Seasonal and habitat variations in diet of the invasive driftwood catfish *Trachelyopterus galeatus* in a Neotropical river basin, Brazil

Running title: Diet of the invasive *Trachelyopterus galeatus*

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Conflict of interest

The authors declare no conflict of interest.

Summary

The characteristics of successful invaders often include generalist traits that enable adaptation to new environments through plastic responses, including their diet. The use of trophic resources of invasive driftwood catfish *Trachelyopterus galeatus* of the Upper Paraná River basin, Brazil, were studied with diet analysis and stable isotopic niche metrics based on $\delta^{15}N$ and $\delta^{13}C$ to test differences between populations in impounded and free-flowing river sections, and between wet and dry season. Stomach content analyses revealed significant differences between the populations. The diet of the free-flowing river population was macroinvertebrate dominated, with Coleoptera and Lepidoptera prominent. In the impounded population, diet was largely plant based, although Coleoptera was also prominent. Trophic niche breadth comparisons revealed a larger niche in the free-flowing river population versus the impounded population that was independent of season. Populations in both sites had dietary differences between the wet and dry season according to stomach contents analyses, although these were less less prominent according to stable isotope metrics. Therefore, the diet of this invader is relatively general and plastic, enabling their exploitation of the varying availability of food resources between free-flowing and impounded river sections, and between wet and dry season.

Key words: food resource, niche breadth, non-native species, stable isotopes, spatial variability.

Introduction

Non-native species are a major factor driving biodiversity loss, and altering ecosystem functioning and services (Dudgeon et al., 2006; Gozlan et al., 2010; Pelicice et al., 2014). Following establishment, invasive populations can become abundant, competing with and predating upon native species, and potentially leading to food web instability (Latini & Petrere, 2004; Li et al., 2015; Sagouis et al., 2015), especially in aquatic ecosystems (Gallardo et al., 2016). The establishment of populations in new habitats is facilitated when the introduced species has generalist traits that are highly plastic, as these enable rapid adaptation to the new biotic and abiotic conditions (Gozlan et al., 2010). These generalist traits include diet composition, with successful invaders often being those able to exploit a wide range of prey items in these novel environments (Gozlan et al., 2010). This ability to alter diet composition is especially important when the species is invading heavily modified waterbodies, including rivers impounded by dams. Food resources in impounded sections are usually more strongly associated with macrophytes and flooded vegetation than in the free-flowing, riverine sections, especially during the wet season (Mérona et al., 2003; Delariva et al., 2013). Indeed, seasonal hydrology is a strong driver of riverine food web structure (Douglas et al., 2005), with fish diet in dry seasons tending to be simpler with narrow diet niche. During the wet season, flooding increases feeding opportunities (Balcombe et al., 2005; Douglas et al., 2005), facilitating the establishment process.

The construction of hydropower dams produces large reservoirs that can then be utilized for aquaculture (Forneck et al., 2016; Lima Junior et al., 2018), with public policies often encouraging this, including the subsequent culture of non-native fish (Alves et al., 2018; Brito et al., 2018). A number of non-native fishes farmed in aquaculture and sport angling activities are now present within the fish faunas of the numerous hydroelectric dams in the Upper Paraná basin (Britton & Orsi, 2012). This is allied to another major introduction pathway for non-native fishes, river engineering schemes (such as hydroelectric plants and canals), that connect previously disconnected biogeographic regions, enabling the movement of species between them (Júlio Júnior et al., 2009; Panov et al., 2009; Vitule et al., 2012; Casimiro et al., 2017). An example is in the Paraná River, where the construction of the Itaipu Reservoir in 1982 flooded the natural barrier of the Sete Quedas Falls, connecting the upper and lower river basins for the first time (Abell et al., 2008; Vitule et al., 2012). This has subsequently resulted in a mass biological invasion involving over 30 fish species from the lower to the upper basin (Júlio Júnior et al., 2009).

Among the species that have invaded the Upper Paraná was the driftwood catfish *Trachelyopterus galeatus* (Linnaeus 1766), which is now relatively abundant in the Upper Paraná River floodplain (Agostinho et al., 2004; Luiz et al., 2004; Tonella et al., 2018). Native to river basins in northern South America (Reis et al., 2003) and Paraguay-Lower Paraná basin (Britski et al., 2007), the species has a lagged internal fecundation (Agostinho et al., 2007), where females may preserve the sperm received from a male for up to several months before it is actually used in egg-laying (Meisner et al., 2000). This strategy allows females to wait for optimal environmental conditions before spawning (Pusey & Stewart, 1989). The species is also considered a trophic generalist with a wide food spectrum (Hahn et al., 1997). Invasive populations are now present in both free-flowing and impounded environments within the Upper Paraná basin (Júlio Júnior et al., 2009; Tonella et al., 2018; Garcia et al., 2018). In the free-flowing sections, their floodplain environments are characterized by high levels of environmental heterogeneity (Agostinho, 1997), whereas their impounded environments are strongly influenced by hydroelectric dams (Garcia et al., 2018). The impact of *T. galeatus* on native species may extend to a larger number of species and therefore have a greater effect on the food web. In addition, high plants may have a positive effect on diet in dammed environments (Mérona et al., 2003).

The aim of this study was to test whether the diet of the invasive *T. galeatus* in the Upper Paraná basin exhibited generalist tendencies by comparing their diet composition and trophic niche size between free-flowing and impounded environments, and between the wet and dry seasons. Using stomach contents analyses, supported by stable isotope analysis, it was predicted that *T. galeatus* in the impounded environments would be more positively associated with high plants than in the lotic habitat, resulting in a narrower trophic niche, and would be more diverse in the wet season than dry season, as shown by larger trophic niches.

Materials and Methods

This study was authorised by the Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio) (survey permit SISBio/16578) and the Animal Ethics Committee of Universidade Estadual de Londrina (30992.2014.33).

Study area

The Paraná River basin is one of the most impacted in the world, mainly due to the large number of hydroelectric plants in the Brazilian stretch (Grill et al., 2015; Agostinho et al., 2016). The Upper Paraná floodplain is located between the Porto Primavera Dam and the Itaipu Reservoir, and is the last stretch that is dam-free and so free-flowing within Brazil. This has preserved its floodplain, which comprises lagoons, rivers and channels of different degrees of connectivity, with this high habitat heterogeneity supporting 211 fish species (Ota et al., 2018). Five sites were sampled in these floodplain areas, hereafter referred to as 'free-from-dam' ('FFD') sites, being two rivers (Baía River 22º43'23.16"S; 53º17'25.5"W and Ivinhema River 22º47'59.64"S; 53º32'21.3"W), one open lagoon (Garças Lagoon 22º43'27.18"S; 53º13'4.56"W), and two closed lagoons (Fechada Lagoon 22º42'37.92"S; 53º16'33.06"W and Ventura Lagoon 22º51'23.7"S; 53º36'1.02"W) (Figure 1). The Baía and Ivinhema rivers have high fish species richness and habitat heterogeneity, and have low transparency (approximately 0.7 m and 0.8 m, respectively) (Reynalte-Tataje et al., 2013).

One of the largest tributaries of the Upper Paraná River basin is the Paranapanema River that has 11 hydroelectric reservoirs constructed along its main channel. Four areas were sampled in this dammed subsystem, two rivers (Pirapozinho River 22º32'13.40"S; 52º1'52.50"W and Anhumas River 22º38'58.59"S; 51º26'48.62"W) and two open lagoons (Lagoon 1 22º38'3.26"S; 52º9'39.94"W and Lagoon 2 22º35'37.74"S; 52º9'29.81"W), in an area under the influence of the Rosana and Taquaruçu reservoirs (Figure 1). These impounded sites are referred to as 'under the influence of dams' ('DAM').

Fish sampling

Fish were sampled quarterly during the dry (from April to September) and wet (from October to March) seasons, between August 2014 and March 2016. In both FFD and DAM sites, fish were captured using gillnets (300 m length, mesh sizes ranging from 3 to 7 cm between opposite knots), which were deployed for 24 hours and inspected at 8:00 a.m., 4:00 p.m., and 10:00 p.m.

Following lifting of nets, all fish were removed, identified to species, with *T. galeatus* specimens retained. They were euthanized using an overdose of anaesthetic (clove oil) and frozen for transport to the laboratory for further analysis (Animal Ethics Committee of Universidade Estadual de Londrina, 30992.2014.33). In the laboratory, the fish were defrosted, measured (standard length, L_S, nearest mm), a sample of dorsal muscle was removed for stable isotope analysis, and then the stomach was removed and preserved in ethanol (70%). Subsequently, the stomachs were dissected, prey items removed and, under a stereo-microscope (magnification x5 to x40), the prey items were identified to lowest taxonomic level possible.

Stable isotope analysis

The fish dorsal muscle samples (FFD: n = 121 (69 in the dry and 52 in the wet season) and DAM: 62 (28 in the dry and 34 in the wet season)) were dried to constant weight at 60 ^{o}C before being ground to a fine powder, weighed and stored in tin capsules before determination of their carbon and nitrogen isotopic ratios. This determination was made on an Isotope Radio Mass Spectrometer from PDZ Europa ANCA-GSL with a PDZ Europe 20-20 interface (Sercon Ltd., Cheshire, UK) at the University of California, Davis Stable Isotope Facility. The values of the carbon and nitrogen isotope ratios were expressed in delta notation (δ; ‰), relative to the international standard for the carbon of the Vienna Pee Dee Belemnite (V-PDB) limestone, and the nitrogen standard was atmospheric nitrogen (*i.e.*, $\delta^{13}C$ (indicator of energy source) and $\delta^{15}N$ (indicator of trophic position)) (Grey, 2006).

As there were no stable isotope data available on the putative food resources of the fish for each site, inter-site comparisons between FFD and DAM are difficult due to the lack of standardization in the data (*i.e.*, conversion of $\delta^{15}N$ to trophic position and

$\delta^{13}C$ to corrected carbon; Jackson & Britton, 2014). Consequently, the stable isotope data were primarily used for intra-site comparisons between the wet and dry season using a suite of stable isotope metrics (Layman et al., 2007; Jackson et al., 2011). The initial metrics were the isotopic ranges of nitrogen (NR) and carbon (CR) that represent the distance between the individual fish with the highest and lowest values of $\delta^{15}N$ and $\delta^{13}C$ within the sample, thus indicate the total extent of nitrogen and carbon isotopes being utilised. Mean centroid distance (CD) was then used as a measure of trophic diversity and was calculated as the mean Euclidean distance of each fish the centroid of $\delta^{13}C$ or $\delta^{15}N$. Finally, standard ellipse areas (SEA) were used as a measure of isotopic niche size, a metric similar to trophic niche size, and were calculated in two ways. Firstly, they were determined using a Bayesian inference model to estimate the covariance matrix of the isotope data that considered data variability (caused both by natural variations and by analytical errors) more efficiently and provides a distribution of solutions rather than a single value (SEA_B). Secondly, they were calculated as sample size corrected ellipse areas (SEAc), calculated from the variance and covariance of the values of $\delta^{15}N$ and $\delta^{13}C$ and where the standard ellipses accommodate 40% of the data.

Stomach contents analyses

The analyses of stomach contents tested differences in the diet composition between wet and dry seasons within the two areas (FFD and DAM), and then between the two areas. To verify the percentage of the populations with individuals with empty stomachs, the vacuity index ($\%I_v$) was completed as the percentage of empty stomachs to the total number of stomachs analysed (Hyslop, 1980). Dietary analyses were then based on the volume of each food item (Hyslop, 1980), obtained by displacing large items in water in a graduated cylinder (0.1 ml) and small items on a millimeter plate (mm^3). The volume obtained (mm^3) was converted to millilitres when the volume was less than 0.1 ml (Hellawel & Abel, 1971). Differences in the diet composition of each population in FFD and DAM areas, and differences between the dry and wet seasons within FFD and DAM areas, were determined by permutational multivariate analysis of variance (PERMANOVA; Anderson et al., 2008), applied to a matrix of food items per analysed stomach versus the volume of the items. The Gower distance was used as a dissimilarity index, and 9999 permutations were used to test the significance of the pseudo-*F* statistic derived from PERMANOVA. Variations in diet composition were synthesized through Principal Coordinate Analysis (PCoA), on a volume data set of prey (individuals in the lines and prey in the columns). The Indicator Value Method (IndVal), based on abundance and relative frequency, was used to detect which food item differed between FFD and DAM, according to Dufrêne and Legendre (1997). The indicator value of a food item ranges from 0 to 100, and reaches its maximum value when all items occur on all sites and hydrological periods within a single group. We tested the significance of the indicator value for each item with a Monte Carlo randomization procedure with 10,000 permutations (significance level adopted was $p < 0.05$).

The trophic niche breadth was estimated for each population using the Levins' standardized niche breadth, according to $B_i = [(E_j P_{ij}^2)^{-1}-1](n-1)^{-1}$, where B_i is the Levins' standardized niche breadth; P_{ij} is the proportion of prey *j* in the diet; and n is the number of food items (Krebs, 1998). Breadth values varies from 0 to 1; higher values indicate a wider range of resource exploitation.

All statistical analyses were performed using R Core Team software. We used the SIAR (Parnnel & Jackson, 2013), SIBER (Jackson et al., 2011) and Vegan packages (The R Project for Statistical Computing, http://www.t-project.prg/: Oksanen et al., 2017).

Results

Stable isotope metrics between wet and dry seasons

Comparisons of metrics between the wet and dry seasons at both sites revealed there were only minor differences in NR, CR and SEAc, with SEA_B indicating that the probability of the isotopic niches being larger in the wet season than the dry season was not significant (Table 1). Moreover, the standard ellipse areas (as SEAc) remained in a similar position in isotopic space between the wet and dry seasons at each site (Figure 2). Whilst the stable isotope metrics indicated that FFD had higher values than DAM for NR and CR, and larger isotopic niches, these remain uncorrected due to the lack of isotopic baseline.

Stomach contents analyses

The vacuity indices indicated that values were higher in the FFD areas compared with the DAM areas; even in DAM, the minimum value was 24% (Table 2). Across the sites, the stomach contents data indicated that *T. galeatus* diet was mainly composed of high plants, insects, fish and crustaceans. In comparison to DAM, their diet in FFD had higher contributions of Coleoptera, irrespective of season, but was lower in high plants and fish. In DAM, the diet of *T. galeatus* mainly consisted of high plants and Coleoptera, with fish and crustaceans present in diet but being less prominent (Table 2).

In general, the diet of *T. galeatus* differed significantly between FFD and DAM (PERMANOVA: $F_{72;44} = 5.66$; $p < 0.01$). The ordination plot of the dietary data revealed a separation between the two environments in axis 1, with FFD being more positioned in the positive scores (Figure 3a). The food items that contributed to this differentiation were Coleoptera and Lepidoptera in FFD and high plants in DAM. In contrast to the stable isotope metrics, the PCoA indicated that the diet between dry and wet seasons differed significantly in both FFD ($F_{33;9} = 2.432$; $p = 0.02$) and DAM ($F_{37;35} = 3.042$; $p < 0.01$) (Figure 3b–c). In FFD, important food items in the dry season were Coleoptera and Lepidoptera, but these were extremely low (5.22%) and absent (0.00) respectively in the wet season (Table 2). In DAM, Coleoptera was only important in the wet season, with Crustacea being more important in the dry season (Table 2).

Across both seasons, the trophic niche breadth of *T. galeatus* was similar in FFD and in DAM (0.18 FFD vs. 0.19 DAM) (Table 2). When compared seasonally, the trophic niche was larger during the wet season in FFD (0.14 Dry vs. 0.34 Wet), with the opposite in DAM (0.28 Dry vs. 0.13 Wet) (Table 2).

Discussion

The results indicated that there was variability in the diet of *T. galeatus*, with differences apparent between the populations in the impounded (DAM) and free flowing (FFD) areas, and between wet and dry season. This variability was consistent with the hypothesis that this invader has a generalist diet that is sufficiently plastic to enable the fish to alter their feeding to exploiting different prey items as their food resource availability alters. It was also hypothesised that their diet would be more varied in the wet season than dry due to flooding providing greater feeding opportunities due to the inundation of floodplain areas and the consequent increase in production from vegetation breakdown (Britton et al., 2009). This larger trophic niche in the wet season was indeed apparent in the free flowing areas, but not the impounded areas. In the free-flowing area, the Baía and Ivinhema rivers are generally important in providing permanent water flows that support high biodiversity, with fish foraging habitat protected by riparian vegetation (Ward et al., 1999; Thomaz et al., 2007). Thus, the larger niche of *T. galeatus* in the wet season here suggests that the high habitat heterogeneity was important in supporting fish diet, with the inundation of floodplain areas being an important process. This was a contrast to the impounded areas, perhaps due to the habitat suffering from a marked decrease in nutrient input in the wet season that limited the extent of food resources available to the fish, as is often typical for impounded rivers (Agostinho et al., 1999).

Fish captured in impoundments had more full stomachs (lower vacuity indices) than those from free-flowing areas. This may be related to the more consistent reservoir levels that ensured constant presence of high plants that were then as a common food item. The diet composition data present here for *T. galeatus* revealed it was omnivorous and highly plastic in its feeding habitat, which is in agreement with other studies on the species more generally (*e.g.*, Moyle & Light, 1996; Ruesink, 2005). For example, Andrian and Barbieri (1996) revealed that *T. galeatus* diet was mainly composed of invertebrates such as Coleoptera and Hymenoptera, with fish and high plants present, similar to the results in the DAM fish. High plants were an important food item during both seasons in DAM. In FFD, the species fed mainly on insects derived from the riparian vegetation, such as Coleoptera, Lepidoptera and Orthoptera. In the Upper Paraná River floodplain, Santin et al. (2015) revealed strong ontogenetic patterns in the diet of *T. galeatus*, where larvae fed mainly on microcrustaceans and aquatic insects, but as the developed and increased in size, their diet switched to being based primarily on aquatic insects. In other studies that have been conducted in the Upper Paraná River floodplain, *T. galeatus* fed mainly on microcrustaceans, insect larvae, aquatic insects and small fish (Peretti & Andrian, 2004; Santin et al., 2015). In Central Amazonia, *T.*

galeatus diet comprises mainly of fruits, seeds and invertebrates (Claro-Jr et al., 2004), while in rivers of the Northern Pantanal, Brazil, the fish is considered as insectivorous (Ximenes et al., 2011). Elsewhere, it is considered omnivorous due to both plant and animal matter in their diet (Santos, 2005). In other Brazilian regions, the fish has also been considered as insectivorous (Gurgel et al., 2002; Oliveira et al., 2016) and carnivorous (Sousa et al., 2017). In entirety, the species is thus highly opportunistic and generalist (Ricciardi & Rasmussen, 1998), able to adapt its diet according to resource availability.

The use of stomach contents analysis and stable isotope analysis to assess the diet composition of fishes is routine, including for dietary assessments of invasive fish populations (*e.g.*, Leunda et al., 2008; Cucherousset et al., 2012; Hamidan et al., 2016). However, when the two dietary methods are used together, the results are not always congruent. For example, a study on the diet of pumpkinseed *Lepomis gibbosus* (Linnaeus 1758) using a combination of methods (data from stomach contents, stable isotopes and their trophically transmitted parasite fauna) revealed no congruence between the methods, with each one providing apparently unrelated information that provided contrasting information on the importance of the different prey items (Locke et al., 2013). Dietary changes of fish might not be reflected in the stable isotope data of their tissues for some time, with this time dependent on a rage of factors including the tissue analysed, and fish growth and metabolic rates (Winter et al., 2019). Thus, a diet change in the transition between wet and dry season might not be detected in stable isotope values of dorsal muscle for some time (e.g. > 90 days) (Sacramento et al., 2016). Indeed, differences in the results of dietary assessments are typical in studies that use both stomach contents and stable isotope analysis, with the differences usually relating to how each method works. For example, Hamidan et al. (2016) revealed that in the desert fish *Garra ghorensis* Krupp 1982, stomach contents data collected through the year was successful at detecting temporal shifts in diet, given that the method indicates the individual, ingested diet of fish over very short time frames (*e.g.*, < 24 h). Stable isotope analysis, however, in providing a much longer temporal perspective on assimilated diet, does not necessarily have the power to detect such short-term dietary changes, unless a tissue has been analysed that has a short isotopic turnover rate, such as epidermal mucus (Winter et al., 2019). The *T. galeatus* tissue used here, dorsal muscle, tends to have a slower turnover rate than mucus, although a faster rate than fin tissue and scales (Winter et al., 2019). Thus, stable isotope data using these tissues tend to be less sensitive to temporal dietary changes than stomach contents data. Consequently, the minor differences observed in the stable isotope metrics between the wet and dry here might relate to the method not being sufficiently sensitive to detect changes over this timeframe.

Field samples of the putative food resources of the fish were also not available to this study and so it could not be tested whether there were seasonal or spatial differences in the stable isotope baseline of the populations. This means that it was difficult to assess temporal and spatial patterns in stable isotope metrics, such as the size of the standard ellipse areas, as the metrics could not account for any changes in variability of the stable isotope data of the main food resources of the fish that might have been apparent (Jackson & Britton, 2014). Consequently, any inferences on dietary changes from the stable isotope data need to be interpreted cautiously.

In summary, the results indicate that *T. galeatus* is a dietary generalist whose diet composition varies over time and space, and habitat type. The data presented here suggest that the species is an unrestricted predator, *i.e.*, it consumes easy-to-catch items in its habitat (albeit resource availability was not measured here), suggesting it is highly opportunistic. There were clear dietary differences between populations in impounded and free-flowing areas of river, and differences between wet and dry season. These results indicate that when introduced into new environments, the diet plasticity of *T. galeatus* facilitates their adaptation, with this likely to be an important trait that enhances their ability establish new invasive populations.

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TABLE 1 Isotopic niche metrics of *Trachelyopterus galeatus* in free-from-dam (FFD) and damming (DAM) environments according to all data and wet and dry season, where NR = nitrogen isotopic range; CR = carbon isotopic range; CD = mean centroid distance; Prob. Wet > Dry = probability that the SEA_B obtained in wet season is greater than the SEA_B obtained in the dry season

Environment/Season		NR	CR	CD	SEAc	Prob. Wet < Dry
FFD	All	7.96	12.51	2.61	9.64	0.29
	Dry	7.65	11.92	2.46	9.00	
	Wet	6.99	10.53	2.66	10.19	
DAM	All	5.41	11.64	2.18	7.08	0.25
	Dry	4.10	11.12	1.94	6.33	

Wet	5.41	8.96	2.30	7.54

TABLE 2 Volumetric percentage of food items in the diet of *Trachelyopterus galeatus*, trophic niche breadth (B*i*), and mean standard length (± standard deviation) in free-from-dam (FFD) and damming (DAM) environments. Values in parentheses show the number of stomach contents analysed

Items	FFD			DAM		
	Dry	Wet	Total	Dry	Wet	Total
	(112)	(26)	(138)	(50)	(46)	(96)
High plants	6.58	28.26	34.84	30.45	47.79	78.24
Fish	0.77	21.87	22.64	17.81	7.41	25.22
Coleoptera	52.04	5.22	57.26	2.57	28.79	31.36

Lepidoptera	19.89	0.00	19.89	0.35	0.00	0.35
Orthoptera	8.00	2.75	10.75	3.23	1.28	4.51
Odonata	4.03	0.82	4.85	5.17	1.69	6.86
Ephemeroptera	0.00	10.93	10.93	0.00	0.00	0
Hymenoptera	0.02	0.01	0.03	3.00	0.84	3.84
Isoptera	2.32	0.00	2.32	0.00	0.00	0
Hemiptera	2.17	0.54	2.71	0.19	0.00	0.19
Homoptera	0.18	0.00	0.18	0.55	1.28	1.83
Crustacea	2.63	0.00	2.63	22.46	0.00	22.46
Gastropoda	0.38	0.00	0.38	1.89	2.37	4.26
Aranae	0.12	3.55	3.67	1.11	0.04	1.15
Algae	0.00	0.86	0.86	0.184	0.07	0.25
$\%I_v$	67.9	57.7	65.9	26.0	24.4	25.0
B*i*	0.14	0.34	0.18	0.28	0.13	0.19
Mean L_S (cm) ± S.D.	13.7 ± 2.1	12.7 ± 2.9	13.5±2.3	14.0 ± 1.1	14.1 ± 1.4	14.1 ± 1.3

List of figure captions

FIGURE 1 Study area and sampling sites in the Upper Paraná River floodplain (free from dam, FFD): 1 – Ventura Lagoon; 2 – Ivinhema River; 3 – Fechada Lagoon; 4 – Baía River; 5 – Garças Lagoon; and Lower Paranapanema (under the influence of dams, DAM): 6 – Lagoon 1; 7 – Lagoon 2; 8 – Pirapozinho River; 9 – Anhumas River; A – Porto Primavera Dam; B – Rosana Dam; C – Taquaruçu Dam; D – Capivara Dam

FIGURE 2 Stable isotope biplot of $\delta^{13}C$ and $\delta^{15}N$ data (expressed in parts per thousand) for each sampling area with the ellipses that represents the isotopic niche area (SEAc ‰^{2}) occupied by *Trachelyopterus galeatus*. (a) all seasons and all areas together; (b) free-from-dam habitat (FFD), each ellipse represent a different season; (c) damming habitat (DAM), each ellipse represent a different season. Each point is an individual fish

FIGURE 3 (a) Diet data ordination of *Trachelyopterus galeatus* based on food items volume consumed in free-from-dam (white circles, FFD) and damming (black squares, DAM) environments during dry and wet season, (b) by dry (white circles) and wet (black squares) season in FFD area, and (c) DAM area. Each point represents the stomach of one fish in each environment