influenciada por mudanças sazonais ou fatores ontogenéticos, mas o tamanho dos indivíduos determinou o número de presas consumidas. Assim, a espécie pode ser classificada como insetívora, sem variação em sua ecologia trófica relacionada à sazonalidade do ambiente ou ao seu tamanho.

Palavras-chave: ecologia trófica; presas bentônicas; insetívoro.

Introduction

The study of fish feeding biology is an important tool to understand the relationship between fish populations and other aquatic organisms (Hahn, Agostinho, & Goitein, 1997). Many Neotropical fishes can modify their diet throughout ontogenetic development, which might be correlated to morphological limitations, habitat use and changes in behavior (Winemiller, 1989; Hahn, Delariva, & Loureiro, 2000). Ontogenetic shifts in the niche of species are changes in the use of food or spatial resources occurring between different stages of development, *e.g.* adults and juveniles (Werner & Gilliam, 1984; Pessanha & Araújo, 2014). Such ontogenetic changes in diet alter the species' functional roles, like the consumption of allochthonous resources and the recycling of autochthonous detritus. Therefore, the assessment of such changes is essential to understand how organisms resource use affects their distribution and abundance (Lowe-McConnell, 1987; Abelha, Agostinho, & Goulart, 2001).

However, the role of morphological change caused by ontogenetic shifts in niche properties is unclear (Galis, Terlouw, & Osse, 1994). Ontogenetic dietary changes are generally induced by alterations associated with the growth of morphological structures correlated with body size that can cause alterations in feeding behavior (Wainwright & Richard, 1995). Generally, fishes may be trophic specialists with a reduced niche breadth through ontogenetic stages, whereas trophic generalists have the opposite trend (Winemiller, 1989; Winemiller & Kelso-Winemiller, 2003). Most of the Neotropical fishes are unspecialized opportunist species, which feed on a wide variety of resources (Lowe-McConnell, 1987; Lima & Behr, 2010).

These opportunist species feeding patterns are related to environmental conditions such as changes throughout the year in resource availability. Seasonality influences the trophic relationships of fish species, which tend to eat the most abundant items in different periods of the year (Lowe-McConnell, 1987; Araújo-Lima, Agostinho, & Fabré, 1995; Hahn, Fugi, & Andrian, 2004). This is even more important in rivers that exhibit a well-defined seasonal regime, as it occurs in the Tocantins River Basin with rainy and dry seasons well-defined (Agostinho, Pereira, Oliveira, Freitas, & Marques, 2007).

The tetraodontiform *Colomesus asellus* (Müller & Troschel, 1849) is a small-sized fish widely distributed along riverbanks of the Tocantins River basin, as well as in numerous northern rivers of South America (Kullander, 2003). Among the family Tetraodontidae, only *Colomesus tocantinensis* Amaral, Brito, Silva, and Carvalho (2013) and *C. asellus* are confined exclusively to freshwaters (Amaral et al., 2013). Like other tetraodontids, *C. asellus* has four tooth plates capable of breaking hard-shelled prey (Amaral et al., 2013), although in a study of trophic characterization of the fish species on the upper and middle Tocantins River basin, *C. asellus* consumed terrestrial and aquatic insects, fishes, sediment, organic matter, and algae (Pereira, Agostinho, Oliveira, & Marques, 2007).

Considering the wide distribution of the freshwater pufferfish in Amazonian river and its peculiar morphology, we describe for the first time the diet of this species from the riverbanks of the upper-middle Tocantins River, Central Brazil. Information about the trophic niche of species may be useful to understand ecological processes and to the monitoring of natural food webs in face of anthropogenic disturbance. In order to assess trophic ecology aspects of *Colomesus asellus*, we investigated trophic dissimilarities between juvenile and adult individuals and between individuals captured in the dry and rainy seasons. We expected that larger individuals consumed a wider array of prey due to decreasing morphological limitations, and that the species would increase the consumption of allochthonous resources in the rainy season due to increased availability.

Material and methods

The Lajeado Hydroelectric Power Plant (HPP) is located in the upper-middle stretch of the Tocantins River, between Lajeado and Miracema do Tocantins municipalities (9º 42' 5.30"S / 48º 21' 56.80" W), Tocantins state, Central Brazil (Figure 1). Its reservoir presents 630 km² and its surroundings are covered by Cerrado savannah. The climate is tropical humid and sub-humid, with two well-defined seasons: a rainy season between October and April with temperatures ranging from 24 to 28°C and a dry season between May and September with temperatures between 28 and 35°C (Agostinho et al., 2007).

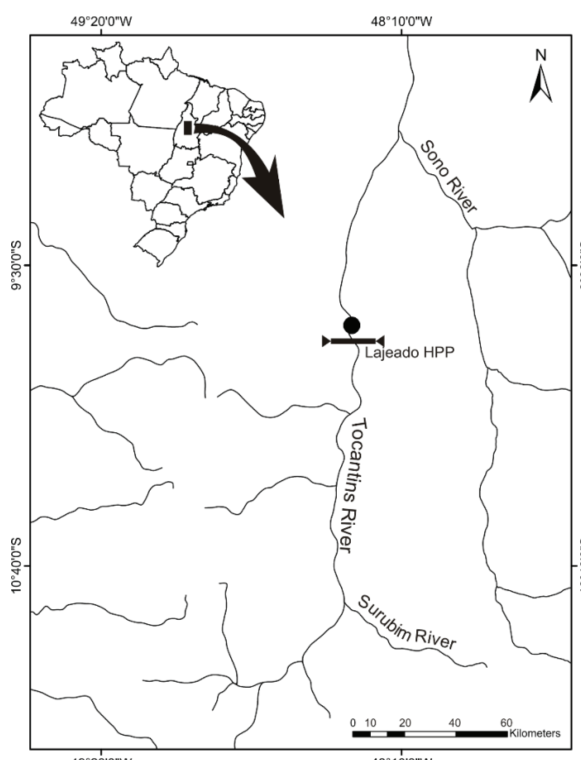

Figure 1. Map of the study area showing the sampling site downstream of the Lajeado Hydroelectric Power Plant (black dot), upper-middle Tocantins river basin, Tocantins State.

Two sampling expeditions were carried out downstream of the Lajeado HPP, one in August 2013 (dry season) and another in October 2013 (rainy season). The sampled area presented Cerrado savannah preserved at the margins, with a depletion zone forming sandbanks away from the water in the dry period (10-20 m) and close to marginal vegetation in the rainy period (1-3 m). The riverbed in this stretch was composed mainly of sand and small gravel (< 10 mm). The water column exhibited a gradual slope until 5 m of margin, followed by a deep channel (dry period). There were no registered aquatic macrophytes in the margins during the sampling period.

Individuals were collected with seine nets (10 x 1.75 m/5 mm mesh) in a stretch of 100 m on the riverbank. Fishes were anesthetized with Eugenol (Lucena, Calegari, Pereira, & Dallegrave, 2013), fixed in 10% formalin and transferred to ethanol 70°GL. After fixing, each individual was weighed (g), measured to standard length (SL-cm) and dissected. The digestive tracts were removed and preserved in ethanol 70°GL. Individuals were sexed and their phase of the reproductive cycle was classified following Brown-Peterson, Wyanski, Saborido-Rey, Macewicz, and Lowerre-Barbieri (2011) as juvenile (never spawned) or adult (sexually mature).

The SL values were tested by the Mann-Whitney U test. We used a non-parametric approach because length data were heteroscedastic.

Stomach contents were analyzed under a stereoscopic microscope and food items were identified. The volume of each item was measured on a 1-mm-high transparent dish with a 1 x 1 mm grid beneath, as described in Albrecht and Caramaschi (2003). Food items were identified to the lowest taxonomic level with specialized literature (Hamada, Nessimian, & Querino, 2014). The relative importance of the food items was calculated by the Feeding Index (Kawakami & Vazzoler, 1980) according Equation 1:

$$IAi = ((Fi * Vi) / (\Sigma Fi * Vi)) * 100 \quad (1)$$

where:
i = 1, 2, ... n food items;
Fi = frequency of occurrence of item i, and
Vi = relative volume of item i.

Differences in diet composition between juveniles and adults and between dry and rainy seasons were analyzed by multivariate techniques using matrices of proportional volume (%) of each item consumed by individuals. We used analysis of similarity (ANOSIM two-way) considering phases in the reproductive cycle (juvenile *vs.* adults) and seasons (dry *vs.* rainy) as factors. ANOSIM was performed with 999 permutations and a Bray-Curtis dissimilarity matrix. The effect of SL (log-transformed values) on the number of food items consumed by the individual (trophic connections) was assessed by a linear regression. Analyses were carried out at a 5% level of significance using the R program (R Core Team, 2015), and multivariate analyses were conducted using the *vegan* package (Oksanen et al., 2016).

Results and discussion

A total of 122 individuals of *C. asellus* were dissected and only 80 digestive tracts were analyzed, because remaining specimens presented empty stomach. Fifty individuals were sampled in the dry season (SL = 2.2-4.5 cm; 3.72 ± 0.64 cm) and 30 in the rainy season (SL = 1.2-3.4 cm; 2.50 ± 0.70). SL was higher in the dry season (U = 80.50; p < 0.01). Juvenile individuals exhibited SL between 1.0-2.5 cm, whereas adults presented SL between 2.6-4.5 cm. Juvenile individuals (N = 32) were caught in both rainy (N = 26) and dry seasons (N = 6), but predominantly in the rainy season. Adults (N = 48) occurred predominantly in the dry season (N = 44) but were also recorded in the rainy season (N = 4) (Figure 2).

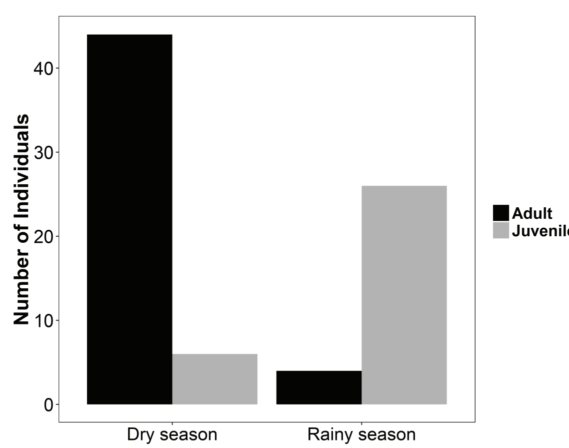

Figure 2. Distribution of adults and juveniles of *Colomesus asellus* in the dry and rainy seasons.

Eighteen food items were identified in stomach contents (Table 1). Ephemeroptera nymphs were the most important item for juvenile (IAi = 49.9) and adult (IAi = 48.63) individuals. Juveniles also consumed high amounts of Chironomidae larvae, sediment, insect remains, and Gastropoda. For adults, Gastropoda (IAi = 25.07), scales (IAi = 8.16), insect fragments (IAi = 6.31), and Chironomidae (L) (IAi = 5.93) were important. Both juveniles and adults consumed vegetal matter (Table 1).

Table 1. Food items consumed by *Colomesus asellus* (values represent the Feeding Index, %IAi) for juvenile (N = 32) and adult (N = 48) individuals in the upper-middle Tocantins River. A – Aquatic; L – Larvae; N – Nymphs; P – Pupae.

Taxon	Food items	Juvenile	Adult
Mollusca	Gastropoda	6.42	25.07
Insecta	Coleoptera (A)	0.01	0.00
Insecta	Coleoptera (L)	0.03	0.00
Insecta	Ceratopogonidae (L)	0.10	0.02
Insecta	Chironomidae (L)	18.05	5.93
Insecta	Diptera (P)	1.76	0.76
Insecta	Ephemeroptera (N)	49.9	48.63
Insecta	Hemiptera	0.47	0.00
Insecta	Insect fragments	9.47	6.31
	Invertebrate Eggs	0.19	0.02
Insecta	Odonata (N)	0.00	0.06
Insecta	Trichoptera	0.03	0.47
Pisces	Fish	0.00	0.06
Pisces	Scales	0.00	8.16
Eukaryota	Filamentous Algae	0.49	0.34
Plantae	Vascular plants	0.01	0.03
	Organic matter	1.37	0.60
	Sediment	11.7	3.54

ANOSIM considering ontogenetic phases and seasons did not indicate significant differences in diet composition ($R = 0.097$; $p = 0.10$). Individuals' SL influenced the number of food items consumed, as more food items were consumed by larger specimens ($R^2 = 0.11$; $p = 0.003$).

Colomesus asellus displayed temporal segregation of juvenile and adult individuals between seasons, with juveniles being predominantly sampled in the rainy season and adults in the dry season. The segregation in the population distribution may be related to the recruitment reported for many fish species in periods of intense rainfall (Araújo-Lima et al., 1995). During the dry season, adults probably occupy the riverbanks to feed and reproduce and, after spawning, adults search for food resources in other sites when the riverbanks become a suitable environment for the growth of juvenile specimens.

These riverbanks provide a wide array of food resources, and fish species can select their food depending on their ontogenetic stage and availability of resources in the environment, which may vary spatially and seasonally (Abelha et al., 2001). Despite the diversified diet of *C. asellus* (18 food items), juveniles and adult specimens consumed mainly Ephemeroptera nymphs during both seasons, characterizing the species as an insectivore. Mayfly nymphs are benthic and extremely abundant in Brazilian Cerrado watercourses (Silva et al., 2005), thus representing an important link in the food web of aquatic environments (Salles, Silva, Serrão, & Francischetti, 2004).

Contrary to what we found, *Colomesus asellus* is described to consume allochthonous arthropods in sandbanks in the Tocantins river (Pereira et al., 2007). Herein, *C. asellus* consumed only autochthonous items, which may be both related to the species' benthic habits or to resources availability, if the marginal vegetation that surrounds the area is providing low abundance of allochthonous items. The predominance of autochthonous items can be modulated by the predator's ability to detect and recognize mainly benthic prey, which agrees with the benthic habit reported for other tetraodontids (Krumme, Keuthen, Saint-Paul, & Villwock, 2007).

Despite feeding in benthic prey, the diet of *C. asellus* was distinct from that of *C. psittacus* sampled in Northern Brazilian mangroves and of other marine tetraodontiform like *Sphoeroides spengleri* (Bloch, 1785) and *S. testudineus* (Linnaeus, 1758), which predominantly consumed hard-shelled crustaceans and mollusks abundant in their environments (Targett, 1978; Krumme et al., 2007). Gastropods are not abundant in Cerrado rivers (Silva et al., 2005) and were consumed only by larger individuals of *C. asellus*, despite its morphological apparatus adapted to consume hard-shelled prey. The lack of correlation between the morphological specialization (teeth plates) and the ecological niche observed in the present study is in accordance with the Liem's Paradox, which predicts that highly specialized phenotypes are maintained for exploration and use of more difficult resources (e.g., gastropods), but do not limit the use of other resources (Liem, 1980).

It is a common assumption that seasonal variation in rainfall contributes to the input of allochthonous resources in rainy months, which may alter the fishes' trophic interactions (Lowe-McConnell, 1987). However, we did not find any influence of seasonality on the feeding patterns of *C. asellus*. This resulted into a benthic behavior and feeding mainly composed by Ephemeroptera nymph, and not by allochthonous prey. In addition, it indicates that the main food items of *C. asellus* was available in all seasons, and a similar lack of seasonality in the feeding of an entire fish community in streams of the Cerrado biome was found by Schneider, Aquino, Silva, and Fonseca (2011).

Despite the lack of seasonality in the species diet that indicates similar resources availability, we observed an increase in the number of food items consumed by larger individuals. This pattern may result from changes in the energy demand or a decrease in morphological limitations (*e.g.* enlarged mouth size may allow consumption of larger resources) throughout ontogenetic development (Abelha et al., 2001). The addition of food items to the diet along its ontogeny revealed a nested pattern of consumption, in which the diet of smaller individuals is a subset of that of larger individuals (Araújo et al., 2010).

Conclusion

The results did not confirm our expectation that the diet composition of *C. asellus* would be influenced by ontogenetic and seasonal factors. Nonetheless, we observed that larger individuals consumed a higher number of prey. Future studies aiming to examine the availability of food resources can provide important information for understanding the absence of seasonal changes and ontogenetic factors in the diet of the species as well as to identify other areas occupied by *C. asellus* outside the riverbanks.

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