

Article

Niche partitioning of two piscivorous fish species
in a river in the western Brazilian AmazonIgor David da Costa^{1,2}  & Natalia Neto dos Santos Nunes³ 

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ABSTRACT. We analyzed the seasonal variation in the diet, trophic niche breadth (Levins index), the partitioning of food resources (Pianka's symmetric index) and trophic level (weighed average of trophic level of each prey determined in FishBase and SeaLifeBase platform) of *Plagioscion squamosissimus* (Heckel, 1840) and *Hydrolycus scomberoides* (Cuvier, 1819) in the Machado River, Rondônia, Brazil. Fish samplings were conducted bimonthly from June 2013 to May 2015 in five sites, using eight sets of gillnets. The occurrence frequency and volumetric frequency were used to quantify the food items. We analyzed the stomach contents of 283 individuals, 134 of *H. scomberoides* and 149 of *P. squamosissimus*. Fish were the most consumed food item by both piscivorous species. However, *H. scomberoides* mostly ingested pelagic fish (e.g. Characiformes fishes and *Prochilodus nigricas* Spix & Agassiz, 1829), while *P. squamosissimus* mostly consumed benthic fish [e.g. *Pimelodus blochii* Valenciennes, 1840 and *Tenellus trimaculatus* (Boulenger, 1898)]. *Hydrolycus scomberoides* presented the trophic level 3.55 for both periods analyzed, while *P. squamosissimus* 4.01 in the flood period and 3.82 in the drought period. Seasonal variations in the diet of *H. scomberoides* and *P. squamosissimus* were observed (PERMANOVA). Specifically, *P. squamosissimus* consumed mainly "Siluriformes" fishes and *P. blochii* in the drought period. The trophic niche breadth of *P. squamosissimus* was greater than that of *H. scomberoides* in the flood period. The species *P. squamosissimus* and *H. scomberoides* had low (0.35) food niche overlap in both seasons analysed. The data indicated that *P. squamosissimus* has a generalist feeding habit, while *H. scomberoides* is specialized in prey selection. The overlap of food niche between the species in both periods of the hydrological cycle was low, indicating that niche partitioning was probably the main mechanism of coexistence of these species, with little relationship with variations of the hydrological cycle.

KEYWORDS. Diet, trophic niche, Machado River, seasonal variation.

RESUMO. Particionamento de nicho de duas espécies de peixes piscívoros em um rio na Amazônia Ocidental Brasileira. Nós analisamos a variação sazonal na dieta, a amplitude do nicho trófico (Índice de Levins), a partição dos recursos alimentares (Índice simétrico de Pianka) e o nível trófico (média do nível trófico de cada presa determinada pela plataforma FishBase e SeaLifeBase) de *Plagioscion squamosissimus* (Heckel, 1840) e *Hydrolycus scomberoides* (Cuvier, 1819) no rio Machado, Rondônia, Brasil. As amostragens de peixes foram realizadas bimestralmente de junho de 2013 a maio de 2015 em cinco locais, utilizando oito conjuntos de redes de emalhar. A frequência de ocorrência e a frequência volumétrica foram utilizados para quantificar os itens alimentares. Analisamos o conteúdo estomacal de 283 indivíduos, 134 de *H. scomberoides* e 149 de *P. squamosissimus*. Peixes foram o item alimentar mais consumido pelas duas espécies piscívoras. No entanto, *H. scomberoides* ingeriu principalmente peixes pelágicos (ex. peixes Characiformes e *Prochilodus nigricas* Spix & Agassiz, 1829), enquanto *P. squamosissimus* consumiu principalmente peixes bentônicos [ex. *Pimelodus blochii* Valenciennes, 1840 e *Tenellus trimaculatus* (Boulenger, 1898)]. *Hydrolycus scomberoides* apresentou nível trófico de 3,55 para ambos os períodos analisados, enquanto para *P. squamosissimus* o nível trófico foi de 4,01 no período da cheia e 3,82 no período de seca. Variações sazonais na dieta de *H. scomberoides* e *P. squamosissimus* foram observadas (PERMANOVA). Especificamente, *P. squamosissimus* consumiu principalmente peixes "Siluriformes" e *P. blochii* no período de seca. A largura do nicho trófico de *P. squamosissimus* foi maior que a de *H. scomberoides* no período da cheia. *Plagioscion squamosissimus* e *H. scomberoides* apresentaram baixa (0,35) sobreposição de nicho alimentar nas duas estações analisadas. Os dados indicaram que *P. squamosissimus* tem hábito alimentar generalista, enquanto *H. scomberoides* é especializado na seleção de presas. A sobreposição de nicho alimentar entre as espécies em ambos os períodos do ciclo hidrológico foi baixa, indicando que a partição de nicho foi provavelmente o principal mecanismo de coexistência dessas espécies, com pouca relação com as variações do ciclo hidrológico.

PALAVRAS-CHAVE. Dieta, nicho trófico, rio Machado, variação sazonal.

The Amazon basin covers approximately 6,000,000 km², discharging about 16% of the world's freshwater into the Atlantic Ocean (VENTICINQUE *et al.*, 2016; LATRUBESSE *et al.*, 2017), and have high global freshwater biodiversity (TISSEUIL *et al.*, 2013). Specifically, the fish fauna is represented by 2,257 species described (including over 1,000 endemic

species; not found anywhere else in the world). Consequently, in the Amazon basin making up approximately 15% of the described global freshwater ichthyofauna (TEDESCO *et al.*, 2017).

The theories related to species coexistence, which consequently try to explain high species diversity, mostly in

Amazonia, are based on two competing theories, Hutchinson's niche theory (HUTCHINSON, 1957) and Hubbell's neutral theory (HUBBELL, 2001). Niche theory states that guilds of competing species will diverge, leading to reduced niche overlap. The ubiquity of ecological niches provides a general explanation for the positive relationship between diversity and functioning: through competitive divergence each species only covers some part of the total niche space available in a community (TILMAN *et al.*, 1997). The neutral theory considers that groups of trophically similar species typically can occur in sympatry and compete for similar resources, because the diversity of the assemblage results from stochastic processes acting on both local and regional scales (GASTON & CHOWN, 2005).

However, MACARTHUR (1965) described that gradients of richness could be explained by two contrary patterns of niche occupation: (i) the niche expansion model, where an increase in richness is linked to the occupation of new regions of niche space (habitat dimensions and resources), which are not available or still need to be explored by more assemblages (MACARTHUR, 1965; KARR & JAMES, 1975); and (ii) the niche packing model that proposes higher diversity is associated to denser niche packing, which arises through more restricted specialization or greater overlap in resource use (KLOPFER & MACARTHUR, 1961; KARR & JAMES, 1975) that, in turn, may reflect differences in the ecological capacity of coexistence or regional differences in speciation rates (HUBBELL, 2006).

One approach for evaluating interactive processes in aquatic assemblages (ESTEVEZ & ARANHA, 1999), is the investigation of the diet of fishes (REIS & SANTOS, 2014), whose feeding habits can be influenced by environmental conditions, the biological traits of the species (ABELHA *et al.*, 2001) and spatial-temporal variations (XIMENES *et al.*, 2011). According to JUNK *et al.* (1989), the hydrological cycle plays an important role in controlling natural fluvial systems by affecting the structure of habitats and the life cycle of species. Seasonal river fluctuations unite large extensions of terrestrial environments in the fluvial system, which promotes greater availability of habitats and food (AGOSTINHO *et al.*, 2007), supports a high diversity of species with distinct morphological traits (WILLIS *et al.*, 2005), and facilitates the coexistence of species via resource partitioning (WINEMILLER *et al.*, 2000).

Piscivorous fish represent a high percentage of the total biomass of Neotropical aquatic environments (PEREIRA *et al.*, 2017). Piscivorous fish play an important role in the dynamics and structuring of fish assemblages (PETRY *et al.*, 2010), coupled with the fact that flooding affects inter- and intraspecific relationships between synoptic species (PEREIRA *et al.*, 2017). Species belonging to this guild are usually top predators and are able to sustain biodiversity and prevent strong trophic cascades (MONTEIRO & FARIA, 2016). Species with similar diets, such as piscivores, but with different feeding strategies, should behave differently in relation to the hydrological cycle and resource availability (LUZ-AGOSTINHO *et al.*, 2009).

Large piscivorous fishes show notable versatility in their feeding habits and high plasticity in feeding due to the high variation in aquatic environments of tropical regions (LOWE-McCONNELL, 1999; MOYLE & CECHE, 2004; CORREA & WINEMILLER, 2014; BARBOSA *et al.*, 2018). In several environments and biomes (HAHN *et al.*, 1999; BENNEMANN *et al.*, 2000, 2006; SANTOS *et al.*, 2016), *Plagioscion squamosissimus* (Heckel, 1840), the South American silver croaker is piscivorous (BARBOSA *et al.*, 2018) or a generalist carnivore (NEVES *et al.*, 2015). This species is a sedentary fish native to the Amazonian region (SANTOS *et al.*, 2006), a valuable resource for human consumption and recreational fishing (BARROS *et al.*, 2012) and preferentially dwells in the water column and at the bottom of rivers and lakes (TEIXEIRA & BENNEMANN, 2007). In recent studies by BARBOSA *et al.* (2018), this species consumed preferably species of the order Siluriformes. Similarly, *Hydrolycus scomberoides* (Cuvier, 1819), the dogtooth characin, is distributed throughout the Amazon basin (QUEIROZ *et al.*, 2013), has a piscivore dietary habit, consumes entire fish, but has insignificant commercial importance (SANTOS *et al.*, 2006).

Considering their ecological importance, this study aimed to evaluate piscivorous fish feeding in a stretch of the Machado River, Amazônia, comparing flood and drought periods. The questions that this survey aims to investigate are: i) The hydrological periods change the diet and trophic niche breadth of *P. squamosissimus* and *H. scomberoides* in the river? ii) There are trophic relationships (niche overlap) between fish species. Whereas water level changes, and the allochthonous and autochthonous inputs varies in their importance for fish assemblages (VAZZOLER, 1996; JUNK *et al.*, 1989, 2010), we hypothesized that the diet composition of both species of fish varies between the seasons of the hydrological cycle (flood and drought periods), in a river in southwestern Amazonia. Considering the occurrence and high abundance of both species in the Machado river, we infer that such species have specialized food habits, however, a smaller niche partitioning between *P. squamosissimus* and *H. scomberoides* occurs.

MATERIAL AND METHODS

Study area. We carried out the study in the Machado River (commonly known as Ji-Paraná River) basin, which covers 75,400 km² in the State of Rondônia, Brazil (Fig. 1).

This seventh-order river annually drains about 700 m³.s⁻¹ into the middle course of the Madeira River (KRUSCHE *et al.*, 2005). The Machado River has large individual rocks, rocky portions, as well as trunks and branches observed during the drought season with low sediment loads, typifying it as a clear-water Amazonian river (GOULDING *et al.*, 2003).

The climate of the region is characterized by temperatures that vary between 19 and 33°C and annual precipitation of around 2,500 mm (KRUSCHE *et al.*, 2005). The hydrological regime is characterized by the peak of the flood in March and the minimum level in September (COMPANHIA DE PESQUISA DE RECURSOS MINERAIS, 2012). The Machado

River runs through the Jarú Biological Reserve (ReBio Jarú, Fig. 1), which has a total area of 47,733 km² (MMA, 2010), with a preserved riparian zone covered by ombrophylous forest that is mainly open and has low floristic variations (IBGE, 1992).

Fish sampling. Samplings were performed bimonthly from June 2013 to May 2015 in five sites (Carmita, Farofa, Suretama, São Sebastião and Poção) (Fig. 1). A total of 12 samples were taken (four samples in 2013, six in 2014 and two in 2015; flood season = six samples and drought

season: six samples). Eight sets of gillnets (2 x 20 m with mesh sizes varying from 30 to 100 mm) were used. Sampling effort was standardized, and scientific fishing was carried out for 24 hours continuously at each sampling site. The gillnets reviews were carried out every three hours. Some specimens were fixed in 10% formalin and preserved in 70% ethanol. Subsequently, these specimens were deposited in the Ichthyology collection at the Universidade Federal de Rondônia (voucher: UFRO-ICT 023107) and Universidade Federal de Mato Grosso (voucher: CPUFMT 3390). License for fish collections was provided by the Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis (IBAMA # 4355-1).

Stomach content analysis. In all analyzed individuals, the standard length (L_s in cm) was measured. A total of 283 stomachs were analyzed: 134 stomachs of *H. scomberoides* and 149 of *P. squamosissimus* (Tab. I).

Fish abdominal cavities were opened and their stomachs were removed. After, the gut contents were stored in 70% alcohol, and food items were analyzed and identified to the lowest taxonomic level (HAMADA & FERREIRA-KEPPLER, 2012; HAMADA *et al.*, 2014). The occurrence frequency ($F_i\%$) and the method of volumetric frequency ($V_i\%$) were used to quantify the gut contents (HYSLOP, 1980). The occurrence frequency method, whereby the number of stomachs in which a particular item is found, is expressed as the percentage of the total number of examined stomachs containing food. For the volumetric frequency, the volume of each item was obtained using the percentage in relation to the total value of all gut contents. The volume was obtained using a gridded dish, and cubic millimeters were converted to milliliter (HELLAWELL & ABEL, 1971). This value was combined in a feeding index (IA_i) proposed by KAWAKAMI & VAZZOLER (1980). The index is given by the equation $IA_i = (F_i * V_i) / \sum F_i * V_i * 100$, where $i = 1$ to number of food items; F_i = Frequency of occurrence of food item i ; and V_i = Volume of food item i . Food items were grouped according to type (animal or plant) and origin (autochthonous or allochthonous). Fullness index (FI) was determined according to HAHN *et al.* (1999) and gut contents were coded as follows: 0 (empty), 1 (volume < 25%), 2 (25% < volume < 75%) and 3 (75% < volume < 100%).

Data analysis. A Permutational Multivariate Analysis of Variance (two-way PERMANOVA – ANDERSON *et al.*, 2005) was performed to test the null hypothesis that diet composition of *P. squamosissimus* and *H. scomberoides* does not differ between hydrological periods. Was applied to a matrix of food items of individual fish, with volume values log transformed. The significance of multivariate dispersion generated by PERMANOVA was assessed using a Monte Carlo test with 9999 permutations, followed by a post hoc pair wise comparison between hydrological seasons.

A non-metric multidimensional scaling analysis (nMDS) was used to examine multidimensional temporal variation in diet using the total volume of each item. The dissimilarity matrix used in the ordination was built using the Bray-Curtis index.

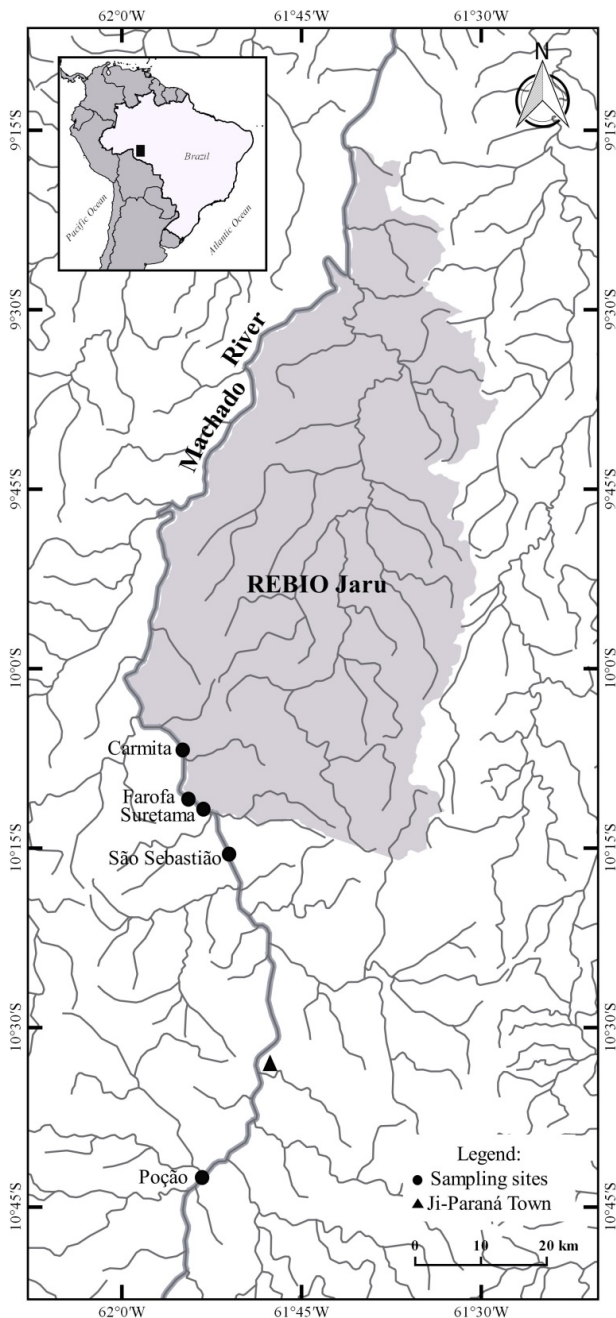


Fig. 1. Sampling site (black circles), Ji-Paraná Town (black triangle) and Machado River basin, Madeira River drainage, Brazil. Samples taken in June 2013 to May 2015. REBIO Jarú = Jarú Biological Reserve; Rondônia State = black square

Tab. I. Sampling site, abundance (N) and standard length ($L_{S, \text{mean}} \pm$ standard deviation) of *Hydrolycus scomberoides* (Cuvier, 1819) and *Plagiosciurus squamosissimus* (Heckel, 1840) at flood and drought periods of Machado River, Brazil (June 2013 to March 2015).

Site	<i>H. scomberoides</i>				<i>P. squamosissimus</i>			
	Flood		Drought		Flood		Drought	
	N	L_s	N	L_s	N	L_s	N	L_s
Carmita	8	57.5 ± 7.4	10	59.6 ± 5.0	8	49.4 ± 4.9	13	47.2 ± 6.8
Farofa	7	49.7 ± 3.9	13	57.2 ± 4.2	22	46.3 ± 3.8	10	47.0 ± 2.2
Suretama	9	50.2 ± 2.9	14	58.6 ± 4.8	19	48.5 ± 5.1	8	48.1 ± 1.8
São Sebastião	26	58.7 ± 3.4	32	51.3 ± 4.9	12	49.3 ± 2.1	40	46.9 ± 1.2
Poção	5	57.9 ± 2.4	10	56.2 ± 4.0	12	48.9 ± 1.6	5	47.3 ± 3.2

To estimate the trophic niche breadth, we used the standardized Levins index (Ba): $Ba = [(\sum_j P_{2ij})]^{-1}(n-1)-1$, where Ba = niche breadth, P_{ij} = proportion of item j in the diet of species i, and n = total number of items (KREBS, 1998). This index ranges from zero (when the species consumes only one type of item) to one (when the species consumes all items in equal proportions). Species feeding overlap in each period was calculated using Pianka's symmetric index (PIANKA, 1974) that varies in a scale from 0 to 1, with 1 indicating complete overlap. Overlap values were arbitrarily set at the following levels: high (>0.6), intermediate (0.4 - 0.6) or low (<0.4) (GROSSMAN, 1986). This index assumes prey to be equally available to all predators (REINTHAL, 1990).

The differences in the niche breadth between species and periods were tested using one-way analysis of variance (ANOVAs), when normality (Shapiro-Wilks test) and homoscedasticity (Levene's test) assumptions were met. The nonparametric Kruskal-Wallis test was used for data with non-normal distributions.

The trophic level (TL) was calculated using the formula $TL = 1 +$ (weighed average of TL's of each prey) (PAULY & CHRISTENSEN, 1995). Trophic level and maximum length of *P. squamosissimus* and *H. scomberoides* fish prey were determined using FishBase platform (FROESE & PAULY, 2019) and SeaLifeBase (<http://sealifebase.org>).

The niche breadth was performed using the software PAST (version 2.1.7) (HAMMER *et al.*, 2001). Statistical tests were performed using the software R (version 3.5.2) (R DEVELOPMENT CORE TEAM, 2018), with the package's vegan, MASS for ANOVA, PERMANOVA, NMDS and SPAA for niche overlap. Results were considered significant when $p \leq 0.05$.

RESULTS

Both species ingested a wide variety of food items, such as fishes, shrimps, terrestrial and aquatic insects at different life stages, and plants. *Hydrolycus scomberoides* consumed a total of 14 food items (flood season: eleven items; drought season: eight items), while *P. squamosissimus* consumed a total of ten items (flood season: ten items; drought season: eight items) (Tab. II). We highlight that *H. scomberoides*

mainly ingested pelagic fish and *P. squamosissimus* mainly ate benthic fish.

Prochilodus nigricans Spix & Agassiz, 1829 was the most important food item (high IAI) for *H. scomberoides* in the flood period, as well as Characiformes fishes and unidentified fish fragments (Tab. I; Fig. 2A). For the drought period, Characiformes fish, nematodes and terrestrial insects were the main items (high IAI) encountered in the diet of *H. scomberoides* (Tab. I; Fig. 2B). Unidentified fish fragments were the most important food item for *P. squamosissimus* in the flood period, as well as *Pimelodus blochii* Valenciennes, 1840 and Siluriformes fishes (Tab. I; Fig. 2C). In the drought period, unidentified fish fragments, Siluriformes fishes and *Tenellus trimaculatus* (Boulenger, 1898) were the most important items in the diet of *P. squamosissimus* (Tab. I; Fig. 2D).

The PERMANOVA indicated that the diet between *H. scomberoides* and *P. squamosissimus* for both periods analyzed was significantly different (pseudo-F = 2.54, $p = 0.02$) (Tab. III). "Siluriformes" (PERMANOVA, pseudo-F = 2.00; $df = 3$; $p = 0.006$) and *Pimelodus blochii* (PERMANOVA, pseudo-F = 1.77; $df = 3$; $p = 0.01$) were the food items consumed mainly by *P. squamosissimus* in the drought period.

In the NMDS analysis, clustering was observed based on the distinct use of food resources between *H. scomberoides* and *P. squamosissimus* for both seasonal periods, with a "stress" of 0.12 (Fig. 3).

Mean values for niche breadth were lower as follows: 0.181 and 0.172 for *H. scomberoides* in the flood and drought periods, respectively. For *P. squamosissimus* the mean of niche breadth was high, 0.813 and 0.632 in the flood and drought periods, respectively. The trophic niche breadth of *P. squamosissimus* was greater than that of *H. scomberoides* in the flood period (ANOVA, $F = 7.1$; $p < 0.05$; $df = 3$) (Fig. 4).

The general niche overlap between *P. squamosissimus* and *H. scomberoides* was low (0.35). There was no niche overlap between the species in the flood period (overlap = 0), whereas in the drought period it was 0.03. Considering the periods, the average overlap between the diets was low (0.10), showing a high degree of food resource partitioning (Fig. 5).

Tab. II. Trophic level (TL), occurrence frequency (Fi%), volumetric frequency (Vi%), and feeding index (IAi) for diet items from *Hydrolycus scomberoides* (Cuvier, 1819) and *Plagiosciurus squamosissimus* (Heckel, 1840) at flood and drought periods of Machado River, Brazil (June 2013 to March 2015). Allochthonous items[†]; autochthonous items[‡].

Food item	TL	<i>H. scomberoides</i>						<i>P. squamosissimus</i>					
		Flood			Drought			Flood			Drought		
		Fi%	Vi%	IAi	Fi%	Vi%	IAi	Fi%	Vi%	IAi	Fi%	Vi%	IAi
Animal origin													
Characiformes [‡]	3.2	0.371	0.057	0.385	0.286	0.259	0.501	0.111	0.041	0.033			
<i>Acestrohynchus falcatus</i> [‡]	4.2	0.057	0.037	0.038									
<i>Prochilodus nigricans</i> [‡]	2.4	0.029	0.815	0.424									
<i>Moenkhausia</i> sp. [‡]	3.2	0.029	0.004	0.002									
Siluriformes [‡]	3.2	0.057	0.008	0.008	0.143	0.074	0.072	0.111	0.077	0.061	0.176	0.300	0.358
<i>Pimelodus blochii</i> [‡]	3.2	0.029	0.020	0.011	0.071	0.111	0.054	0.074	0.152	0.080	0.176	0.013	0.016
<i>Tenellus trimaculatus</i> [‡]	2							0.111	0.077	0.061	0.118	0.140	0.111
Gymnotyformes [‡]	3.2							0.111	0.049	0.039	0.176	0.035	0.042
Fish no identified [‡]	3.2	0.200	0.029	0.107	0.071	0.037	0.018	0.185	0.483	0.639	0.176	0.345	0.412
Shrimp [‡]	2							0.111	0.067	0.053	0.059	0.022	0.009
Scales [‡]	3.2	0.086	0.009	0.013	0.071	0.037	0.018	0.111	0.046	0.037	0.059	0.002	0.001
Nematodes [‡]	2				0.214	0.111	0.161						
Aquatic insects [‡]	2							0.037	0.005	0.001			
Terrestrial insects [†]	2				0.071	0.296	0.143	0.037	0.003	0.001	0.059	0.142	0.056
Coleoptera [†]	2	0.057	0.008	0.008									
Annelida [†]	2	0.057	0.008	0.008									
Plant origin													
Seeds [†]	1	0.029	0.004	0.002									
Unidentified Material													
Detritus/mud [†]	1				0.071	0.074	0.036						

In both periods, *H. scomberoides* showed similar trophic level values (mean of $TL_{\text{flood}} = 3.55$; $TL_{\text{drought}} = 3.55$; $\chi^2 = 0.0$; $df = 1$; $p = 0.95$), which was also found for *P. squamosissimus* (mean of $TL_{\text{flood}} = 4.01$; $TL_{\text{drought}} = 3.82$; $\chi^2 = 0.0$; $df = 1$; $p = 0.99$).

DISCUSSION

In our study, *H. scomberoides* and *P. squamosissimus* consumed different food items. For each fish species analyzed, we did not observe significant differences in the items ingested between the periods. Further, the trophic level values for both species were similar between the drought and flood periods. Our results could indicate that the high TLs and the similarity between them refer to habitat use, which is used by *H. scomberoides* in the pelagic region, to capture prey, and to *P. squamosissimus* in the benthic region. According to BENNEMANN & SHIBATTA (2002), variations in the pelagic and benthic food chains and opportunistic behavior was already identified for these species in other environments. The competitive exclusion and limiting similarity are expected to favor the co-occurrence of dissimilar species by promoting the exploitation of different resources ("niche partitioning" hypothesis; PIANKA,

1974). However, microhabitat heterogeneity or resource availability can greatly influence the partitioning of resources among species (MOUQUET *et al.*, 2002). We highlight that structurally complex environments, such as the Machado River (comprising rapids, rocks, trunks, and branches from the forest margin), are stable and have resources (PELICICE *et al.*, 2005; WILLIS *et al.*, 2005), favoring the exploration of resources in a compartmentalized way.

Generalist carnivorous species has large feeding spectrum, consuming different food resources that are appropriate for its feeding behavior, digestive capacity and morphology (NEVES *et al.*, 2015). The greater consumption of pelagic fish by *H. scomberoides* can be explained by the ecomorphological traits of the species. In general, *H. scomberoides* is able to eat whole prey due their large mouth with underslung jaw (BEAUMORD, 1991; CARDOSO *et al.*, 2019), but have also been shown to capture their prey using their long canine teeth (HOWES, 1976). Due to their large and upward-oriented mouths, these species focus prey-capture at the water surface or at the limnetic zone (SAINT-PAUL *et al.*, 2000). The *H. scomberoides* is predator with surface-oriented vision that have remarkably similar morphology. The narrow head allows stereoscopic vision anteriorly, ventrally, and dorso-anteriorly (HOWES, 1976).

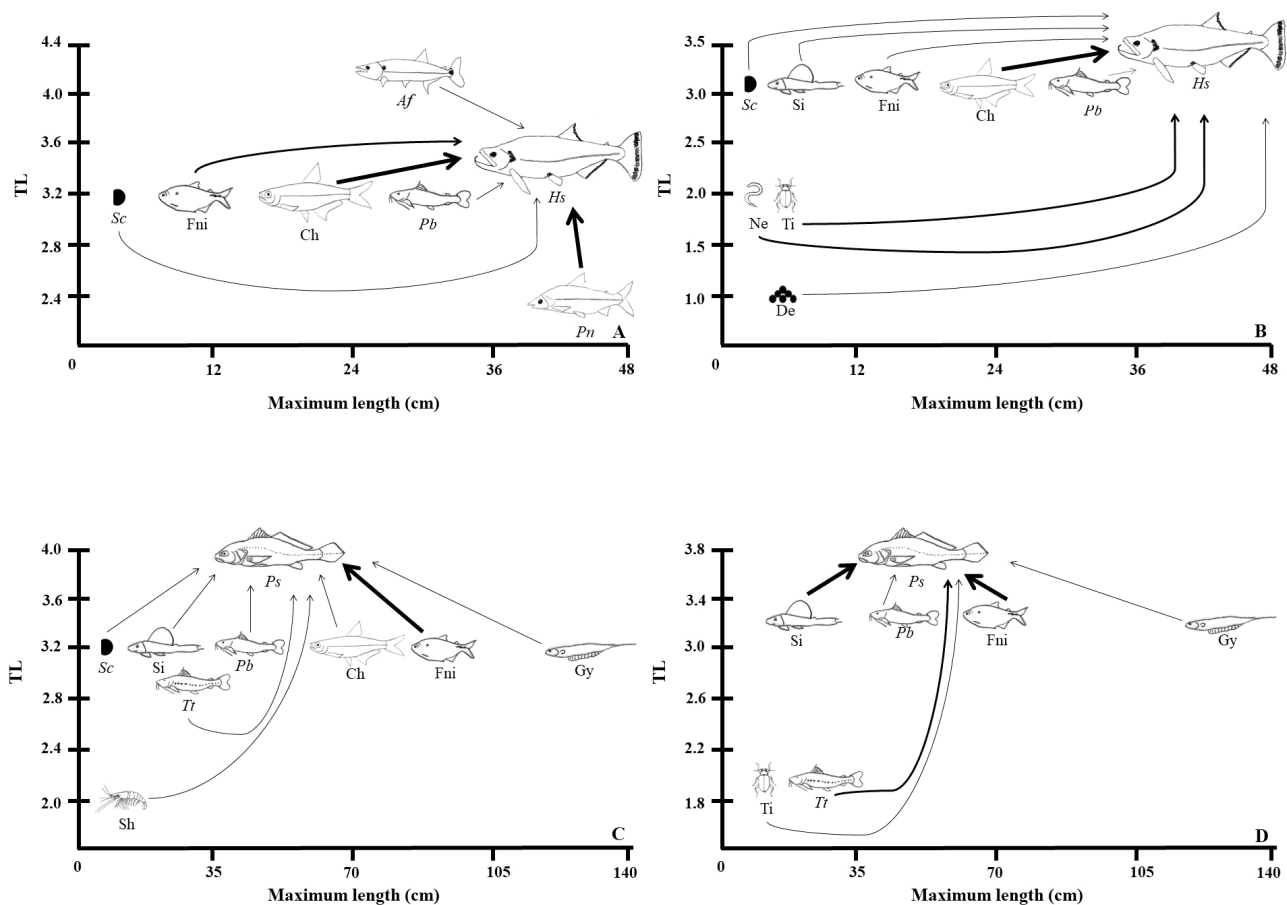


Fig. 2. Simplified food chain for *Hydrolycus scomberoides* (Cuvier, 1819) (*Hs*) in the flood (A) and drought (B), and for *Plagioscion squamosissimus* (Heckel, 1840) (*Ps*) in the flood (C) and drought (D) periods in Machado River (Brazil), June 2013 to May 2015. Arrow width illustrates importance in the diet Y-axis = trophic level (TL), X-axis: maximum length (cm). TL and maximum length are from fishbase.org and CASATTI (2003). *Ps* = *Plagioscion squamosissimus* (Heckel, 1840), *Hs* = *Hydrolycus scomberoides* (Cuvier, 1819), *Af* = *Acestrohynchus falcatus* (Bloch, 1794), *Pn* = *Prochilodus nigricas* Spix & Agassiz, 1829, *Pb* = *Pimelodus blochii* Valenciennes, 1840, *Tt* = *Tenellus trimaculatus* Boulenger, 1898, Ch = Characiformes, Si = Siluriformes, Gy = Gymnotiformes, Fni = Fish no identified, Sc = Scales, Ne = Nematoda, Sr = Shrimp, Ti = Terrestrial insect and De = Detritus.

Tab. III. Results of Two-way PERMANOVA applied to diet of *Hydrolycus scomberoides* (Cuvier, 1819) and *Plagioscion squamosissimus* (Heckel, 1840) in flood and drought periods of Machado River, Brazil (June 2013 to March 2015). F = Flood; D = Drought.

Species	Pseudo-F = 2.75; p = 0.0002
Hydrological periods	Pseudo-F = 2.54; p = 0.02
<i>H. scomberoides</i> (F) x <i>H. scomberoides</i> (D)	p = 0.172
<i>H. scomberoides</i> (F) x <i>P. squamosissimus</i> (D)	p < 0.0001
<i>H. scomberoides</i> (D) x <i>P. squamosissimus</i> (F)	p = 0.014
<i>P. squamosissimus</i> (F) x <i>H. scomberoides</i> (F)	p = 0.001
<i>P. squamosissimus</i> (D) x <i>H. scomberoides</i> (D)	p = 0.009
<i>P. squamosissimus</i> (F) x <i>P. squamosissimus</i> (D)	p = 0.786

The enlarged pectoral fins of these fish probably are used for rapid upward acceleration, followed by prey capture either by impalement on large inferior canines in the upturned mouth, or by suction caused by expansion of the buccal cavity (HOWES, 1976; GOULDING, 1980).

Given their morphology, *P. squamosissimus* is efficient swimmer and have the capacity of expanding their mouths to

ingest entire prey (RODRIGUES & MENIN, 2006; TEIXEIRA & BENNEMANN, 2007). These characteristics allow this species to exploit the most accessible and abundant feeding items, which could change seasonally from fish to shrimp, insects, among others (PRUDENTE *et al.*, 2016). The *P. squamosissimus* is a silvery fish with a large mouth and a flattened ventrum. This species often lives in turbid waters and have elaborate

sound producing and receiving systems and a well-developed lateral line (MOYLE & CECHE, 2004). Also, NICO & TAPHORN (1984) have shown that *P. squamosissimus* feeds near or on the bottom during the night.

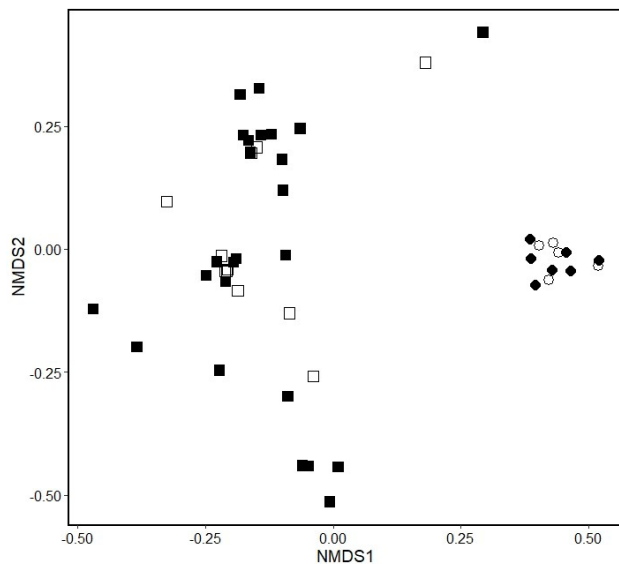


Fig. 3. Non-metric multidimensional scaling analysis (nMDS) of IAi data of *Plagioscion squamosissimus* (Heckel, 1840) and *Hydrolycus scomberoides* (Cuvier, 1819) in the flood and drought periods in the Machado River, Rondônia State, Brazil, June 2013 to May 2015. *Hydrolycus scomberoides* (Cuvier, 1819)/flood (square); *Hydrolycus scomberoides*/drought (square opened); *Plagioscion squamosissimus* (Heckel, 1840)/flood (circle) and *Plagioscion squamosissimus* (Heckel, 1840)/drought (circle opened).

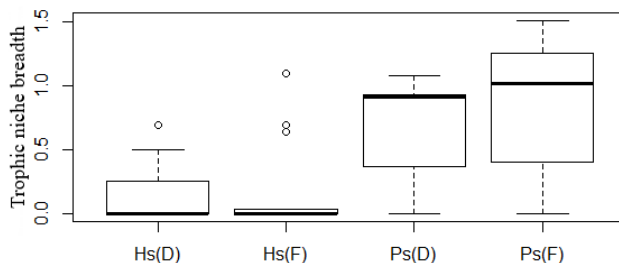


Fig. 4. Values of trophic niche breadth (mean ± standard error) of *Plagioscion squamosissimus* (Heckel, 1840) (Ps) and *Hydrolycus scomberoides* (Cuvier, 1819) (Hs) in the flood (F) and drought (D) periods in the Machado River, Rondônia State, Brazil, June 2013 to May 2015.

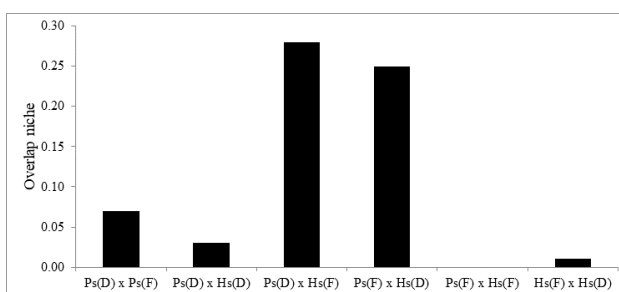


Fig. 5. Trophic niche overlap between *Plagioscion squamosissimus* (Heckel, 1840) (Ps) and *Hydrolycus scomberoides* (Cuvier, 1819) (Hs) in the flood (F) and drought (D) periods in the Machado River, Rondônia State, Brazil, June 2013 to May 2015.

Thus, fish is the main food item for *P. squamosissimus*, but with reduced fish availability this species becomes opportunistic (BENNEMANN & SHIBATTA, 2002). However, the optimal foraging theory must be considered, this predicts that optimal patterns of behavior based on the costs and benefits are associated with various strategies of species survival (BROUGHTON, 2002). According to predictions of optimal foraging theory, foragers are expected to have more specialized diets when preferred resources are abundant, and to broaden their diets during periods of food scarcity (STEPHENS & KREBS, 1986; PERRY & PIANKA, 1997). Aside from the differences between pelagic and benthic food webs, it is common to associate deforestation with increased inputs of organic matter (THOMAZ *et al.*, 2004), as well as upwelling organic matter to eutrophication (BRASIL *et al.*, 2016), which could lead to blooms of toxin-producing microalgae and force detritivory (BEZERRA *et al.*, 2018), limiting the pelagic trophic network (PAERL & PAUL, 2012). Under these circumstances, resources are available to benthic organisms and other generalist species that could drive the omnivorous fishes to benthivory (BEZERRA *et al.*, 2018). Such alternative state increases energy dissipation in the upper trophic levels (D'ALELIO *et al.*, 2016), which is also linked to omnivory (GONZÁLEZ-BERGONZONI *et al.*, 2016) and the consumption of benthos (BEZERRA *et al.*, 2018). This phenomenon can be described as “benthification” in oligotrophic waters (MAYER *et al.*, 2014), representing a sudden change from turbidity to clarity caused by invertebrate filter feeders consuming phytoplankton, a change which benefits generalist fish (KARATAYEV *et al.*, 2007). This concept could also be used in environments as the Machado River.

The relation between Amazonian ichthyofauna and the hydrological cycle has been discussed in many studies (JUNK *et al.*, 1989; FREITAS *et al.*, 2010). The period with high water is expected to be advantageous to prey species, since there is more space for dispersal and refuge (GOMES *et al.*, 2012), and flooded forest areas with tree roots, trunks, branches, rocks and holes (ARAÚJO-LIMA & GOULDING, 1998; CLARO-JR *et al.*, 2004). Drought season favors predators because of the restricted environment in the region of the river channel and low availability of refuge areas, making it easy to find prey (LUZ-AGOSTINHO *et al.*, 2009).

In our study, significant differences were not identified for the diet of *H. scomberoides* and *P. squamosissimus* between the drought and flood periods. The consumed items were compatible with ecomorphological of each species, as previously described. The only exception was the greater contribution, but not statistically significant, of terrestrial insects in the diet of *H. scomberoides* in the drought period. The increased presence of terrestrial insects in the diet of fish during a flood period has been reported in many studies (ANGERMEIER & KARR, 1983; WINEMILLER, 1990; ZAVALA-CAMIN, 1996; LOWE MCCONNELL, 1999; YAMAMOTO *et al.*, 2004), which is because these insects are carried by rain water and water courses expand along marginal areas during this period. Our results were contrary to those described in the literature and the consumption of terrestrial insects by

H. scomberoides could be related to the life cycle of the arthropods eaten by this species.

Additional studies have shown that seasonal variation in the overlap of species' niches can occur within some systems (POKHAREL *et al.*, 2015). As a result, there have been renewed efforts to explore species' trophic plasticity and the influence natural and/or human factors have on the adaptability of food web structures (CORRÊA *et al.*, 2011). Opposite to that described by POKHAREL *et al.* (2015), the overlap of food niche between *H. scomberoides* and *P. squamosissimus* in both periods of the hydrological cycle was low, showing that niche partitioning was probably the main mechanism promoting the coexistence of these species, with little relationship with variations of the hydrological cycle. According to PEREIRA *et al.* (2017), low diet overlap between species would reflect the high heterogeneity of habitats that these species are able to reach; this fact is highlighted by the consumption of and selectivity for different prey types. The niche differentiation will lead to a reduction in the niche overlap between possible competitors, reducing competition and allowing coexistence (MACARTHUR, 1958; PIANKA, 1974). These differences in niche might involve changes in some combination of strategies for habitat use, such as feeding time, energy allocation, defense, and diet restrictions, through feeding selectivity or niche retraction (WINEMILLER *et al.*, 2015).

Thus, understanding and predicting how extreme inundation and flood events (which are increasing with climate change) influence the diet of fish assemblages are of relevant importance to the development of control programs and reducing impacts on ichthyofauna. As fishing pressure is eased through management efforts to restore overexploited stocks, making it necessary to enter information about interactions between species, especially trophic interactions between prey and predators, in models that promote the prediction and management of recovered fish stocks effectively (JENNINGS & KAISER, 1998). For this, it is necessary to understand the trophic relationships between species and the factors that influence prey-predator interactions.

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