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## Seasonal changes at population and individual levels in the diet of juvenile catfish in a Neotropical floodplain

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### ABSTRACT

Intra-population variation in niches is a widespread phenomenon in animal populations, but, in fish, this knowledge is still scarce. Here, we investigated the population and between-individuals variations in the diet of juvenile *Pimelodus maculatus*, in dry and wet seasons, in a floodplain from Pantanal, Brazil. A significant difference was verified, being that during the dry season, the diet was mainly composed of fish remains and detritus, while in the wet season, the main food item was fruit/seed. Values of trophic niche breadth were low and seasonally similar. High values of diet variation between individuals and low values of clustering degree, as well as the nestedness metric based on overlap and decreasing fill (NODF), were found. This combination showed that there are generalist and specialist individuals within the population, in which the diet of the last is composed of a subset of food items consumed by generalists. In addition, the median individual specialization index was statistically lower in the wet season, suggesting that individuals could be more diet specialists during this period. Thus, the seasonality in the food resources supply seems to be the main mechanism driving diet variations of juvenile *P. maculatus* at both population and individual level.

### ARTICLE HISTORY

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### KEYWORDS

Pimelodidae; niche breadth; omnivory; nested diets; food availability

## Introduction

Studies on trophic ecology generally characterize the feeding habits and/or the trophic group of an animal based on the predominant food item occurring in the diet of all individuals within a population. In this sense, all individuals are treated as ecological equivalents (Bolnick et al. 2003, 2011) disregarding possible individual differences, such as those related to behavior, physiology, and morphology (Persson et al. 1997), or even those related to environmental factors. Any given population may be composed entirely by trophic generalists, specialists, or a combination of both (Araújo et al. 2010). In the latter case, if the diet of specialists is an ordered subset of the diet of the generalists, then, the diet follows a nested pattern (Atmar and Patterson 1993). However, the diet of the individuals may be overdispersed when individual niches have low overlap with each other (Bolnick 2004; Eklöv and Svanbäck 2006; Araújo et al. 2010), or when groups of niche-specialized individuals (i.e. individuals that rely on different resources) are formed (Araújo et al. 2008, 2009).

Individual specialization is a key mechanism that contributes to the variation of a population's niche and may have important ecological and evolutionary consequences in maintaining the populations (Fox 2005). One specialist individual may be defined as an individual whose niche is

substantially narrower than its population's niche for reasons not attributable to its sex, age, or discrete morphological group (Bolnick et al. 2003). Thus, many apparent generalist populations could be, in fact, composed of relatively specialized individuals (Araújo et al. 2010). However, the individual variations have been usually neglected in trophic ecology studies of fish (Lima-Júnior and Goitein 2004; Silva et al. 2007), because the population is treated as a homogeneous group of individuals (Svanbäck et al. 2015), when the stomach contents are analyzed. In addition, it has been shown that the variation among individuals may comprise a large proportion of the population's niche breadth, especially for some species that exhibit generalized (or omnivorous) feeding habit at the population level (Bolnick et al. 2003, 2007; Svanbäck et al. 2015), such as many freshwater fish (Abelha et al. 2001).

In freshwater fish populations, diet variations in the use of resources can be conditioned by seasonal differences in food availability (Prejs and Prejs 1987; Winemiller and Kelso-Winemiller 2003). In this, since floodplains are typical seasonal ecosystems that present a dry period, the retraction of water-level constrains the fish populations to more reduced areas of foraging, especially in bays adjacent to river channels. The other period is the rainy season, where the return of high water-level expands the bays and increases the variety and availability of seasonal food, such as fruits, seeds, and allochthonous invertebrates for fish (Hanh et al. 2004; Corrêa et al. 2009). It seems to conduct to more specialized diets during high-water season in floodplains, when the foods are varied, and the fish species can use different resources to overlap less with each other (Prejs and Prejs 1987; Lowe-McConnell 1999), although the same pattern has not been verified in ecosystem streams (Zaret and Rand 1971).

At the individual level, the effects of variety and availability of food resources on diet variation have been little investigated (Araújo et al. 2008), even though there are evidences that new types of prey are included in the diet of individuals when fish density is increased (Araújo et al. 2008). Something similar could happen during low-water season in floodplain bays, constraining the individuals to cease or reduce the use of a preferential food item, and consume other ones, in function of its low availability (Hanh et al. 2004). This hypothesis gains support, because species populations have shown highest diet overlapping during dry periods (Prejs and Prejs 1987; Lowe-McConnell 1999), which is probably a result of the diversification of its individuals in the use of food items. In addition, many fish populations are more specialized during rainy periods (Lowe-McConnell 1999). It suggests that the amount of preferential food items favors individual specializations, because any individual, in function of its foraging experience, may consume some item previously consumed, simply because of it easier access (Abelha et al. 2001).

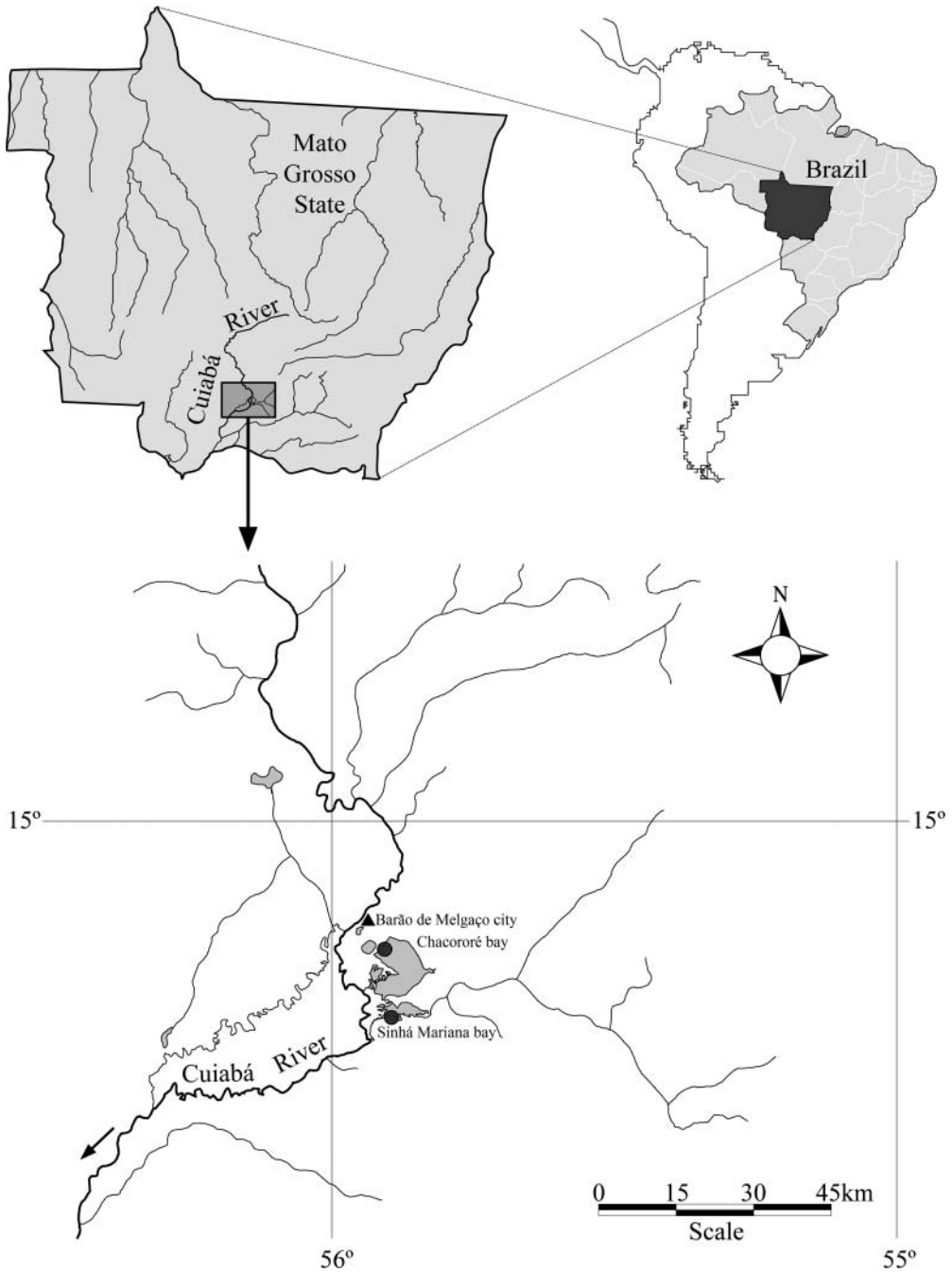
In this case, omnivorous fish living in floodplains are suitable habitat models for investigating seasonal trophic variation at population and individual levels. The medium-sized catfish, *Pimelodus maculatus* Lacépède, 1803 (Siluriformes, Pimelodidae), is abundant in the northern Pantanal wetland. This fish is widely distributed in South America and many studies have reported its generalist feeding habit (e.g. Lobón-Cerviá and Bennemann 2000; Lima-Júnior and Goitein 2003, 2004; Silva et al. 2007). Moreover, this species also shows a pronounced diet ontogenetic shift, with the juveniles being omnivorous and the adults piscivorous (Silva et al. 2007).

Considering that *P. maculatus* have a flexible diet in early life stages, we aimed to provide a quantitative estimation of the food composition for juvenile individuals of this species (at population and individual levels) in a floodplain from northern Pantanal, Brazil. Thus, we predict that (i) the diet composition differs between dry and wet seasons at the population and individual levels, due to the differential availability of food resources along seasonal scales; and that (ii) in the wet season, trophic specialization is expected at the individual level because during this season, there is a greater amount of preferential food resources, which promote better individual opportunities for foraging.

## Materials and methods

### Study area

Samples were taken from two bays that belong to the Cuiabá River basin. This basin covers an area of approximately 9365 km<sup>2</sup>, comprising two important Brazilian biomes: the Cerrado



**Figure 1.** Study area, Chacororé–Sinhá Mariana bays system, Mato Grosso state, Brazil. Black circles indicate the sampling sites and arrow the flow direction.

(a savannah area) and the Pantanal wetland, located in the Mato Grosso state, Brazil. Specifically, we sampled fish from lentic bay environments located on the left bank of the Cuiabá River, near the municipality of Barão de Melgaço, Mato Grosso state (Figure 1). The Chacororé bay ( $16^{\circ}14'6.8''S/55^{\circ}55'17''W$ ), the third largest bay on the wetland, is connected to the Cuiabá River to the west and to the Sinhá Mariana bay ( $16^{\circ}20'27''S/55^{\circ}54'10''W$ ), the second

sample site, to the south. The Sinhá Mariana bay is also connected to the Cuiabá River by a channel which is about 5 km long. The substrate is composed of a gradient of sandy/silty, sandy/loamy, and sandy bottom. The Chacororé bay has a range of 9.88–10.9 km width (6 km average width) and 2.75 m average depth. The size of this bay is  $178 \times 10^6 \text{ m}^3$  and  $64.92 \text{ km}^2$  of volume and area, respectively. The Sinhá Mariana bay has between 2.67 and 8.75 km width (1.29 km of average width) and an average depth of 3.58 m, which represent an average volume of  $40.4 \times 10^6 \text{ m}^3$  and an area of  $11.25 \text{ km}^2$  (Nunes and Silva 2005).

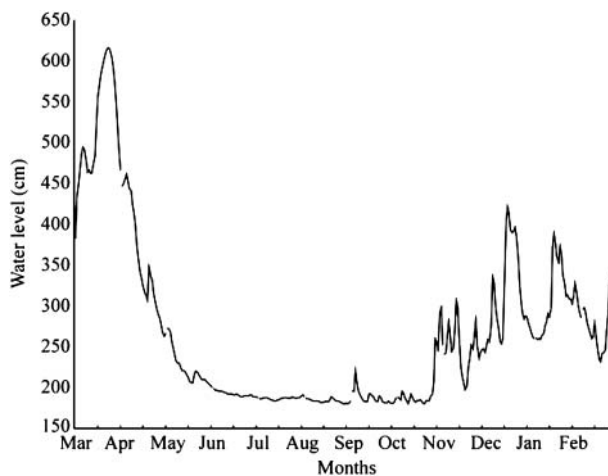
These sites represent the place where a wide floodplain begins and are characterized by a strong seasonal flood pulse (Junk et al. 1989). These bays have very similar seasonal dynamics in availability of food resources for fish. Besides, they are connected along the channel of the Cuiabá River and therefore, were treated as a single system (Agostinho et al. 2004). In addition, the fluvial communication between the bays, makes it impossible for us to treat the individuals as two distinct populations, since *P. maculatus* perform short reproduction migrations (Agostinho et al. 2004). We followed the sampling protocol of Pacheco and Silva (2009), describing both the lentic environments as Chacororé–Sinhá Mariana bays system.

### Sampling and diet analysis

Fish were sampled monthly from March 2000 to February 2001. The wet season occurred during the months of March, April, November, and December of 2000, and January and February of 2001; and the dry season from May to October of 2000. These seasons were defined according to the water-levels of the Cuiabá River (Figure 2).

In each sampling (i.e. in each month and in each bay), we set 10 m gill nets with different mesh sizes (i.e. ranging from 2.4 to 30.0 cm between opposite knots) for 24 hours with inspections every 8 hours. Three drift nets were set simultaneously in the littoral region of each sampling site (each 20 m long and with 1 cm mesh size).

Fish were identified based on Britski et al. (1999) and specimens were measured to the nearest 1 mm standard length (Ls), weighed to the nearest 0.1 grams total weight (Wt), and eviscerated. Stomachs were preserved in 4% formaldehyde and, in the laboratory, transferred and preserved in 70% ethanol. Sex and maturity stage were evaluated (Vazzoler 1996) and gonads were removed. Voucher specimens of *P. maculatus* were deposited in the Ichthyological Collection of Nupélia at the State University of Maringá, Brazil (<http://www.nupelia.uem.br/colecao>).



**Figure 2.** Relative water-levels in the study area, Chacororé–Sinhá Mariana bays system, Mato Grosso state, Brazil, from March 2000 to February 2001, showing the dry and wet seasons. Data were provided by the Brazilian Water Agency (Agência Nacional de Águas – ANA in Portuguese).

We identified the food items to the lowest possible taxonomic level, using specific literature. The insects were identified to the order level and, in some cases, to the family level (e.g. Ceratopogonidae, Chaoboridae, and Chironomidae). Other invertebrates were identified to the finest taxonomic level as possible, given the difficulty of their recognition (e.g. legs, broken shells, and digested organisms). However, in regard to some other resources, such as plants (leaf fragments), fruit (generally fragments or seeds), and fish (scales, spines, and muscle), the taxonomic identification was not possible. Due to the advanced stage of digestion of some items, combined with the fact that *P. maculatus* have pharyngeal teeth that grind foods (Lolis and Andrian 1996) and that this fish feed on plants and animals' debris, we could not accurately identify some food items. The limitation of this approach (taxonomic identification) to diet determination is expected due to the differential digestibility of the food items (Araújo et al. 2010).

To describe the diet composition of *P. maculatus*, we calculated the frequency of occurrence ( $O\%$ ), that is the occurrence of a determined food item in relation to the overall items of all stomach contents, and the volumetric frequency ( $V\%$ ), that is the volume of a determined food item in relation to the overall volume of all stomach contents (Hyslop 1980). Volumes were obtained by the displacement of water column of graduated cylinders (items  $> 0.1$  mL), and by a glass counting plate (items  $< 0.1$  mL) where volumes were obtained in  $\text{mm}^3$  and subsequently transformed into mL.

### Data analysis

For all analyses, we used the volume data of food items. In order to assess the significant differences in diet composition between sexes and seasons, we applied a multivariate permutational analysis of variance (PERMANOVA; Anderson 2005) to a matrix of food items of each individual, the volume values of which were transformed to  $\log(x + 1)$ . We used the Bray–Curtis dissimilarity as a measure of distance with the transformed data obtained by 9999 random permutations with appropriate units. All statistical analyses were conducted in the *R Programming Environment* using the Vegan package (the R Project for Statistical Computing, <http://www.r-project.org/>).

Trophic niche breadth was calculated using the Levins index (1968), which assumes that the diet breadth can be estimated using the uniformity in the distribution of the items among several feeding resources. Trophic niche breadth values range from 1 to  $n$ , with higher values representing a wider trophic niche breadth and, therefore, a wider resource exploitation by the consumer.

To assess how the degree of between-individual niche variation shifted across the seasons, we used the individual-level diet variation index ( $E$ ), obtained by averaging the pairwise dietary dissimilarity among all individuals (Araújo et al. 2008).  $E$  is positively related to the variation of the niche and ranges from 0, when the individual diets are identical and there is no diet variation, to 1 as the variation in the diet increases.

For a given level of diet variation ( $E$ ), individuals may vary continuously along the trophic niche-axis or form discrete groups specialized in distinct resources sets (Araújo et al. 2010). These patterns of organization are known as clustering (Watts and Strogatz 1998), and can be captured with the proposed  $C_{ws}$  index, which varies from  $-1$  to  $+1$  (Araújo et al. 2008).  $C_{ws}$  will be positive and tend towards  $+1$  when diet variation is clustered, and it will be negative and tend to  $-1$  when diet variation is continuous. Combined with  $E$ , for example, if there is no diet variation, both  $E$  and  $C_{ws}$  tend to zero. If diet variation is continuous, so that individual niches overlap little with each other, then  $E$  tends to 1 and  $C_{ws}$  tends to  $-1$  (diets are overdispersed). If diet variation is discrete so that individuals form discrete dietary groups,  $E$  tends to 1 and  $C_{ws}$  tends to  $+1$  (diets are clustered). Finally, if there are specialist and generalist individuals within the population, but the diets of the specialists are ordered and predictable subsets of the generalists' diets, then  $E$  tends to 1 and  $C_{ws}$  tends to 0 because although there is a diet variation in individuals, they neither form distinct clusters nor have overdispersed diets (Araújo et al. 2010). To measure the nestedness, a property of complex networks that describes the structural links among interactive species (Atmar and Pettersson 1993) (here to investigate the

individual–resource interactions), we use the nestedness metric based on overlap and decreasing fill (NODF) index (Almeida-Neto et al. 2008). NODF tends to 100 for highly nested individual–resource matrices, that is, when the diet of specialist individuals is a perfect subset of the diet of generalist individuals and tend to zero when it shows other non-random patterns, such as clustering or overdispersed diets (Almeida-Neto et al. 2008). We use the software ANINHADO version Bangu 3.0 (Guimarães and Guimarães 2006) to calculate the NODF and to test its significance by a null distribution model, in accordance with Araújo et al. (2010). The DIETA 1.0 software was used to calculate  $E$  and  $C_{ws}$  (Araújo et al. 2008). The software DIETA1.exe, its source code, and its manual can be found in *Ecological Archives E089-115-S1*.

We estimated individual trophic specialization using the proportional similarity index ( $PS_i$ ) (Schoener 1968), which measures the diet overlap between an individual  $i$  and its population. The degree of specialization was quantified by the  $PS_i$  between the distribution of resources in the diet of each individual and the distribution of resources in the diet of the population (Bolnick et al. 2002).  $PS_i$  ranges from 0 (maximum individual specialization) to 1 (no individual specialization). The  $PS_i$  values of all individuals can be calculated and summarized as a measure of the individual specialization of the whole population, which is the average of the  $PS_i$  values (Bolnick et al. 2002; Araújo et al. 2009). Median  $PS_i$  values were interpreted as the average individual specialization of the population and were compared between the hydrological seasons using the Mann–Whitney  $U$  nonparametric test, with the significant level set at  $\alpha = 0.05$ . We calculated the  $PS_i$  of each individual in the IndSpec 1.0 software, using a quantitative matrix of items consumed by the individuals (Bolnick et al. 2002).

## Results

### Population-level variation

Differences in diet between males and females were not found (PERMANOVA –  $F = 1.66$ ;  $p = 0.06$ ); then, these data were grouped for all analyses. Stomach content analysis of immature *P. maculatus* ( $n = 54$  in the dry season,  $L_s = 4.4$ – $18.0$  cm;  $n = 40$  in the wet season,  $L_s = 3.6$ – $18.0$  cm) showed a diversified diet because the individuals consumed aquatic and terrestrial invertebrates, fish, plants, and detritus, however, most of the items were rare. During the dry season, the diet consisted mainly of fish remains and detritus ( $>44\%$  and  $>78\%$ , in occurrence and volume, respectively). On the other hand, in the wet season, we observed shifts in the use of feeding resources. Fruit/seed comprised  $>10\%$  and  $43\%$  (occurrence and volume, respectively) and the consumption of fish remains and detritus decreased to  $18\%$  in occurrence and approximately  $37\%$  in volume (Table 1). This diet shift between dry and wet seasons was captured by the PERMANOVA analysis, which showed significant differences between the two periods ( $F = 3.65$ ;  $p < 0.001$ ). Despite the differences in diet composition, the trophic niche breadth was low and similar in both seasons, with a slight increase in the dry season ( $B_{dry} = 4.52$  and  $B_{wet} = 4.04$ ).

### Individual-level variation

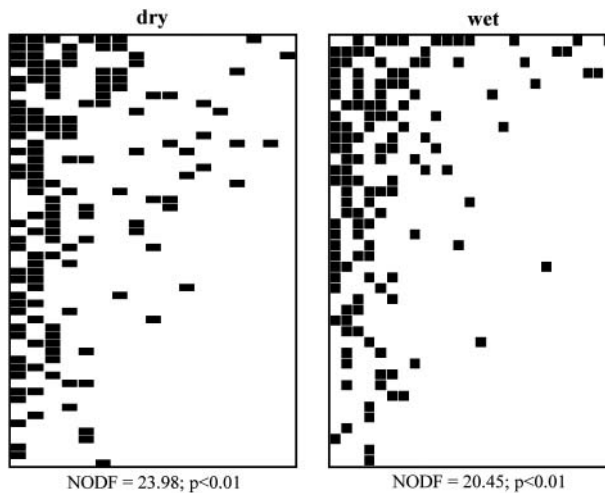
We found high values of variation among individuals' diet ( $E$ ) in both dry and wet seasons ( $E = 0.7516$  and  $E = 0.8213$ , respectively). On the other hand, the clustering degree ( $C_{ws}$ ) was low in both hydrological seasons ( $C_{ws} = -0.0030$  in the dry season and  $C_{ws} = 0.0352$  in the wet season). Similarly, low nestedness values (NODF  $\sim 20$ ) were found, but significant in both seasons ( $p < 0.05$ ; Figure 3).

Thus, the combination of the values of  $E$ ,  $C_{ws}$ , and NODF showed that there are specialist and generalist individuals within this population, with the diet of specialists forming ordered subsets of the generalist diets.

Values of the individual specialization index ( $PS_i$ ) ranged from 0.063 to 0.667 during the dry season, and from 0.036 to 0.586 in the wet season. The median individual specialization index ( $PS_i$ )

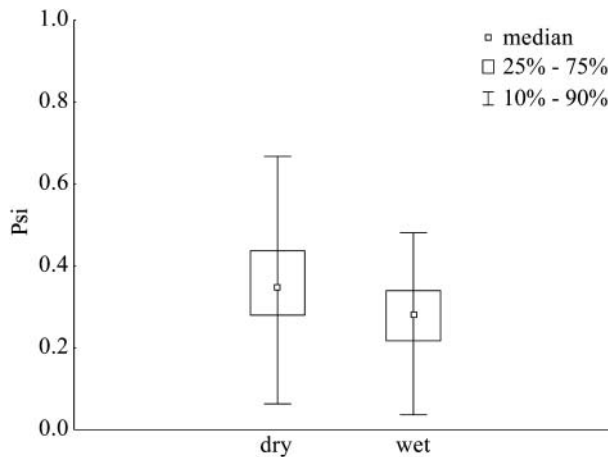
**Table 1.** Percentage of occurrence (O%) and volume (V%) of each food resource consumed by immature *Pimelodus maculatus* during the dry and wet seasons. Chacororé–Sinhá Mariana bays system, Mato Grosso state, Brazil. Bold values indicate the main food item.

Food Resources/Items	Dry		Wet	
	O%	V%	O%	V%
<b>Aquatic insects</b>				
Ceratopogonidae	1.39	0.01		
Chaoboridae	0.69	0.01	0.75	0.01
Chironomidae	15.97	0.75	9.09	0.18
Coleoptera			0.75	0.05
Diptera (others)	4.86	1.16	4.54	0.30
Ephemeroptera	0.69	0.01	0.75	0.38
Odonata			1.51	0.52
Trichoptera	2.77	0.05	0.75	0.08
<b>Terrestrial insects</b>				
Coleoptera	4.16	1.07	2.27	0.59
Diptera			0.75	0.01
Hemiptera			1.51	0.08
Hymenoptera	0.69	0.03	3.03	0.09
Isoptera			0.75	0.01
Lepidoptera			0.75	0.09
Orthoptera			0.75	0.01
Remain	9.02	4.31	15.15	8.69
<b>Aquatic invertebrates</b>				
Decapoda	2.08	6.13	0.75	1.26
Hydracarina			0.75	0.01
Nematoda	1.39	0.26	0.75	0.01
Ostracoda	2.08	0.01	2.27	0.42
<b>Terrestrial invertebrates</b>				
Annelida			0.75	0.19
Araneae			0.75	0.01
<b>Fish remains</b>	24.30	57.24	16.66	26.70
<b>High plants</b>	6.94	4.91	12.12	6.78
<b>Fruit/seeds</b>	2.77	2.81	11.36	43.40
<b>Detritus</b>	20.13	21.24	10.60	10.13
Number of stomachs		54		40



**Figure 3.** Incidence matrices describing the food items (columns) used by juvenile individuals (lines) of *Pimelodus maculatus* during dry and wet periods in Chacororé–Sinhá Mariana bays system. Black squares indicate that a given individual consumed a given food item.





**Figure 4.** Median and quartiles of the individual specialization index (PSi) of *Pimelodus maculatus* juveniles. Inner square indicates the 50th percentile (median), the box includes 50% of the data, from the 25th to the 75th percentile, and the vertical line extends to the values included between the 10th and the 90th percentile.

was statistically lower in the wet season ( $U = 761$ ;  $n = 94$ ;  $p < 0.05$ ), showing that individuals were more specialist during this season (Figure 4).

## Discussion

Seasonal change in the population diet of juveniles of *P. maculatus* was evident, with significant results. In the dry season, the high intake of detritus (more than a half of the stomachs) may be an evidence of trophic niche contraction (*sensu* Pires et al. 2013). According to Lima-Junior and Goitein (2003), the preferential food of juvenile individuals is the benthic fauna (i.e. high-quality food items), but in the absence of this resource (due to retraction of the environment during droughts), the fish may feed on detritus. In addition, the expressive consumption of fish remains, may be explained by its densification with other characiforms fish during water retraction in the bays. In this case, the seasonal increase in turbidity could facilitate the approximation to bit scales from other larger fish, since juveniles of *P. maculatus* could not intake entire preys due to morphological constrains, such as the size of the mouth. These assumptions are supported by the fact that juveniles of *P. maculatus* consumed fish scales and detritus in more than 30% of the stomach contents analyzed in this study.

During the wet season, there was a remarkable change in the population diet, when the predominant item was fruit/seed, and there was an increase in the consumption of different taxa of terrestrial and aquatic insects and invertebrates (i.e. 25 food items in the wet and 16 in the dry season), indicating a trophic niche expansion (*sensu* Pires et al. 2013). Although we found evidence of expansion in the wet season, we observed similar trophic niche breadth between dry and wet seasons, showing that this index could not be sensitive enough to detect such variation. These findings support the idea that generalist fish could change their diet according to food availability in the environment (Gerking 1994; Hahn and Fugi 2007). In floodplain systems, changes in resources are mainly due to seasonal water-level fluctuations (Hahn and Fugi 2007; Coleman et al. 2011), and several authors agree that river–floodplain ecosystems have cycles of abundant food in the wet season, and limited availability during the dry season (Prejs and Prejs 1987; Winemiller and Jepsen 1998; Agostinho et al. 2004). In this sense, river–floodplain ecosystems are subjected to changes in habitat availability which, in turn, influence fish mobility and its pursuit for food in areas not available in the dry season.

Diet variation among juveniles of *P. maculatus* was high ( $E \sim 1$ ) regardless of the hydrological season, but slightly higher during the wet season. Besides, in the Chacororé–Sinhá Mariana bays

system, as well as in other Neotropical floodplains, the diversity and availability of food resources for fish seem to be high (Corrêa et al. 2009), allowing trophic segregation among individuals by using alternative food sources, even during the dry season. Thus, the assumption that the competition for food will increase the degree of between-individual diet variation in animal populations (Svanbäck and Persson 2004; Svanbäck et al. 2011), does not seem to fit for the *P. maculatus* population from Pantanal, because food resources were abundant in this floodplain.

Matching the individual variation ( $E$ ) with the clustering degree ( $C_{ws}$ ), which was about zero in both seasons, our results indicated that although high diet variations occurred, the individuals neither formed distinct clusters (specialized in a given food resource) nor presented overdispersed diet (Araújo et al. 2010). On the other hand, despite the low values of NODF, both diets (dry and wet) were significantly nested, indicating that the juvenile population of *P. maculatus* is composed of generalist and specialist individuals, but the diet of specialists is an ordered subset of the generalist's diet. Therefore, the diets were nested in both hydrological seasons, indicating that generalist individuals interacted with a larger array of resources, whereas specialists interacted more with subsets of these generalists, than with resources of other specialists, as discussed by Kondoh et al. (2010). In a specific sense, the generalist individuals of *P. maculatus* interacted (preyed) on a broader core of resources, which was composed of 5–11 food items, such as fish remains, detritus, Chironomidae, plants, fruit/seeds, and by more rare items, such as Ephemeroptera, Odonata, Chaoboridae, and Hemiptera. Already, the more specialized individuals interacted with subgroups of this larger food spectrum, including often the most consumed items by the population (i.e. fish remains and detritus in the dry season and fruit/seeds in the wet season), besides other few food items that were frequent or rare in the diet population.

This outcome suggests the presence of asymmetric individual specialization within the population of *P. maculatus*, corroborating studies on temperate fish, that verified clustering diets for the perch *Perca fluviatilis* (Svanbäck and Eklöv 2002) and for the stickleback *Gasterosteus aculeatus* (Araújo et al. 2008). According to Araújo et al. (2008), if individuals within a population differ in their diet preferences, they might be organized into discrete groups; however, the nested pattern also indicates diet specialization (Araújo et al. 2010) since some individuals may feed on different subsets of resources. Nonetheless, Araújo et al. (2008) observed that when sticklebacks experience situations of high population density, they start to consume alternative and more abundant prey. Similar alternative consume could occur for juveniles of *P. maculatus* during the dry season in function of water-level retraction. However, this did not happen probably because of the availability of fish scales, making the diet between individuals to vary below the expected, when compared to the wet season.

The low values of individual specialization index ( $PSi$ ) showed that during the wet season, *P. maculatus* juveniles were significantly more specialist. This may be related to the fact that in the wet periods, there is a high input of allochthonous resources in the floodplain system, increasing the food supply and allowing individuals to forage at different ranges of the population's trophic niche, with little overlap with each other. Furthermore, this increased individual specialization can be due to the spatial distribution of resources because, according to Pringle et al. (1988), in aquatic environments, resources have a patchy distribution and, therefore, are variable in time and space. During floods, large terrestrial areas are incorporated into the aquatic system, and some fish individuals can find resources often undetected by others due to greater swimming ability.

Heterogeneous food resources in the environment (Luo et al. 1996; Lehtiniemi et al. 2007) may result in temporal individual specialization in fish. Specziár (1999) showed a marked duality in the feeding strategy of *Rutilus rutilus* individuals, especially in the littoral zone (e.g. lagoons, rivers, bays, etc.), where they exhibited short-term specialization either on mollusks or filamentous algae. Sometimes, temporal individual specialization is highly stochastic (Luo et al. 1996) and the stochastic component is related to the small-scale heterogeneity in the density and taxonomic composition of the food resources (Specziár and Erős 2014). For immature *P. maculatus*, trophic differences (in both population and within-population variation) seem to have been governed by the stochastic

component, which is responsible for short-term individual specialization. Wilson and Yoshimura (1994) argue if changes in environment are stochastic, no trait is favored, being the evolution of specialist animals less probable.

In short, the pattern of resource use by the juveniles of *P. maculatus* showed that the seasonality in food supply was the main responsible driver to the degree of feeding specificity, at both the population and individual levels. Thus, changes in the diet and occurrence of individual specialization were more related to food availability than with other mechanisms. The access to larger foraging areas during the wet season by some individuals combined with individual foraging ability enabled individual specialization to this juvenile catfish. Besides providing additional support on individual specialization, especially for fish whose knowledge is still scarce, we encourage other studies to explore another aspect of individual specialization not evaluated herein, such as long-term studies and the assessment of phenotypic individual characteristics. Additionally, we suggest that future studies should use integrated methodologies (i.e. carbon and nitrogen stable isotope + stomach content analysis) to better understand individual niches.

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