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Diet of *Hemigrammus marginatus* (Characiformes: Characidae) in the Upper Contas River, Diamantina Plateau (Bahia, Brazil)

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ABSTRACT. Studies on the composition of fish diet and on how species exploit food resources are especially relevant in tropical freshwater systems, where dietary plasticity is a commonly used strategy. In this study, we analysed the food spectrum and the environmental, seasonal and ontogenetic variations in the diet of a characid species [*Hemigrammus marginatus* Ellis, 1911 (Characidae)] in the region of the Upper Contas River, in the Diamantina Plateau, Brazil. We verified an omnivorous/invertivorous and opportunistic food habit, with predominance of insects and microcrustaceans, followed by filamentous algae. Seasonality did not alter the food resources used by the species. However, differences were detected in the dominant categories when comparing the two sampled rivers, as well as in the food consumption throughout the development of the species. These data increase the knowledge about the biology of *H. marginatus* and allow understanding the influence of the characteristics of the rivers and their surroundings in the trophic ecology of the species, as our findings have shown that, although insects have been expressive in both studied localities, microcrustaceans exhibit a greater relative importance in the more lentic environment, which is probably related to the variation in the availability of these resources in the environment.

KEYWORDS. Feeding, coastal drainage, trophic ecology, freshwater fishes.

RESUMO. Dieta de *Hemigrammus marginatus* (Characiformes: Characidae) no Alto Rio de Contas, Chapada Diamantina (Bahia, Brasil). Estudos sobre a composição da dieta de peixes e de como as espécies exploram os recursos alimentares são especialmente relevantes em sistemas de água doce tropicais, onde a plasticidade alimentar é uma estratégia comumente utilizada. Neste trabalho, analisamos o espectro alimentar e as variações ambientais, sazonais e ontogenéticas na dieta de uma espécie de caracídeo [*Hemigrammus marginatus* Ellis, 1911 (Characidae)] na região do Alto Rio de Contas, na Chapada Diamantina, Brasil. Verificamos um hábito alimentar onívoro/invertívoro e oportunista, com predominância de insetos e microcrustáceos, seguido de algas filamentosas. A sazonalidade não alterou os recursos alimentares utilizados pela espécie. No entanto, foram detectadas diferenças nas categorias dominantes ao comparar os dois rios amostrados, bem como no consumo do alimento ao longo do desenvolvimento da espécie. Esses dados ampliam o conhecimento acerca da biologia de *H. marginatus* e permitem entender a influência das características dos rios e de seus entornos na ecologia trófica da espécie, visto que, embora o item insetos tenha sido expressivo em ambos os locais estudados, microcrustáceos exibiram maior importância relativa no ambiente mais lêntico, o que possivelmente está relacionado à variação na disponibilidade destes recursos no ambiente.

PALAVRAS-CHAVE. Alimentação, drenagem costeira, ecologia trófica, peixes de água doce.

Neotropical freshwater fishes, in general, present trophic plasticity, varying their diet according to space, time and ontogeny (Abelha *et al*., 2001). This lack of specialization allows the use of the most variable food items available in the environment, favouring the sharing of resources among the members of the community as well as reduction of the intra- and interspecific competition for food (Lowe-McConnell, 1999; Araújo *et al*., 2005; Mise *et al*., 2013). The items used as food resource by the fish are quite diverse, differing in type (animal, plant or detritus/sediment) and origin (autochthonous or allochthonous), and their availability in the aquatic environments is also variable (Bennemann *et al*., 2005). This variation is influenced by the characteristics of the water body and its surrounding and can occur seasonally and/or spatially, mainly as a function of the longitudinal gradient of the watercourse (Vannote *et al*., 1980; Esteves & Aranha, 1999; Gomiero & Braga, 2005).

In this context, the structure of the riparian vegetation can directly and indirectly influence the availability of food resources to the fishes, since many species consume items from the adjacent terrestrial environment, such as detritus, fruits, leaves, invertebrates and, although uncommon, small vertebrates (Sabino & Castro, 1990; Abelha *et al*., 2001; Esteves & Lobón-Cerviá, 2001; Souza *et al*., 2015). Moreover, even if not consumed directly, the allochthonous material corresponds to the nutritional base of several autochthonous aquatic organisms (*e.g.* detritivores aquatic invertebrates), which represent an important food source for several fish species in freshwater environments (Ueida *et al*., 1997; Gomiero & Braga, 2008).

Due to their importance in the energy flow and nutrient cycling, small-sized fishes represent an indispensable link in the trophic chain of aquatic environments (Lowe-McConnell, 1999; Corrêa *et al*., 2009; Fiori *et al*., 2016). Among these species, there is *Hemigrammus marginatus* Ellis 1911, a small characid widely distributed in the Neotropical region, occurring in the basins of Guaporé, Orinoco, Amazonas, Paraná, Paraguai, and São Francisco rivers, as well as in some rivers of the Brazilian Northeast (*e.g.* Jaguaribe, Itapicuru, Paraguaçu, and Contas rivers) (Buckup *et al*., 2007; Eschmeyer *et al*., 2018). *Hemigrammus marginatus* dwells in large shoals (30 to 50 individuals, according to Casatti *et al*., 2003), exploits the middle of the water column, and mainly consumes food items carried by the current, preferentially inhabiting margin environments (both lentic and lotic) in association with aquatic macrophytes (Grant & Noakes, 1987; Casatti *et al*., 2003; Crippa *et al*., 2009; Brandão-Gonçalves *et al*., 2010; Ceneviva-Bastos *et al*., 2010).

The Contas River basin, where *Hemigrammus marginatus* is widely spread, is a coastal hydrographic system that occupies an area of 55,483 km^2 in the south-central region of the Bahia state, Brazil, and belongs to the Northeastern Mata Atlântica freshwater ecoregion (Abell *et al*., 2008). This basin can be subdivided into three regions with well-differentiated characteristics: upper, medium and lower Contas (SRHSH, 1993), and *H. marginatus* has been recorded in these three portions of the basin (André Teixeira da Silva, pers. com.). This study has as sampling area the upper course of the Contas River, in the Diamantina Plateau, where the climatic and physiographic characteristics of the Bahia semi-arid region predominate (Juncá *et al*., 2005). This area is notable for sheltering several endemic species, such as *Hyphessobrycon brumado* Zanata & Camelier 2010, *Trichomycterus tete* Barbosa & Costa 2011, a probable new species of *Nematocharax* (Barreto *et al*., 2016), and *Hasemania piatan* Zanata & Serra 2010, being the latter considered endangered due to anthropic impacts (Silva *et al*., 2016).

To date, there are no data about the feeding or any other aspect of the biology of *Hemigrammus marginatus* in the Contas River basin. In addition, Hortal *et al.* (2015) highlight that the knowledge gaps on the ecological characteristics of the species (functional traits, abiotic niches and biotic interactions) have restricted the elaboration of models that adequately describe the biodiversity worldwide. In view of this, we analysed the diet of *H. marginatus* in two water bodies belonging to the drainage of the Upper Contas River in order to determine its food spectrum and verify the variations in the diet of this species in function of the environments, seasons, and along the ontogeny.

MATERIAL AND METHODS

Study area. The specimens of *Hemigrammus marginatus* (Fig. 1) were captured in two rivers: Contas River (13°31'58.53"S / 41°36'7.29"W) and Água Suja River (13°24'34.79"S / 41°38'1.28"W) (Fig. 2), one of its tributaries. These rivers differ in limnological characteristics and degradation level (Fig. 3). In the Contas River, a section dammed by a bridge in an intermittent region of the river was sampled, representing a lentic environment, being possible to observe the use of its surrounding by cattle and degraded marginal vegetation. In turn, the Água Suja River is a perennial drainage with running water and constitutes therefore a lotic environment. It also has a lower eutrophication level and its riparian vegetation is better preserved.

Fish sampling and analysis. The collections of the *Hemigrammus marginatus* specimens in the two aforementioned rivers were performed in July 2012 (campaign 1; dry season) and March 2013 (campaign 2; rainy season). The specimens were captured during the day and near the margins of the water bodies using trawl nets. Still in the field, the individuals were placed in plastic bags, duly labelled and fixed in formalin 5% for the preservation of the stomach content, and later transported to the Universidade Estadual do Sudoeste da Bahia (UESB), campus of Jequié.

In the laboratory, the fish were transferred to flasks containing a 70% ethanol solution. The standard length (mm) of each specimen was determined using a pachymeter, and

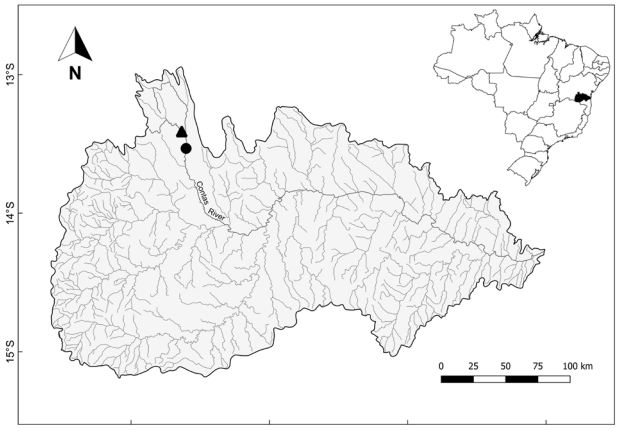

Fig. 1. Map of the Contas River basin, in the south-centre region of the Bahia state (Brazil), with its main drainages and indication of the two collection sites: Contas River (circle) and Água Suja River (triangle).

Fig. 2. Living specimen of *Hemigrammus marginatus* Ellis, 1911 collected during the study (standard length = 32 mm).

the total weight (g) was measured with an analytical balance. After the abdominal incision under stereomicroscope, the stomach of each specimen was removed. The duly identified stomachs with food were placed in flasks containing a 70% ethanol solution for further analysis.

Data analysis. The stomach contents were observed under stereomicroscope and the food items were identified with the aid of specialized literature (*e.g.* Borror *et al*., 1989; Ruppert *et al*., 2005; Brusca & Brusca, 2007; Mugnai *et al*., 2010), and then distributed in nine food categories (Tab. I). These data were distinguished according to the environments (Contas and Água Suja rivers), campaigns (dry and rainy seasons), and length classes (classes 1, 2 and 3) in order to verify if the diet of the species differs between lentic and lotic waters, seasons, and along the ontogeny. The length classes were established based on the variation of the standard length of the specimens, using an interval of 9 mm, as follows: 9.5 |— 18.5 (class 1), 18.5 |— 27.5 (class 2) and 27.5 |— 36.5 (class 3).

The most representative food categories in the general diet of the species and for each aforementioned condition were determined based on the methods of Frequency of Occurrence (F%), Dominance (D%) (Frost & Went, 1940), and Feeding Index (IAi) (Kawakami & Vazzoler, 1980) with modification, since the volumetric values were substituted by the D%. Furthermore, the dietary data for each environment, campaign, and length class were ordered by a Non-Metric Multidimensional Scaling (NMDS) analysis based on the IAi values of the food categories, and using the Bray-Curtis Index as distance measure (Magurran, 2004).

RESULTS

From the analysis of the stomach content of 338 specimens of *Hemigrammus marginatus*, 183 of which were captured in the Contas River and 155 in the Água Suja River, we verified the consumption of a wide variety of food items (Tab. I). Tables II and III present the values of F%, D% and IAi of the food categories identified in the diet of specimens from the Contas and Água Suja rivers, respectively. In general, the predominant categories were microcrustaceans, insects and, secondarily, filamentous algae. Detritus was a representative item in some stomachs only, while the other categories were considered occasional or accidental, since they occurred in a smaller number of stomachs and were not dominant in any of them.

Fig. 3. Collection sites of *Hemigrammus marginatus* Ellis, 1911 in the Upper Contas River basin: Contas River (above) and Água Suja River (below).

When comparing the two sampled rivers (Fig. 4), we observed that different food categories predominated in the diet of the species. In the Contas River, there was a considerable consumption of insects and microcrustaceans,

Tab. I. Food categories in which the items found in the stomachs of specimens of *Hemigrammus marginatus* Ellis, 1911 in drainages of the Upper Contas River, Diamantina Plateau, Brazil, were classified.

Food categories	Description
Microcrustaceans	Cladocera, Ostracoda and Copepoda
Insects	Ephemeroptera nymph, Plecoptera nymph, Diptera larva, Diptera pupa, Trichoptera larva, Trichoptera cocoon, Coleoptera larva, fragments of autochthonous insects, Coleoptera, Hemiptera, Hymenoptera, Diptera, and fragments of allochthonous insects
Plant fragment	Plant material and seeds
Unicellular algae	
Filamentous algae	
Detritus	Organic particulate matter
Sediment	Mineral particles (materials from the bottom of the river, such as grains of sand)
Non identified material (NIM)	Unspecified material (animal or plant)
Other invertebrates	Spiders, mites, nematodes, and Thecamoeba

Tab. II. Frequency of occurrence (F%), Dominance (D%), and Feeding Index (IAi) of the food categories in the diet of *Hemigrammus marginatus* Ellis, 1911 in the Contas River, Diamantina Plateau, Brazil, between campaigns (Campaign 1 and Campaign 2) and among length classes (C1, C2 and C3).

	Campaign 1 (dry season)									Campaign 2 (rainy season)					
	C1			C2			C3			C2			C3		
Stomachs analysed	40			40			23			40			40		
	F%	D%	IAi	F%	D%	IAi	F%	D%	IAi	F%	D%	IAi	F%	D%	IAi
Microcrustaceans	100.0	40.0	0.49	92.5	33.8	0.41	91.3	8.7	0.09	65.0	27.5	0.27	87.5	61.3	0.71
Insects	75.0	50.0	0.46	90.0	38.8	0.46	100.0	73.9	0.86	90.0	40.0	0.54	82.5	23.8	0.26
Plant fragment	0.0	0.0	0.0	2.5	0.0	0.0	8.7	0.0	0.0	37.5	6.3	0.03	27.5	5.0	0.02
Unicellular algae	10.0	0.0	0.0	32.5	0.0	0.0	4.3	0.0	0.0	20.0	0.0	0.00	12.5	0.0	0.0
Filamentous algae	2.5	0.0	0.0	42.5	10.0	0.06	17.4	4.3	0.01	45.0	17.5	0.12	10.0	6.3	0.01
Detritus	5.0	0.0	0.0	20.0	2.5	0.01	17.4	4.3	0.01	47.5	5.0	0.03	17.5	0.0	0.0
Sediment	2.5	0.0	0.0	15.0	0.0	0.0	0.0	0.0	0.0	5.0	0.0	0.00	7.5	0.0	0.0
Non identified material	35.0	10.0	0.05	35.0	15.0	0.06	39.1	4.3	0.02	2.5	2.5	0.00	2.5	2.5	0.0
Other invertebrates	15.0	0.0	0.0	7.5	0.0	0.0	13.0	4.3	0.01	27.5	1.3	0.01	32.5	1.3	0.01

Tab. III. Frequency of occurrence (F%), Dominance (D%), and Feeding Index (IAi) of the food categories in the diet of *Hemigrammus marginatus* Ellis, 1911 in the Água Suja River, Diamantina Plateau, Brazil, between campaigns (Campaign 1 and Campaign 2) and among length classes (C1, C2 and C3).

	Campaign 1 (dry season)									Campaign 2 (rainy season)								
	C1			C2			C3			C1			C2			C3		
Stomachs analysed	5			39			26			3			43			39		
	F%	D%	IAi	F%	D%	IAi	F%	D%	IAi	F%	D%	IAi	F%	D%	IAi	F%	D%	IAi
Microcrustaceans	80.0	0.0	0.00	92.3	0.0	0.00	73.1	0.0	0.00	100.0	0.0	0.00	69.8	0.0	0.00	41.0	0.0	0.00
Insects	100.0	100.0	1.00	100.0	78.2	0.92	100.0	40.4	0.46	100.0	83.3	0.83	100.0	86.0	0.95	100.0	89.7	0.97
Plant fragment	0.0	0.0	0.00	10.3	0.0	0.0	23.1	0.0	0.00	0.0	0.0	0.00	9.3	4.7	0.00	25.6	7.7	0.02
Unicellular algae	20.0	0.0	0.00	48.7	2.6	0.01	7.7	0.0	0.00	33.3	0.0	0.00	14.0	0.0	0.00	2.6	0.0	0.00
Filamentous algae	0.0	0.0	0.00	30.8	19.2	0.07	80.8	59.6	0.54	0.0	0.0	0.00	2.3	1.2	0.00	0.0	0.0	0.00
Detritus	0.0	0.0	0.00	12.8	0.0	0.00	53.8	0.0	0.00	100.0	16.7	0.17	51.2	8.1	0.05	48.7	2.6	0.01
Sediment	20.0	0.0	0.00	28.2	0.0	0.00	46.2	0.0	0.00	100.0	0.0	0.00	37.2	0.0	0.00	35.9	0.0	0.00
Non identified material	0.0	0.0	0.00	10.3	0.0	0.00	11.5	0.0	0.00	0.0	0.0	0.00	2.3	0.0	0.00	2.6	0.0	0.00
Other invertebrates	80.0	0.0	0.00	48.7	0.0	0.00	30.8	0.0	0.00	33.3	0.0	0.00	46.5	0.0	0.00	33.3	0.0	0.00

followed by filamentous algae. In the Água Suja River, there was a predominance of insects, followed by filamentous algae and detritus. Regarding the campaigns (dry and rainy seasons), no differences were detected in the dominant categories. In the Contas River, insects and microcrustaceans predominated in both seasons. On the other hand, in the Água Suja River, insects predominated in both seasons, and a considerable consumption of filamentous algae in the dry season and detritus in the rainy season was also observed.

The three length classes in the Contas River consumed predominantly categories of animal origin (microcrustaceans and insects), and no individual belonging to the class 1 was sampled in the rainy season (Fig. 4). In the Água Suja River, the diet of *H. marginatus* was constituted predominantly by insects, but caveats should be made for class 3 in the dry season, due to a greater consumption of filamentous algae if compared with the other items.

DISCUSSION

Our analyses allowed the identification of a varied food spectrum for *Hemigrammus marginatus* of the Upper Contas River, with a diet based on autochthonous items mainly of animal origin, besides algae, detritus and sediment, so that the species, in general, was characterized as omnivorous/invertivorous and opportunistic. The occurrence of a flexible diet is an important strategy in variable environments such as the locality of the Contas River, since it allows the species to change the type of food consumed when oscillations occur in the relative abundance of resources or when the preferred item is in small supply (Knöppel, 1970; Abelha *et al*., 2001). In the present case, the fact that some populations of *H. marginatus* inhabit intermittent drainages with large variation in limnological parameters and resource availability highlights the importance of this feeding strategy to the species.

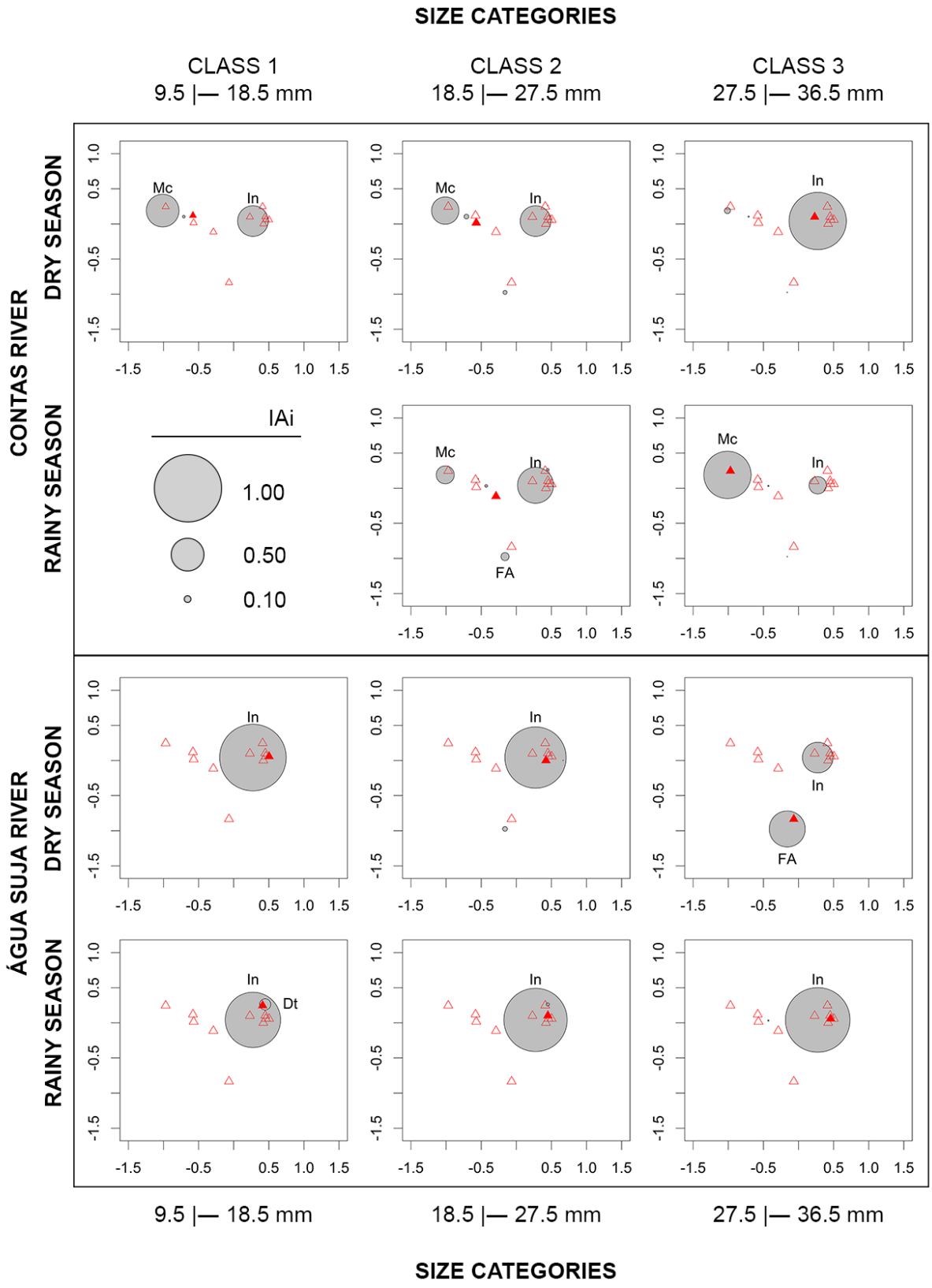

Fig. 4. Plots of the first two axes resulting from the Non-Metric Multidimensional Scaling (NMDS) ordination of individuals of *Hemigrammus marginatus* Ellis, 1911 from drainages of the Upper Contas River, Diamantina Plateau, Brazil, based on the Feeding Index (IAi) of the food categories consumed. The triangles correspond to the groups of individuals according to collection sites (Contas and Água Suja rivers), campaigns (dry and rainy seasons), and length classes (classes 1, 2 and 3), and the circles correspond to the food categories. For each graph, the respective fish group was highlighted as a filled triangle and the diameter of the circles is proportional to the IAi values observed for each food category (Mc, microcrustaceans; In, insects; FA, filamentous algae; Dt, detritus).

Regarding studies in lentic systems such as the locality in the Contas River, microcrustaceans represent a significant component of the species' diet (see Casatti *et al*., 2003; Pelicice & Agostinho, 2006). In fact, environments with lentic characteristics, mainly in the marginal regions, favour the development of the zooplankton community (Esteves, 1988; Russo & Hahn, 2006). On the other hand, for the *H. marginatus* population from the Água Suja River, an environment with lotic characteristics, the category insects resulted in the greatest importance, a fact that was also observed in the Franco stream, Mato Grosso do Sul state (Brandão-Gonçalves *et al*., 2010), and in a preserved stream of the Atlantic Forest in São Paulo state (Fragoso-Moura *et al*., 2017). In the Água Suja River, the better conservation state of the marginal vegetation can be responsible for the considerable contribution of allochthonous material for the water body (Afonso *et al*., 2000). This material could be used directly or indirectly as food resource by the fish. In the latter case, the fish may consume organisms that are part of the detritivore food chain, as many aquatic insects (Angermeier & Karr, 1983; Pusey & Arthington, 2003).

In the Água Suja River, the filamentous algae were also important in the diet of the species. This can be related to the greater availability of light and nutrients favouring the development of algae (Pusey & Arthington, 2003). Since the Água Suja River presents a lower depth and a more transparent water, it possibly provided an increase of this food item in this locality, increasing in this way the availability of this resource to the fishes. Thus, the variation found in the diet of *H. marginatus* can be related to the different environmental conditions and availability of resources in the different locations, which reflects the opportunistic character of the species.

Despite of being described as a species sensitive to the consequences of the degradation of the marginal vegetation (Teresa & Casatti, 2010), the survival of *H. marginatus* in an altered environment such as the Contas River can be related to its capacity to consume the various food resources available in the locality. Another factor that can be related to this dietary plasticity is the possibility that *H. marginatus* corresponds to a species complex and therefore the populations from the Paraná River basin represent a taxonomic unit distinct from the populations from other basins (Ota *et al*., 2015). However, this issue has not yet been properly revised and *H. marginatus* remains as the only valid taxonomic nomenclature for these fish (Eschmeyer *et al*., 2018).

Variation between different environments in the diet of *H. marginatus* was also verified between two floodplain lakes of the Upper Paraná River, where the species ingested as main item detritus/sediment in the Figueira lake and insects in the Pousada lake (da Luz *et al*., 2001). Also in the floodplain of the Upper Paraná River, the preferential items in the diet of the species differed between two open lakes connected to the Paraná River (Santana-Porto & Andrian, 2009). Although *H. marginatus* has been classified as zooplanktivore, there was a greater consumption of insects (Diptera and Hymenoptera) in Ressaco do Manezinho and Cladocera in Ressaco do Bile. In this approach, it is important to highlight that some food resources found in the diet of species with generalist or opportunistic habits do not necessarily means a preference for that food, but may reflect the abundance of this resource in the environment or represent an accidental ingestion (Bennemann *et al*., 2000; Silva *et al*., 2012).

The predominant categories in the diet of *H. marginatus* did not substantially differ between the dry and rainy seasons within each environment analysed, indicating that, in this case, the seasonality probably did not alter the offer of food resources consumed by the species. This result differs from that observed in other studies with the same approach. For example, in the Franco stream, the items of plant origin presented higher importance in the diet of *H. marginatus* in the autumn, while in the summer and spring the items of animal origin predominated (Brandão-Gonçalves *et al*., 2010). According to the authors, the lower feed importance of invertebrates in the autumn may be a result of lower metabolism and, consequently, lower activity of these animals in colder periods due to their ectothermal character. In addition, the higher rainfall in the flood period may be directly related to food availability. In this period, there is an increase of organic input into the water body, which is used as substrate by autochthonous invertebrates, thus favouring an increase in the abundance of this resource to the fishes as well as in the contribution of allochthonous food items, such as terrestrial insects, fruits, and seeds (Deus & Petrere-Junior, 2003; Bonato *et al*., 2012). It is worth noting that in the present study we did not observe representative variation in the climatic characteristics throughout the year, both in terms of water temperature and amount and intensity of rainfall, although all the collections were carried out in a period of drought which was considered one of the most intense of the last decades (Marengo *et al*., 2013, 2018).

Analysing the variations in the diet of *H. marginatus* in function of the length classes, we observed, for both rivers, a notable consumption of items of animal origin in the first classes and, for the Água Suja River, an increase in the consumption of filamentous algae in the third class. During the juvenile phase, since they are in a period of increase in the body size, fishes tend to consume mainly items of animal origin, given their higher protein value (Wootton, 1998; Motta & Uieda, 2004). Adults, in turn, are able to amplify their food spectrum (Andrian *et al*., 2001), and can also include items of plant origin to their diet (Gerking, 1994). Inclusion of items of plant origin as animals become adults is a common pattern in the diet of omnivorous tropical fishes, like in many members of the Characidae family, such as *Deuterodon langei* Travassos 1957 in the Ribeirão River basin (Vitule *et al*., 2008) and three species of the genus *Astyanax*: *A.* **aff.** *fasciatus* Cuvier 1819 in the Pedras River, Paraná (Wolff *et al*., 2009), *A. janeiroensis* Eigenmann 1908 in the Ubatiba River, Rio de Janeiro (Mazzoni *et al*., 2010), and *A. taeniatus* Jenyns 1842 in the Mato Grosso River, also in Rio de Janeiro (Manna *et al*., 2012).

The change in the diet over the course of growth can also be seen as an adaptation of the population in order to take advantage of a wider range of available resources, enabling the species as a whole to assimilate a greater variety of foods (Nikolsky, 1963). Moreover, variation in the food habit of a species during its development has as advantage reducing the intraspecific competition for food or supplying the physiological, morphological or energetic needs that fish could have due to migration, sexual maturation, and/or reproduction (Braga & Braga, 1987). The fact of showing remarkable ontogenetic variation also restricts the determination of *H. marginatus* as a single trophic unit in studies that relate its food character to that of other sympatric species, without admitting the covariant size or maturation stage (Vitule *et al*., 2008).

Finally, the results show that, in drainages of the Upper Contas River, *Hemigrammus marginatus* presents an omnivorous/invertivorous food habit, including in its diet resources of different types and origins. Some items considered uncommon in the diet of the species may have been consumed because they are highly available in the environment, denoting the opportunism of *H. marginatus*. Thus, these unprecedented results are fundamental to increase the knowledge about the biology of fishes from the Upper Contas River and provide a better understanding of how the fish communities of this region are structured.

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