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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.

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ABSTRACT. The stomach contents of 172 individuals of *Hypostomus plecostomus* and 94 specimens of *Hypostomus emarginatus* from the Coaracy Nunes reservoir in northern Brazil were analyzed in order to evaluate the feeding ecology of the two fish species from this site. Data were collected in eight campaigns conducted every two months between May, 2010 and July, 2011, four in the dry season and four during the flood period. The analysis of the stomach contents was based on the volumetric frequency (VF%) and frequency of occurrence (FO%), combined with the feeding index (FI). Nine different dietary items were identified: detritus, plant fragments, zooplankton, arthropods, chlorophytes, bacillariophytes, cyanobacteria, dinophytes, and unidentified material. Detritus was the principal component of the diet during both seasons, with all the other items representing only complementary or accidental portions of the diets of both species. Niche breadth was low overall, but slightly greater in *H. plecostomus* in comparison with *H. emarginatus*. Niche overlap was accentuated in both seasons, which indicates that seasonality is not a major factor influencing the characteristics of the niches of these species, possibly because of the marked abundance of detritus in the study area, specifically in the impounded sector. The two species can be characterized as detritivores, which share dietary resources with no clear evidence of any negative effects of interspecific competition on the coexistence of the two populations.

Keywords: Feeding ecology, niche breadth, Araguarí River, Amazonia

RESUMO: Dieta, amplitude e sobreposição de nicho entre *Hypostomus plecostomus* (Linnaeus, 1758) e *Hypostomus emarginatus* (Valenciennes, 1840) (Siluriformes) do reservatório da UHE Coaracy Nunes, Ferreira Gomes, Amapá-Brasil. O presente estudo teve como objetivo analisar a ecologia trófica de 172 exemplares de *Hypostomus plecostomus* e 94 indivíduos de *Hypostomus emarginatus* do reservatório da UHE Coaracy Nunes, Ferreira Gomes-Amapá, coletados em oito campanhas, bimensalmente de maio de 2010 a julho de 2011, sendo quatro no período seco e quatro no período de cheia. A análise baseou-se nos métodos de freqüência volumétrica (FV%) e de ocorrência (FO%), combinados no índice alimentar (IAi). Foram encontradas nove categorias de alimentos: Detritos, fragmentos vegetais, zooplâncton, artrópodes, chlorophyta, bacillariophyta, cyanobacteria, dinophyta e material não identificado. Nos dois períodos sazonais, detritos foi o item mais consumido, sendo os demais considerados itens de consumo acidental ou de complementação para ambas as espécies. Em geral, a amplitude de nicho foi baixa, porém entre as duas espécies houve pequena diferença, sendo a amplitude de *H. plecostomus* maior que a de *H. emarginatus*. Nos dois períodos sazonais, a sobreposição de nicho apresentou valores elevados, indicando que a sazonalidade não é um fator decisivo na alteração de nicho dessas espécies, provavelmente em virtude da alta disponibilidade de detritos, particularmente na região do represamento. Conclui-se que as duas espécies apresentam hábito alimentar detritívoro, realizando a partilha deste recurso, sem existir processos de competição interespecífica evidentes, que comprometam a sua coexistência.

Palavras-chave: Ecologia trófica, amplitude alimentar, rio Araguarí, Amazônia.

1. Introduction

Ecological theory predicts that each species of animal occupies a unique niche which characterizes its relationship with the dietary resources available in the environment (BRADLEY; BRADLEY 1985). In particular, understanding the trophic dimension of a species niche provides important insights into the coexistence of different species in the same community. Reliable data on the trophic dynamics of fish species represent an important approach to the understanding of other aspects of the biology of these animals, such as their reproduction, ontogeny, demographic patterns, migration and niche partitioning (HANN et al., 1996).

In reservoirs, the fish fauna tends to suffer modifications during the impoundment, and subsequently as a consequence of the conversion of a lotic environment into a lentic one (HANN; FUGI, 2007). An increase in interspecific competition is expected in impounded environments, especially in the period immediately following the damming of the river, when the species have yet to develop effective resource partitioning strategies, which might eventually contribute to a reduction in competition (RABORN et al., 2004). Closely-related species tend to be similar, in ecological terms, especially in their exploitation of resources. In general, while an optimal environment might offer sufficient resources for the coexistence of closely-related species, in practice, niche partitioning is often based on spatial and/or temporal differentiation, including the occupation of distinct microhabitats (SHOENER, 1974; ROSS, 1986). In this context, reliable data on feeding ecology may be important for the understanding of the factors that segregate sympatric species (GERKING, 1994).

The fishes of the family Loricariidae are known as sucker mouth armored catfishes, and are widely distributed in South America. The family includes around 600 species distributed in 70 genera and six subfamilies: Lithogeninae, Neoplecostominae, Loricariinae, Hypoptopomatinae, Ancistrinae, and Hypostominae (ISBRÜCKER, 1980). The members of this family are among the most specialized catfishes of the order Siluriformes (REIS et al., 1990).

Hypostomus is one of the most diverse and complex genera of the South American armored catfishes, with approximately 140 known species (MULLER; WEBER, 1992; REIS et al., 1990; JEREP et al., 2006). These species are normally found in habitats with fast-flowing water. However, they may also inhabit lentic environments, where they feed on mud and detritus. Species of this genus are popular as food as well as aquarium fishes (ANGELESCU; GNERI, 1949).

The Araguarí River in the State of Amapá, Brazil, is one of the least studied in the Amazon basin, principally in terms of the ecology of its fish fauna. The available data (GAMA, 2004; SÁ-OLIVEIRA, 2012) indicate a relatively diverse fish fauna throughout the Araguarí basin, with a large number of loricariid species, which include *Hypostomus plecostomus* and *Hypostomus emarginatus.* The present study analyzes the diet, and niche breadth and overlap of the syntopic populations of these congeneric species in the Coaracy Nunes reservoir on the Araguarí River during the flood and low water seasons, with the primary aim of characterizing the possible strategies that underpin their coexistence in the reservoir.

2. Material and Methods

Study area

The Araguari is the principal river of the Brazilian state of Amapá, with a total length of 498 km and a drainage basin of 38,000 km^2. This river arises in the Tumucumaque range and discharges into the Atlantic Ocean, although it is strongly influenced by the Amazon River. The study area is located in the middle Araguari River basin, in the Coaracy Nunes reservoir. The Coaracy Nunes reservoir lies between the municipalities of Ferreira Gomes and Porto Grande in the state of Amapá, and is located approximately 200 km from the Atlantic Ocean. The reservoir drains a total area of 23.5 km^2, and has a mean discharge of 976 m^{3}s^{-1}, mean depth of 15 m, and a total volume of 138 Hm^3. The local climate is typical of the Amazon basin, with a rainy season between January and June, and a dry season from July to December (BEZERRA et al., 1990; IBGE, 2010).

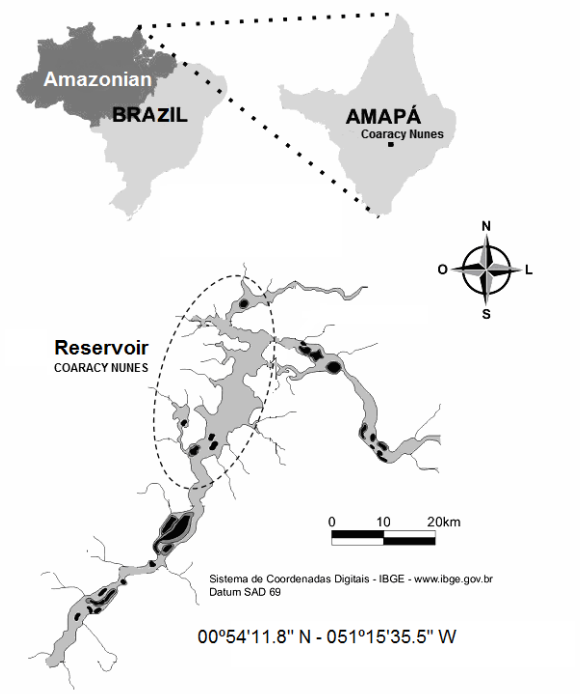

Figure 1. Study area: reservoir of the Coaracy Nunes hydroelectric power station in Ferreira Gomes, Amapá, Brazil.

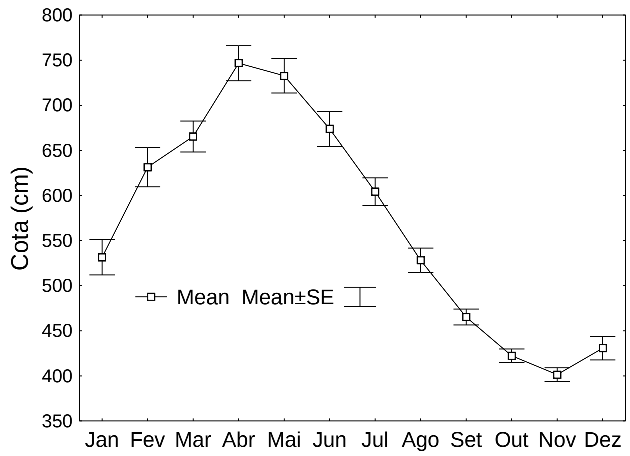

Figure 2. Mean (± standard deviation) monthly variation in the level (cm) of the Araguari River at the Porto Platon station, between 1952 and 2010 (source: ANA, 2011).

Data collection and analysis

Fish specimens were captured with cast and drag-nets throughout the area of the reservoir every two months between May, 2010 and July, 2011. The specimens captured were stored on ice in a cooler for immediate removal to a field laboratory for analysis and biometric measurements. The stomachs of the all the specimens were removed, weighed, and were preserved in 5% formaldehyde.

The diet of each species was analyzed separately for the flood and dry seasons. Dietary items were observed under stereoscopic and optical microscopes, and identified with the help of published reference material and identification keys.

All captured specimens were identified to the lowest possible taxonomic level, measured (total length in mm), weighed (g), and photographed. Species identification was based on the available literature and was confirmed by specialists. Dietary analysis was based on the examination of the stomach contents of booth species. Dietary items were classified in ten standardized categories: 1 – plant material (unidentified remains of leaves, flowers, and algae); 2 – insect (whole individual or animal parts); 3 – larva (terrestrial or aquatic); 4 – zooplankton; 5 – phytoplankton; 6 – crustacean (crab or shrimp); 7 – fish (whole animals or remains, including scales and fins); 8 – arthropod (other representatives of the phylum Arthropoda, whole animals or parts); 9 – detritus (organic detritus at different stages of decomposition, associated with sediments, algae, and organic material such as mud or slime); 10 – animal parts (unidentified parts of non-fish vertebrates).

The composition of the diet was analyzed by volume (VO%) and the frequency of occurrence (FO%) using an optical microscope (HYNES, 1950; HYSLOP, 1980). These two parameters were combined to produce Kawakami and Vazzoler's (1980) Feeding Index (FI). Based on this analysis, the dietary preferences and feeding specializations of the different species were evaluated on the basis of a FI $\geq$ 0.5 criterion for a given category or type of item. In some specific cases, where a number of different items were consumed in relatively reduced proportions, a criterion of FI $\geq$ 0.4 was adopted (GASPAR DA LUZ et al., 2001). Species that presented a co-dominance of plant and animal items, or a relatively balanced consumption (difference of no more than 20%) of the two types of items, were considered to be omnivorous.

The importance of the different items in the diet was classified according to the system of Guillen and Granado (1984), in which items with a contribution of >30% were classified as the principal components of the diet, with those of 15-30% being classified as additional items, and those of <15% as accidental.

The niche breadth of each species was based on Levin's standardized index, Bi (HURLBERT, 1978), the values of which vary from 0 (when the species consumes a single dietary item) to 1 (when the species exploits the available items in equivalent proportions). The index is provided by $Bi = [(\Sigma jPij2)-1 -1] (n - 1)^{-1}$, where Bi = the standardized index of niche breadth, Pij = the proportion of resource j in the diet of species i, and n = the total number of dietary resources. Values of Bi are considered high when they exceed 0.6, moderate, when they are between 0.4 and 0.6, and low when they are below 0.4 (NOVAKOWSKI et al., 2004). The analysis of niche overlap between the most common species was based on Pianka's index (1973), which is derived from the composition of the diet (percentages) of the different species. The values obtained for this index were classified according to the scheme of Grossman et al (1985) and Novakowski et al. (2004), in which values of over 0.6 are considered high, those of 0.4-0.6, moderate, and those below 0.4, low.

Niche overlap between a pair of species is given by the equation $O_{jk} = \sum_{(n;\, i)} P_{ij} * P_{ik} / \sqrt{\sum_{(n;\, i)} P_{ij}^2 * \sum_{(n;\, i)} P_{ik}^2}$, where O_{jk} = Pianka's index of niche overlap between species j and k, pij = the proportion of the ith resource in the diet of species j, p_{ik} = the proportion of the ith resource in the diet of species k, and n = the total number of items. For both niche breadth and overlap indices, a basic assumption adopted here was that the different dietary resources are equally accessible to all species, given that no data were collected on the availability of resources within the study area (ABELHA, 2007).

Seasonal differences in the mean indices (niche breadth and overlap) were evaluated in the diets of the two species separately and for both species together. The data were analyzed for normality and homoscedasticity before the application of Student's t, with a 5% significance level (α = 0.05) (SOKAL; ROHLF, 1997; ZAR, 1999).

In order to verify whether observed dietary overlap differed significantly from a random pattern, the original matrix of the diet of the two species was randomized, using a null model. The observed proportions of the volume of each item were randomized 10,000 times, and Pianka's index was calculated at each step. Statistical significance (α = 0.05) was determined by the comparison of the observed overlap with that determined by the null model. This analysis was run in the EcoSim program (GOTELLI; ENTSMINGER, 2004).

3. Results

A total of 172 specimens of *H. plecostomus* were collected during the study period (63 during the flood period, and 109 at low water), and 94 of *H. emarginatus* (39 in the flood, and 51 in the dry season). Nine dietary items were identified through the analysis of stomach contents (Table 1), of which detritus was by far the most abundant (98.00%), providing virtually the whole of the diet of the two species throughout the study period. The other items consumed were plant fragments (1.025%), zooplankton (0.05%), arthropods (0.42%), chlorophytes (0.1%), bacillariophytes (0.1%), cyanobacteria (0.1%), dinophytes (0.1%), and unidentified material (0.1%). All these items were present in extremely low percentages (< 15%), and were thus classified as accidental. Apart from detritus, three items, such as, plant fragments, arthropods, and unidentified material, were most consumed during the flood period (Table 2).

Table 1. Composition of the diet (FI) of *H. plecostomus* and *H. emarginatus* from the Coaracy Nunes reservoir in Ferreira Gomes, Amapá (Brazil). (N_{sto}= number of stomachs; Detr = detritus; Fragp = plant fragments; Zoop = Zooplankton; Arthr = Arthropoda; Chlo = Chlorophyta; Bacill = Bacillariophyta; Cyan = Cyanobacteria; Din = Dinophyta; Unmat = unidentified material).

Species	Period	N	N_{sto}	Detr	Fragv	Zoop	Arthr	Chlo	Bacill	Cyan	Din	Unmat
H. plecostomus	Dry	109	30	0.99	0.006			0.001	0.001	0.001	0.001	
	Flood	63	30	0.98	0.01		0.005	0.001	0.001	0.001	0.001	0.001
H. emarginatus	Dry	51	20	0.98	0.01	0.001	0.004	0.001	0.001	0.001	0.001	0.001
	Flood	39	20	0.97	0.015	0.001	0.008	0.001	0.001	0.001	0.001	0.002

In general, the diet of *H. emarginatus* was slightly more diverse than that of *H. plecostomus* throughout the study period. In the dry season, zooplankton, arthropods, and unidentified material were absent from the diet of *H. plecostomus*, although in the flood period, only zooplankton was absent from the diet of this species. However, the diet of neither *H. plecostomus* (*t* test: p = 0.061) nor *H. emarginatus* (*t*: p = 0.93) varied significantly between seasons (Table 1). Similarly, no seasonal difference was found (*t* test: p = 0.57) when the data for the two species were combined (Table 2).

Table 2. Composition of the combined diet of *H. plecostomus* and *H. emarginatus* from the Coaracy Nunes reservoir in Ferreira Gomes, Amapá (Brazil Detr = detritus; Fragp = plant fragments; Zoop = Zooplankton; Arthr = Arthropoda; Chlo = Chlorophyta; Bacill = Bacillariophyta; Cyan = Cyanobacteria; Din = Dinophyta; Unmat = unidentified material).

Season	Detr	Fragv	Zoop	Arthr	Chlo	Bacill	Cyan	Din	Unmat
Dry %	98.50	0.80	0.05	0.20	0.10	0.10	0.10	0.10	0.05
Flood %	97.50	1.25	0.05	0.65	0.10	0.10	0.10	0.10	0.15

The niche breadth (*Bi*) values recorded in the present study indicated that *H. marginatus* fed on a wider variety of items (Bi_{dry} = 0.005; Bi_{flood} = 0.008) than *H. plecostomus* (Bi_{dry} = 0.003; Bi_{flood} = 0.005). Both species presented a narrow niche, as indicated by the *Bi* values of less than 0.3. This reflects the predominance of detritus in the diets of both species. While both species presented broader niches during the flood period (Figure 3), the difference between seasons was not significant for either *H. plecostomus* (*t*: p = 0.052) or *H. emarginatus* (*t*: p = 0.95).

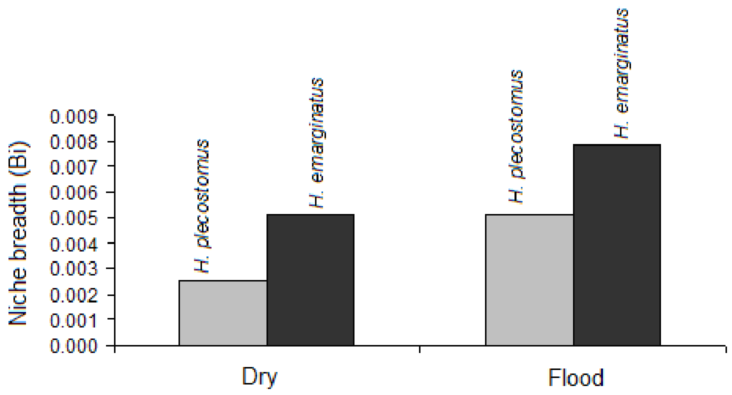

Figure 3. Niche breadth of *H. plecostomus* and *H. emarginatus* during the flood and dry seasons at the Coaracy Nunes reservoir in Ferreira Gomes, Amapá, Brazil.

The overlap recorded between the niches of the two species in the dry season ($O_{jk} = 0.99$) was significantly greater than expected according to the null model (mean = 0.11; χ^2: p = 0.009). A similar pattern was recorded during the flood period, with an observed overlap of $O_{jk} = 0.99$, and mean expected overlap of 0.11 (χ^2: p = 0.00000). In both seasons, then, niche overlap was significantly greater than expected by chance.

4. Discussion

The available data on the trophic ecology of the fishes of the genus *Hypostomus* indicate that these species feed predominantly on detritus. A number of other items may also complement the diet, but in very small proportions (HAHN et al., 1997; DELARIVA; AGOSTINHO, 2001; CASTRO, et al., 2003; ALVIM; PERET, 2004; CARDONE et al., 2006; LEITE, 2008). A predominance of detritus was also recorded in the diets of both species in the Serra da Mesa reservoir on the Tocantins River, in central Brazil (CASTRO, 2003; LEITE et al., 2009), and in non-reservoir habitats (FERREIRA e CASATTI, 2006).

The detrivorous behavior of the loricariids is considered to be a specialization associated with an adaptation of the morphology of the digestive tract (shape and position of the mouth and length of the intestine). These adaptations allow loricariids to inhabit environments with an abundance of detritus (AGOSTINHO et al.1997; HAHN et al.1997; GARAVELLO; GARAVELLO, 2004).

The abundance of decomposing organic matter available in most South American river basins means that the energy flow and nutrient cycling in these aquatic systems is based on the detrital food chain (BOWEN, 1983). This detritus is derived primarily from riverside forests, especially those that are flooded during high water (ARAUJO-LIMA et al., 1995). The lentic nature of reservoirs favors the deposition of a wide range of organic material carried in by the feed rivers, resulting in an abundance of detritus in the sediments of these bodies of water (THORNTON, 1990). This abundance of resources obviously favors the survival of detritivorous fishes in these environments.

Fragments of plants were also a relatively frequent item in the diets of both species throughout the study period, which may also reflect the abundance of this resource in the reservoir. The riparian forest that lines the margins of the reservoir may provide a range of material, including leaves, fruits, and seeds. While the diet of *Hypostomus* species is based on detritus and plant material, these fishes are considered to be detrivores (LUIZ et al., 1998; HANN et al., 1998).

The nutrients available in the detritus may also favor the development of phytoplankton (ARAUJO-LIMA et al., 1995), which is ingested incidentally by the fish when feeding on sediments. The phytoplankton present in the detritus appears to be the principal source of energy for detrivorous fishes. While abundant detritus appears to be energy-poor, this would account for the relatively large amounts of this material ingested by detritivores.

The ingestion of specific dietary items may vary seasonally according to their availability in the environment (EDDS et al., 2002). In reservoirs, the composition of the diets of specialized fishes, such as piscivores and detritivores, may not vary seasonally due to the relatively constant level of the reservoir (HANN et al., 1998; MERONA et al., 2005; AGOSTINHO et al. 2005). In the present study, this lack of seasonal variation was recorded for *H. emarginatus*, although in the case of *H. plecostomus*, arthropods and unidentified material were recorded only during the flood period, indicating possible seasonal fluctuations in the availability of these resources in the Coaracy Nunes reservoir. The apparent broadening of the diet of *H. emarginatus* during the flood period may reflect the evolution of a mechanism for the avoidance of competition with *H. plecostomus*.

In the present study, the narrower niche of *H. plecostomus*, together with its greater abundance within the study area in comparison with *H. emarginatus* (SÁ-OLIVEIRA, 2012), indicates that *H. plecostomus* may have colonized the area more successfully, leading to the less competitive species (*H. emarginatus*) complementing its diet with resources classified as accidental. While detritus appears to be a homogeneous resource, Delariva and Agostinho (2001) concluded that detritivorous fishes may still partition dietary items.

Both species ingested more arthropods during the flood period, which is probably related to an increase in the number of invertebrates washed out by the rain from the riparian forest and other habitats surrounding the reservoir during this part of the year (LOWE-MCCONNELL, 1999). The absence of zooplankton from the diet of *H. plecostomus* may be related to the substrate on which this species forages, which may also be avoided by *H. emarginatus* as part of its strategy to minimize competition. Where resources are abundant, species are likely to exploit preferential resources or occupy the most accessible habitats. In the present study, *H. plecostomus* appears to be using resources and space in a dominant way, forcing *H. emarginatus* to complement its diet with zooplankton and feed at alternative sites.

A number of studies have shown that *Hypostomus* may feed on algae as a secondary or accidental dietary item (ARCIFA; MESCHIATTI 1993; CASSATI; CASTRO, 1998; CARDONE et al., 2006; LEITE et al., 2009; MANZZONI et al., 2010). While recorded in low proportions, this item was frequent in the diet of the two *Hypostomus* species analyzed in the present study. The presence of chlorophytes, bacillariophytes, cyanobacteria, and dinophytes in the diets of both species indicate that they may be relatively abundant in the Coaracy Nunes reservoir.

The marked niche overlap recorded in the present study during both seasons appears to be related to the predominance of detritus in the diets of the two species. A high degree of niche overlap appears to be typical of detritivores (BUXTON, 1984). However, the syntopy of species with the same feeding niche may be facilitated by the overall abundance of resources and differences in the utilization of these resources by the two species (REINTHAL, 1990; ABELHA, 2007).

In the present study, observed niche overlap was significantly greater than that expected by chance, which suggests that, in addition to the abundance of detritus within the study area, other abiotic factors may contribute to the coexistence of the two *Hypostomus* species, supporting their similar foraging patterns (ALBRECHT; GOTELLI, 2001). Pianka (2000) concluded that competition will be absent where species share abundant resources. In the present case, the permanent modification of the water level within the area of the reservoir may have affected the interactions between the two species, and the form in which they share the available resources.

The results of the present study indicate that the *H. plecostomus* and *H. emarginatus* populations of the Coaracy Nunes reservoir have highly similar diets, feeding preferentially on detritus, but also consuming other resources in small proportions, which differ between the species. The minimal difference in the diet of the two species may be the factor that permits their coexistence in the study area, principally during the dry season, when the sharing of resources may have been more accentuated. The results indicate that the two species are well adapted to the hydrological cycle of the reservoir, even after many years following the impoundment. The analysis of the diet also permits certain inferences on the availability of dietary resources at a given site, as in the present case in relation to the presence of microalgae in the diets of the two fish species.

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