

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

3

4 **Running title: Diet of the invasive *Trachelyopterus galeatus***

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38

39 **Conflict of interest**

40 The authors declare no conflict of interest.

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42

43 **Summary**

44

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

62

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

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66

67 **Introduction**

68

69 Non-native species are a major factor driving biodiversity loss, and altering ecosystem
70 functioning and services (Dudgeon et al., 2006; Gozlan et al., 2010; Pelicice et al.,
71 2014). Following establishment, invasive populations can become abundant, competing
72 with and preying upon native species, and potentially leading to food web instability
73 (Latini & Petreere, 2004; Li et al., 2015; Sagouis et al., 2015), especially in aquatic
74 ecosystems (Gallardo et al., 2016). The establishment of populations in new habitats is
75 facilitated when the introduced species has generalist traits that are highly plastic, as
76 these enable rapid adaptation to the new biotic and abiotic conditions (Gozlan et al.,
77 2010). These generalist traits include diet composition, with successful invaders often
78 being those able to exploit a wide range of prey items in these novel environments
79 (Gozlan et al., 2010). This ability to alter diet composition is especially important when
80 the species is invading heavily modified waterbodies, including rivers impounded by
81 dams. Food resources in impounded sections are usually more strongly associated with
82 macrophytes and flooded vegetation than in the free-flowing, riverine sections,
83 especially during the wet season (Mérona et al., 2003; Delariva et al., 2013). Indeed,
84 seasonal hydrology is a strong driver of riverine food web structure (Douglas et al.,
85 2005), with fish diet in dry seasons tending to be simpler with narrow diet niche. During
86 the wet season, flooding increases feeding opportunities (Balcombe et al., 2005;
87 Douglas et al., 2005), facilitating the establishment process.

88 The construction of hydropower dams produces large reservoirs that can then be
89 utilized for aquaculture (Forneck et al., 2016; Lima Junior et al., 2018), with public
90 policies often encouraging this, including the subsequent culture of non-native fish
91 (Alves et al., 2018; Brito et al., 2018). A number of non-native fishes farmed in

92 aquaculture and sport angling activities are now present within the fish faunas of the
93 numerous hydroelectric dams in the Upper Paraná basin (Britton & Orsi, 2012). This is
94 allied to another major introduction pathway for non-native fishes, river engineering
95 schemes (such as hydroelectric plants and canals), that connect previously disconnected
96 biogeographic regions, enabling the movement of species between them (Júlio Júnior et
97 al., 2009; Panov et al., 2009; Vitule et al., 2012; Casimiro et al., 2017). An example is
98 in the Paraná River, where the construction of the Itaipu Reservoir in 1982 flooded the
99 natural barrier of the Sete Quedas Falls, connecting the upper and lower river basins for
100 the first time (Abell et al., 2008; Vitule et al., 2012). This has subsequently resulted in a
101 mass biological invasion involving over 30 fish species from the lower to the upper
102 basin (Júlio Júnior et al., 2009).

103 Among the species that have invaded the Upper Paraná was the driftwood
104 catfish *Trachelyopterus galeatus* (Linnaeus 1766), which is now relatively abundant in
105 the Upper Paraná River floodplain (Agostinho et al., 2004; Luiz et al., 2004; Tonella et
106 al., 2018). Native to river basins in northern South America (Reis et al., 2003) and
107 Paraguay-Lower Paraná basin (Britski et al., 2007), the species has a lagged internal
108 fecundation (Agostinho et al., 2007), where females may preserve the sperm received
109 from a male for up to several months before it is actually used in egg-laying (Meisner et
110 al., 2000). This strategy allows females to wait for optimal environmental conditions
111 before spawning (Pusey & Stewart, 1989). The species is also considered a trophic
112 generalist with a wide food spectrum (Hahn et al., 1997). Invasive populations are now
113 present in both free-flowing and impounded environments within the Upper Paraná
114 basin (Júlio Júnior et al., 2009; Tonella et al., 2018; Garcia et al., 2018). In the free-
115 flowing sections, their floodplain environments are characterized by high levels of
116 environmental heterogeneity (Agostinho, 1997), whereas their impounded environments

117 are strongly influenced by hydroelectric dams (Garcia et al., 2018). The impact of *T.*
118 *galeatus* on native species may extend to a larger number of species and therefore have
119 a greater effect on the food web. In addition, high plants may have a positive effect on
120 diet in dammed environments (Mérona et al., 2003).

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

129

130 **Materials and Methods**

131

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

135

136 **Study area**

137 The Paraná River basin is one of the most impacted in the world, mainly due to the
138 large number of hydroelectric plants in the Brazilian stretch (Grill et al., 2015;
139 Agostinho et al., 2016). The Upper Paraná floodplain is located between the Porto
140 Primavera Dam and the Itaipu Reservoir, and is the last stretch that is dam-free and so
141 free-flowing within Brazil. This has preserved its floodplain, which comprises lagoons,

142 rivers and channels of different degrees of connectivity, with this high habitat
143 heterogeneity supporting 211 fish species (Ota et al., 2018). Five sites were sampled in
144 these floodplain areas, hereafter referred to as ‘free-from-dam’ (‘FFD’) sites, being two
145 rivers (Baía River 22°43’23.16”S; 53°17’25.5”W and Ivinhema River 22°47’59.64”S;
146 53°32’21.3”W), one open lagoon (Garças Lagoon 22°43’27.18”S; 53°13’4.56”W), and
147 two closed lagoons (Fechada Lagoon 22°42’37.92”S; 53°16’33.06”W and Ventura
148 Lagoon 22°51’23.7”S; 53°36’1.02”W) (Figure 1). The Baía and Ivinhema rivers have
149 high fish species richness and habitat heterogeneity, and have low transparency
150 (approximately 0.7 m and 0.8 m, respectively) (Reynalte-Tataje et al., 2013).

151 One of the largest tributaries of the Upper Paraná River basin is the
152 Paranapanema River that has 11 hydroelectric reservoirs constructed along its main
153 channel. Four areas were sampled in this dammed subsystem, two rivers (Pirapozinho
154 River 22°32’13.40”S; 52°1’52.50”W and Anhumas River 22°38’58.59”S;
155 51°26’48.62”W) and two open lagoons (Lagoon 1 22°38’3.26”S; 52°9’39.94”W and
156 Lagoon 2 22°35’37.74”S; 52°9’29.81”W), in an area under the influence of the Rosana
157 and Taquaruçu reservoirs (Figure 1). These impounded sites are referred to as ‘under the
158 influence of dams’ (‘DAM’).

159

160 **Fish sampling**

161 Fish were sampled quarterly during the dry (from April to September) and wet (from
162 October to March) seasons, between August 2014 and March 2016. In both FFD and
163 DAM sites, fish were captured using gillnets (300 m length, mesh sizes ranging from 3
164 to 7 cm between opposite knots), which were deployed for 24 hours and inspected at
165 8:00 a.m., 4:00 p.m., and 10:00 p.m.

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

175

176 **Stable isotope analysis**

177 The fish dorsal muscle samples (FFD: n = 121 (69 in the dry and 52 in the wet season)
178 and DAM: 62 (28 in the dry and 34 in the wet season)) were dried to constant weight at
179 60 °C before being ground to a fine powder, weighed and stored in tin capsules before
180 determination of their carbon and nitrogen isotopic ratios. This determination was made
181 on an Isotope Radio Mass Spectrometer from PDZ Europa ANCA-GSL with a PDZ
182 Europe 20-20 interface (Sercon Ltd., Cheshire, UK) at the University of California,
183 Davis Stable Isotope Facility. The values of the carbon and nitrogen isotope ratios were
184 expressed in delta notation (δ ; ‰), relative to the international standard for the carbon
185 of the Vienna Pee Dee Belemnite (V-PDB) limestone, and the nitrogen standard was
186 atmospheric nitrogen (*i.e.*, $\delta^{13}\text{C}$ (indicator of energy source) and $\delta^{15}\text{N}$ (indicator of
187 trophic position)) (Grey, 2006).

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

191 $\delta^{13}\text{C}$ to corrected carbon; Jackson & Britton, 2014). Consequently, the stable isotope
192 data were primarily used for intra-site comparisons between the wet and dry season
193 using a suite of stable isotope metrics (Layman et al., 2007; Jackson et al., 2011). The
194 initial metrics were the isotopic ranges of nitrogen (NR) and carbon (CR) that represent
195 the distance between the individual fish with the highest and lowest values of $\delta^{15}\text{N}$ and
196 $\delta^{13}\text{C}$ within the sample, thus indicate the total extent of nitrogen and carbon isotopes
197 being utilised. Mean centroid distance (CD) was then used as a measure of trophic
198 diversity and was calculated as the mean Euclidean distance of each fish the centroid of
199 $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$. Finally, standard ellipse areas (SEA) were used as a measure of isotopic
200 niche size, a metric similar to trophic niche size, and were calculated in two ways.
201 Firstly, they were determined using a Bayesian inference model to estimate the
202 covariance matrix of the isotope data that considered data variability (caused both by
203 natural variations and by analytical errors) more efficiently and provides a distribution
204 of solutions rather than a single value (SEA_B). Secondly, they were calculated as sample
205 size corrected ellipse areas (SEA_c), calculated from the variance and covariance of the
206 values of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ and where the standard ellipses accommodate 40% of the data.

207

208 **Stomach contents analyses**

209 The analyses of stomach contents tested differences in the diet composition between wet
210 and dry seasons within the two areas (FFD and DAM), and then between the two areas.
211 To verify the percentage of the populations with individuals with empty stomachs, the
212 vacuity index ($\%I_v$) was completed as the percentage of empty stomachs to the total
213 number of stomachs analysed (Hyslop, 1980). Dietary analyses were then based on the
214 volume of each food item (Hyslop, 1980), obtained by displacing large items in water in
215 a graduated cylinder (0.1 ml) and small items on a millimeter plate (mm^3). The volume

216 obtained (mm^3) was converted to millilitres when the volume was less than 0.1 ml
217 (Hellawel & Abel, 1971). Differences in the diet composition of each population in FFD
218 and DAM areas, and differences between the dry and wet seasons within FFD and
219 DAM areas, were determined by permutational multivariate analysis of variance
220 (PERMANOVA; Anderson et al., 2008), applied to a matrix of food items per analysed
221 stomach versus the volume of the items. The Gower distance was used as a dissimilarity
222 index, and 9999 permutations were used to test the significance of the pseudo- F statistic
223 derived from PERMANOVA. Variations in diet composition were synthesized through
224 Principal Coordinate Analysis (PCoA), on a volume data set of prey (individuals in the
225 lines and prey in the columns). The Indicator Value Method (IndVal), based on
226 abundance and relative frequency, was used to detect which food item differed between
227 FFD and DAM, according to Dufrêne and Legendre (1997). The indicator value of a
228 food item ranges from 0 to 100, and reaches its maximum value when all items occur on
229 all sites and hydrological periods within a single group. We tested the significance of
230 the indicator value for each item with a Monte Carlo randomization procedure with
231 10,000 permutations (significance level adopted was $p < 0.05$).

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

237 All statistical analyses were performed using R Core Team software. We used
238 the SIAR (Parnnel & Jackson, 2013), SIBER (Jackson et al., 2011) and Vegan packages
239 (The R Project for Statistical Computing, <http://www.t-project.prg/>: Oksanen et al.,
240 2017).

241

242 **Results**

243

244 **Stable isotope metrics between wet and dry seasons**

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

253

254 **Stomach contents analyses**

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

262 In general, the diet of *T. galeatus* differed significantly between FFD and DAM
263 (PERMANOVA: $F_{72;44} = 5.66$; $p < 0.01$). The ordination plot of the dietary data
264 revealed a separation between the two environments in axis 1, with FFD being more
265 positioned in the positive scores (Figure 3a). The food items that contributed to this

266 differentiation were Coleoptera and Lepidoptera in FFD and high plants in DAM. In
267 contrast to the stable isotope metrics, the PCoA indicated that the diet between dry and
268 wet seasons differed significantly in both FFD ($F_{33;9} = 2.432$; $p = 0.02$) and DAM ($F_{37;35}$
269 $= 3.042$; $p < 0.01$) (Figure 3b–c). In FFD, important food items in the dry season were
270 Coleoptera and Lepidoptera, but these were extremely low (5.22%) and absent (0.00)
271 respectively in the wet season (Table 2). In DAM, Coleoptera was only important in the
272 wet season, with Crustacea being more important in the dry season (Table 2).

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

277

278 **Discussion**

279

280 The results indicated that there was variability in the diet of *T. galeatus*, with
281 differences apparent between the populations in the impounded (DAM) and free
282 flowing (FFD) areas, and between wet and dry season. This variability was consistent
283 with the hypothesis that this invader has a generalist diet that is sufficiently plastic to
284 enable the fish to alter their feeding to exploiting different prey items as their food
285 resource availability alters. It was also hypothesised that their diet would be more varied
286 in the wet season than dry due to flooding providing greater feeding opportunities due
287 to the inundation of floodplain areas and the consequent increase in production from
288 vegetation breakdown (Britton et al., 2009). This larger trophic niche in the wet season
289 was indeed apparent in the free flowing areas, but not the impounded areas. In the free-
290 flowing area, the Baía and Ivinhema rivers are generally important in providing

291 permanent water flows that support high biodiversity, with fish foraging habitat
292 protected by riparian vegetation (Ward et al., 1999; Thomaz et al., 2007). Thus, the
293 larger niche of *T. galeatus* in the wet season here suggests that the high habitat
294 heterogeneity was important in supporting fish diet, with the inundation of floodplain
295 areas being an important process. This was a contrast to the impounded areas, perhaps
296 due to the habitat suffering from a marked decrease in nutrient input in the wet season
297 that limited the extent of food resources available to the fish, as is often typical for
298 impounded rivers (Agostinho et al., 1999).

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

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

324 The use of stomach contents analysis and stable isotope analysis to assess the
325 diet composition of fishes is routine, including for dietary assessments of invasive fish
326 populations (e.g., Leunda et al., 2008; Cucherousset et al., 2012; Hamidan et al., 2016).
327 However, when the two dietary methods are used together, the results are not always
328 congruent. For example, a study on the diet of pumpkinseed *Lepomis gibbosus*
329 (Linnaeus 1758) using a combination of methods (data from stomach contents, stable
330 isotopes and their trophically transmitted parasite fauna) revealed no congruence
331 between the methods, with each one providing apparently unrelated information that
332 provided contrasting information on the importance of the different prey items (Locke et
333 al., 2013). Dietary changes of fish might not be reflected in the stable isotope data of
334 their tissues for some time, with this time dependent on a range of factors including the
335 tissue analysed, and fish growth and metabolic rates (Winter et al., 2019). Thus, a diet
336 change in the transition between wet and dry season might not be detected in stable
337 isotope values of dorsal muscle for some time (e.g. > 90 days) (Sacramento et al.,
338 2016). Indeed, differences in the results of dietary assessments are typical in studies that
339 use both stomach contents and stable isotope analysis, with the differences usually
340 relating to how each method works. For example, Hamidan et al. (2016) revealed that in

341 the desert fish *Garra ghorensis* Krupp 1982, stomach contents data collected through
342 the year was successful at detecting temporal shifts in diet, given that the method
343 indicates the individual, ingested diet of fish over very short time frames (*e.g.*, < 24 h).
344 Stable isotope analysis, however, in providing a much longer temporal perspective on
345 assimilated diet, does not necessarily have the power to detect such short-term dietary
346 changes, unless a tissue has been analysed that has a short isotopic turnover rate, such as
347 epidermal mucus (Winter et al., 2019). The *T. galeatus* tissue used here, dorsal muscle,
348 tends to have a slower turnover rate than mucus, although a faster rate than fin tissue
349 and scales (Winter et al., 2019). Thus, stable isotope data using these tissues tend to be
350 less sensitive to temporal dietary changes than stomach contents data. Consequently, the
351 minor differences observed in the stable isotope metrics between the wet and dry here
352 might relate to the method not being sufficiently sensitive to detect changes over this
353 timeframe.

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

362 In summary, the results indicate that *T. galeatus* is a dietary generalist whose
363 diet composition varies over time and space, and habitat type. The data presented here
364 suggest that the species is an unrestricted predator, *i.e.*, it consumes easy-to-catch items
365 in its habitat (albeit resource availability was not measured here), suggesting it is highly

366 opportunistic. There were clear dietary differences between populations in impounded
367 and free-flowing areas of river, and differences between wet and dry season. These
368 results indicate that when introduced into new environments, the diet plasticity of *T.*
369 *galeatus* facilitates their adaptation, with this likely to be an important trait that
370 enhances their ability establish new invasive populations.

371

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

Environment/Season		NR	CR	CD	SEAc	Prob. Wet < Dry
All		7.96	12.51	2.61	9.64	0.29
FFD	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

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618 TABLE 2 Volumetric percentage of food items in the diet of *Trachelyopterus galeatus*,
 619 trophic niche breadth (B_i), and mean standard length (\pm standard deviation) in free-
 620 from-dam (FFD) and damming (DAM) environments. Values in parentheses show the
 621 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
<hr/> <i>%I_v</i>	<hr/> 67.9	<hr/> 57.7	<hr/> 65.9	<hr/> 26.0	<hr/> 24.4	<hr/> 25.0
<hr/> <i>Bi</i>	<hr/> 0.14	<hr/> 0.34	<hr/> 0.18	<hr/> 0.28	<hr/> 0.13	<hr/> 0.19
<hr/> Mean <i>L_S</i> (cm) ±	<hr/> 13.7 ±	<hr/> 12.7 ±	<hr/> 13.5±2.3	<hr/> 14.0 ±	<hr/> 14.1 ±	<hr/> 14.1 ±
<hr/> S.D.	<hr/> 2.1	<hr/> 2.9		<hr/> 1.1	<hr/> 1.4	<hr/> 1.3

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645 List of figure captions

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

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653 FIGURE 2 Stable isotope biplot of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ data (expressed in parts per thousand)
654 for each sampling area with the ellipses that represents the isotopic niche area (SEAc
655 $\%o^2$) occupied by *Trachelyopterus galeatus*. (a) all seasons and all areas together; (b)

656 free-from-dam habitat (FFD), each ellipse represent a different season; (c) damming
657 habitat (DAM), each ellipse represent a different season. Each point is an individual fish
658

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