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Article

Diet and resource sharing by two Pimelodidae species in a Southeastern Brazilian reservoir

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Abstract: Fish can vary their diet and feeding dynamics according to biotic and abiotic factors. There is insufficient knowledge regarding these factors in reservoirs, which limits the management of these areas. The aim of this study was to determine the diet of two related and most collected fish species, verify the influence of biotic and abiotic factors on their diet, and also verify the existence of resource sharing by them in an upstream Brazilian reservoir. Fish abundance in the reservoir was calculated and data were provided by 176 specimens of *Iheringichthys labrosus* (Lütken, 1874) and 255 specimens of *Pimelodus maculatus* Lacépède, 1803 collected in Camargos reservoir, MG, Brazil. Stomach contents were analysed through the frequency of occurrence and volumetric methods. PERMANOVA analysis was done to evaluate the influence of biotic (Species and Size class) and abiotic factors (Season and Site) on the diets. The Alimentary Index (AI) and feeding overlap Index (Pianka) were also estimated. A NMDS analysis was conducted to visualize the food categories responsible for interspecific difference. The ingested items were grouped into 18 categories, of which 17 were found in both species. Feeding resources were significantly related to the biotic (Species: Pseudo F = 2.583, P = 0.001; Size Class: Pseudo F = 1.646, P = 0.001) and abiotic (Season: Pseudo F = 2.458, P = 0.006) factors. *I. labrosus* showed an invertivorous diet while *P. maculatus* an omnivorous diet and both species were not exclusively benthophagus as typically reported. Food overlap occurred intraspecifically and interspecifically (Pianka 0.61 to 0.97 and 0.61 to 0.66, respectively) and overlap also occurred in three of the four analysed seasons (Pianka 0.66 to 0.91). The diet overlap found between two of the most fished species and the low fish productivity may indicate the limitation of resources in this reservoir and should be considered for management of this area.
Keywords: *Feeding ecology, Iheringichthys labrosus, Pimelodus maculatus, Rio Grande Basin, upstream reservoir.*

Alimentação e compartilhamento de recursos por duas espécies de Pimelodidae em um reservatório do sudeste brasileiro

Resumo: Os peixes podem variar suas dietas e dinâmicas alimentares de acordo com fatores bióticos e abióticos. O conhecimento insuficiente desses fatores em reservatórios limita o manejo dessas áreas. O objetivo deste estudo foi determinar a dieta de duas espécies de peixes aparentados e mais coletados; verificar a influência de fatores bióticos e abióticos na dieta, e também verificar a existência da partilha de recursos entre essas espécies em um reservatório brasileiro de cabeceira. A abundância de peixes foi calculada e dados foram fornecidos por 176 espécimes de *Iheringichthys labrosus* (Lütken, 1874) e 255 espécimes de *Pimelodus maculatus* Lacépède, 1803 coletados no reservatório de Camargos, MG, Brasil. O conteúdo estomacal foi analisado pelos métodos de frequência de ocorrência e volumétrico. A análise de PERMANOVA foi realizada para avaliar a influência de fatores bióticos (Espécies e Classe de tamanho) e abióticos (Estação e Local) nas dietas. O Índice Alimentar (IA) e o Índice de sobreposição alimentar (Pianka) também foram estimados. Uma análise de NMDS foi conduzida

para visualizar as categorias alimentares responsáveis pela diferença interespecífica. Os itens ingeridos foram agrupados em 18 categorias, das quais 17 foram encontradas em ambas as espécies. Os recursos alimentares foram significativamente relacionados aos fatores bióticos (Espécies: Pseudo F = 2.583, P = 0.001; Classe de tamanho: Pseudo F = 1.646, P = 0.001) e abióticos (Estação: Pseudo F = 2.458, P = 0.006). *I. labrosus* mostrou uma dieta invertívora e *P. maculatus* uma dieta onívora e ambas as espécies não foram exclusivamente bentófagas como normalmente descritas. A sobreposição alimentar ocorreu intraespecífica e interespecífica (Pianka 0,61 a 0,97 e 0,61 a 0,66, respectivamente) e a sobreposição também ocorreu em três das quatro estações analisadas (Pianka 0,66 a 0,91). A sobreposição de dieta encontrada entre duas das espécies mais pescadas e a baixa produtividade pesqueira podem indicar a limitação de recursos nesse reservatório e devem ser consideradas para o manejo dessa área.
Palavras-chave: *Ecologia alimentar, Iheringichthys labrosus, Pimelodus maculatus, Bacia do Rio Grande, reservatório de cabeceira.*

Introduction

Fish ecology studies provide information on species biology and the dynamics of aquatic ecosystems. This in turn contributes to the development of measures for the conservation and management of fishery resources (Braga et al. 2012, Martins et al. 2017). Fish present different adaptations in their feeding habits, usually associated with spatial and seasonal changes in food availability (Wooton 1992). Thus, it is necessary to consider the influence of biotic and abiotic factors for a more accurate evaluation of their trophic ecology (Prejs & Colomine 1981, Vitule et al. 2008). The role of biotic and abiotic factors structuring freshwater fish communities was demonstrated by Magnan et al. (1994) and Jackson et al. (2001). Magnan et al. (1994) also reported the importance of works that simultaneously analyse the biotic, abiotic and spatial factors to determine the resource use by a species. In addition, resource partitioning regulates the biomass and the functioning of the Neotropical ichthyofauna (Abilhoa et al. 2016) and its study contributes to a better understanding of how species interact (Ross 1986).

The growing number of hydroelectric plants built in Brazil since the 1950s has made necessary to study the ichthyofauna in reservoirs. However, the dispersed and fragmented nature of these studies in time and space (Agostinho et al. 2007, Agostinho et al. 2016) compromises the correct management of reservoirs, especially with the growing demand for its multiple uses (Tundisi & Matsumura-Tundisi 2003).

The influence of biotic and abiotic factors on food resources was studied in some Brazilian reservoirs (Arcifa et al. 1992, Araújo et al. 2005, Pamplin et al. 2006). However, according to Araújo-Lima et al. (1995), trophic structure trends in reservoirs are associated to the characteristics of each reservoir. Food resource partitioning by related fish species has already been studied in Brazilian natural environments (Bonato & Fialho 2014, Abilhoa et al. 2016) and reservoirs (Arcifa et al. 1991, Albrecht et al. 2009). However, studies on the long-term consequences of impoundment are necessary to establish feeding ecology patterns in reservoirs (Luz-Agostinho et al. 2006, Hahn & Fugi 2007).

Both *Iheringichthys labrosus* (Lütken, 1874) and *Pimelodus maculatus* Lacépède, 1803 can be found among the native species of the Grande River. They belong to the order Siluriformes, family Pimelodidae, have common anatomical characteristics described by Lundberg & Littmann (2003) that are generally associated with benthic foraging habits (Nomura et al. 1972, Fugi et al. 1996, Abes et al. 2001, Fugi et al. 2001). *I. labrosus* has been classified as omnivorous, invertivorous or insectivorous species (Manetta et al. 2003, Luz-Agostinho et al. 2006, Fagundes et al. 2008, Ribeiro et al. 2014) and there is little information on its interaction with other species (Masdeu et al. 2011). *P. maculatus* is usually classified as an (opportunistic) omnivorous species (Basile-Martins et al. 1986, Silva et al. 2007) with tendency towards piscivory in rivers (Andrade & Braga 2005) or insectivory in reservoirs (Luz-Agostinho et al. 2006).

In the ichthyofauna surveys conducted between 1991 and 1995 in the Camargos reservoir, *I. labrosus* and *P. maculatus* were among the most collected species. In light of the numerous Brazilian reservoirs, it is important to understand the use of the resources, their variation and interaction among the most abundant fish species. Thus, the aim of the present study was: i) to determine the diet of *I. labrosus* and *P. maculatus*; ii) verify the influence of biotic and abiotic factors and iii) verify the existence of resource sharing between species, such *I. labrosus* and *P. maculatus*, in the Camargos reservoir, MG, Brazil.

Materials and Methods

1. *Study area*

The upper Paraná River basin, located in Southeastern Brazil, is the most affected basin by dams in the country and in the Grande River, one of its largest tributaries, there are 71 hydroelectric plants in operation (IPT 2008). The Camargos hydroelectric plant, which started operating in 1960, is the most upstream of the 12 plants located along the mainstream of the Rio Grande but licensing assessment for other upstream construction was underway (IPT 2008). Camargos is a storage reservoir (average water retention time of 58.8 days) that has a dendritic aspect with an area of 74 km^2 and volume maximum of 672 x 10^6 m^3 at an altitude of 913 m above sea level. This reservoir located in the upper section of the river has characteristics typical of many old, deep reservoirs (maximum depth of 32 m) as described by Agostinho et al. (2007), such as thermal and dissolved oxygen (DO) stratification (DO ranging from 6.2 mg/l at the bottom to 13.4 mg/l in the middle of the photic zone) (SISÁGUA, 2018). Additionally, the surrounding area is dominated by degraded native pasture (grass).

The region under the influence of the Camargos reservoir has transitional features between Cwb and Cwa according to Köppen-Geiger climate classification (Antunes 1986). These features are characterised by two distinct periods: one warmer and rainy (spring and summer:

October to March) and other less warm and dry (autumn and winter: from April to September) (Guimarães et al. 2010). The reservoir is at its highest level in autumn (April, May and July) due to the accumulation of summer rains. The lowest level occurs in spring (October, November and December) along with energy production prior to the next rainy season (Fig. 1). In this reservoir, three study sites were established after local investigation and fishing pre-test considering the different distances of the dam, the physical properties of the sites and the surrounding area (Table 1, Fig. 2).

2. *Data collection and laboratory procedures*

Twenty-four monthly samples were taken between February 1991 and January 1993. They occurred alternately in the three study sites and four seasons of the year, so that each site was sampled once per season in each year of study. In each sample, approximately 1200 m^2 of gill nets (20 m long and 1.6 to 1.8 m high), having sizes of 3, 4, 5, 6, 7, 8, 10, 12, 14 and 16 cm between opposing nodes, were set up in the late afternoon and removed the next morning. When it was possible, complementary trawling was also used to capture smaller specimens (5 m long, 1.5 m high and 5 mm mesh, used for 1 h). Thirty seven species were collected and the fish abundance in the reservoir was obtained by the catch per unit effort (CPUE) in number (CPUEn = number of fishes caught /100 m^2/12h) and biomass (CPUEb = weight of fishes caught in kg/100 m^2/12h). At the end of the 24 monthly samples, 1298 individuals of *I. labrosus* and 405 of *P. maculatus* were captured.

In the field, all collected fishes were kept in ice. They were subsequently labelled, identified, measured and dissected. The stomach was removed and fixed in 4% formalin for further analysis. The specimens were selected for the current study considering the species, site, capture date and different sizes. The number of size classes was defined to avoid the low representation of the largest individuals within the population (Chipps & Garvey 2007). Thus, three size classes were defined according to their total length: A = Small (*I. labrosus* between 60.0 - 116.0 mm, n = 60 and *P. maculatus* between 49.0 - 149.6 mm, n = 94); B = Medium (*I. labrosus* between 116.1 - 186.0 mm, n = 78 and *P. maculatus* between 149.7-239.9 mm, n = 103) and C = Large (*I. labrosus* between 186, 1 - 256.0 mm, n = 30, and *P. maculatus* between 240.0 - 390.4 mm, n = 37).

In the laboratory, each selected stomach was opened in a gridded Petri dish under and then assigned its Repletion State (RS) in one of five stages: 0 = empty stomach; 1 = stomach 1% to 25% full; 2 = stomach 26% to 50% full; 3 = stomach 51% to 75% full and 4 = stomach above 76% full. Stomach contents were analysed using the volumetric (quantitative) and frequency of occurrence (qualitative) methods proposed by Hynes (1950). For this, food items of each stomach were identified and quantified under optical microscope, whose volume was fractionated within the RS value and later grouped into categories. The volumetric data tabulation provided information for the calculation of frequency of occurrence. The use of cumulative prey curves determined the number of stomachs with food to be analysed (Chipps & Garvey 2007) and adding the stomach without food, at the end 176 specimens of *I. labrosus* and 255 of *P. maculatus* were used.

3. *Data analysis*

In order to analyse the diet of the two species and the influence of biotic (Species and Size class) and abiotic factors (Season and Site) the PERMANOVA analysis (Anderson et al. 2008) was performed. In order to carry out this analysis, we first transformated the volume data to log (X + 1). After this, a similarity matrix was created using the Bray-Curtis index and the analytical design with hierarchical factors: Season (four levels, fixed); Site (three levels, random) nested in Season; Species (two levels, random) nested in Season and Site; and Size class (three levels, random) nested in Species. The relative importance of each category was presented for PERMANOVA significant results through the Alimentary Index (AIi) (Kawakami & Vazzoler 1980):

$$AI_i = \frac{F_i \times V_i}{\sum_{i=1}^{L} F_i \times V_i}$$

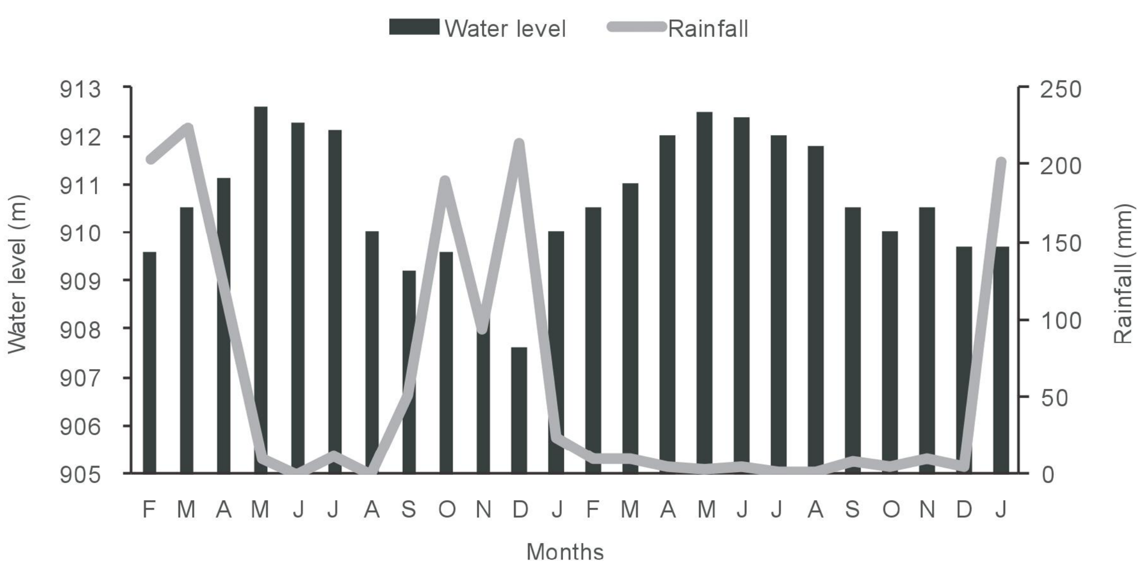

Figure 1. Rainfall and water level from February 1991 up to January 1993 at Camargos reservoir, MG, Brazil

Table 1. Site description, Camargos reservoir, MG, Brazil

Site	Distance from the dam (km)	Channel/ Margin	Maximum depth (m)	Mean depth (m)	Environment	Surrounding area
1	1	Main channel/left margin	18.6	7.4	Lentic	Degraded native pasture
2	7	Side channel/right margin	13.8	5.4	Backwater/ lentic	Group of vacation homes, few banks of aquatic plants; small riparian and semideciduous forest
3	13	Main channel/right margin	16.2	7.2	Temporally lotic	Permanent tributary; small riparian and semideciduos forest

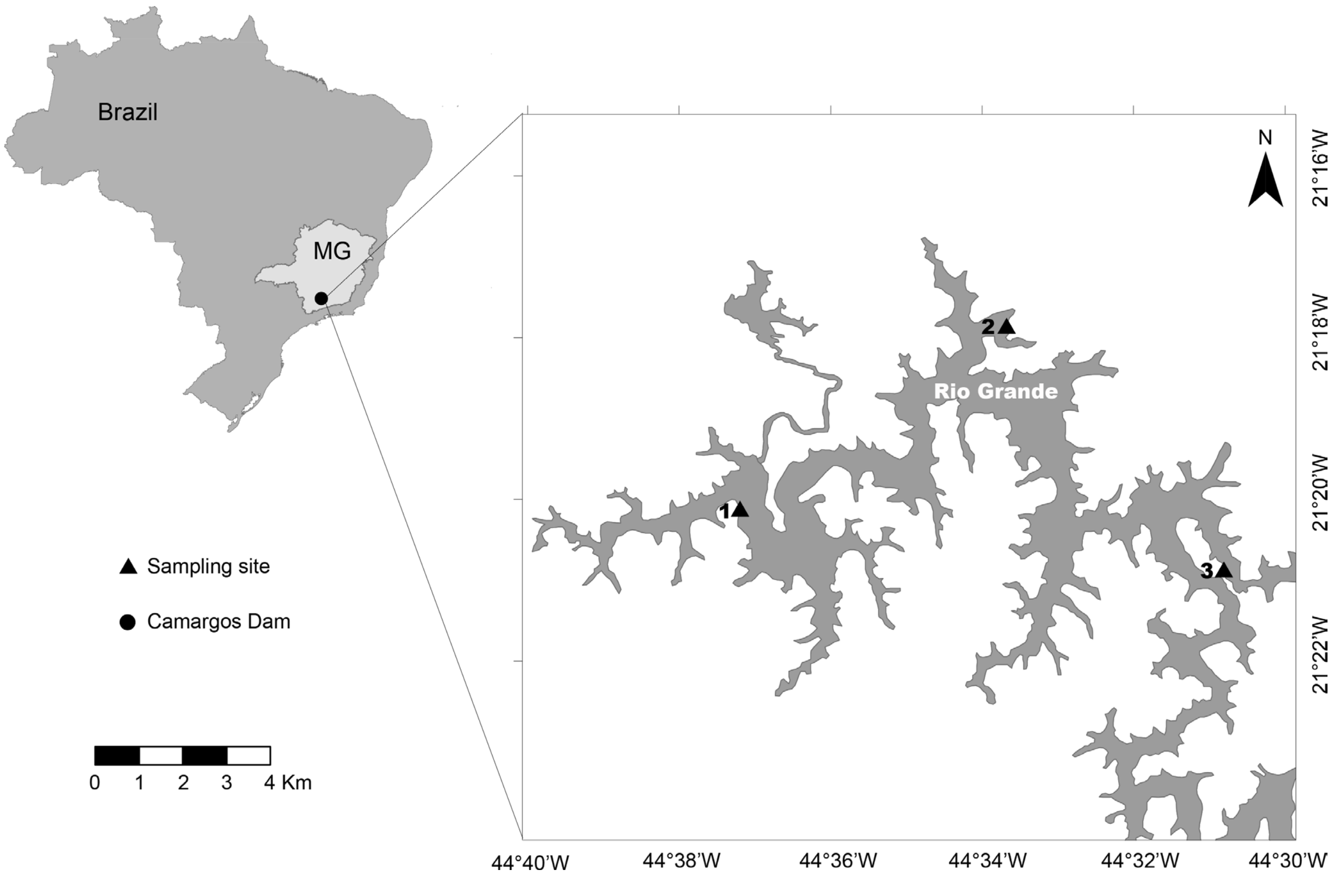

Figure 2. Map of study region showing sampling sites (1, 2 and 3), along Camargos reservoir, MG, Brazil

where i = 1, 2, 3, ... n given food category; L= number of categories; Fi = Frequency of occurrence of category i (%) and Vi = relative volume of category i (%). Resource sharing was measured by the similarity of the species diet using Pianka Index (Pianka 1974):

$$O_{jk} = \frac{\sum_{i}^{n} P_{ij} P_{ik}}{\sqrt{\sum_{i}^{n} P_{ij^2} \sum_{i}^{n} P_{ik^2}}}$$

where Ojk = Pianka overlap measure between species j and k; Pij and Pik = Proportion of resource i in a total of resources used by species j and k, respectively and n = number total of categories. The visualization of food category responsible for the interspecific difference was done through the Non-metric multidimensional scaling (NMDS) analysis (Clarke & Gorley 2006).

Results

Camargos reservoir presented mean catch per unit effort (CPUE) of 11.8 individuals/100 m^2 of gill net/12h and 0.58 kg/100 m^2 of gill net/12h. *I. labrosus* and *P. maculatus* represented the first (36.1%) and third (9.1%) species most collected with gill nets.

Food was found in 119 of the 176 stomachs (67.6%) of *I. labrosus* and in 234 of the 255 stomachs (91.8%) of *P. maculatus*. While the proportion of empty stomachs increased throughout ontogeny in *I. labrosus*, this increase was not observed in *P. maculatus* (Fig. 3). The ingested items were grouped into eighteen food categories, seventeen of which were found in both species and greater diversity of items, within the categories, was recorded for *P. maculatus* (Table 2). Influences of the biotic and abiotic factors tested through PERMANOVA (Table 3) indicated that there were differences in diet associated with species (Pseudo F = 2.583, P = 0.001), size class (Pseudo F = 1.646, P = 0.001) and season (Pseudo F = 2.458, P = 0.006).

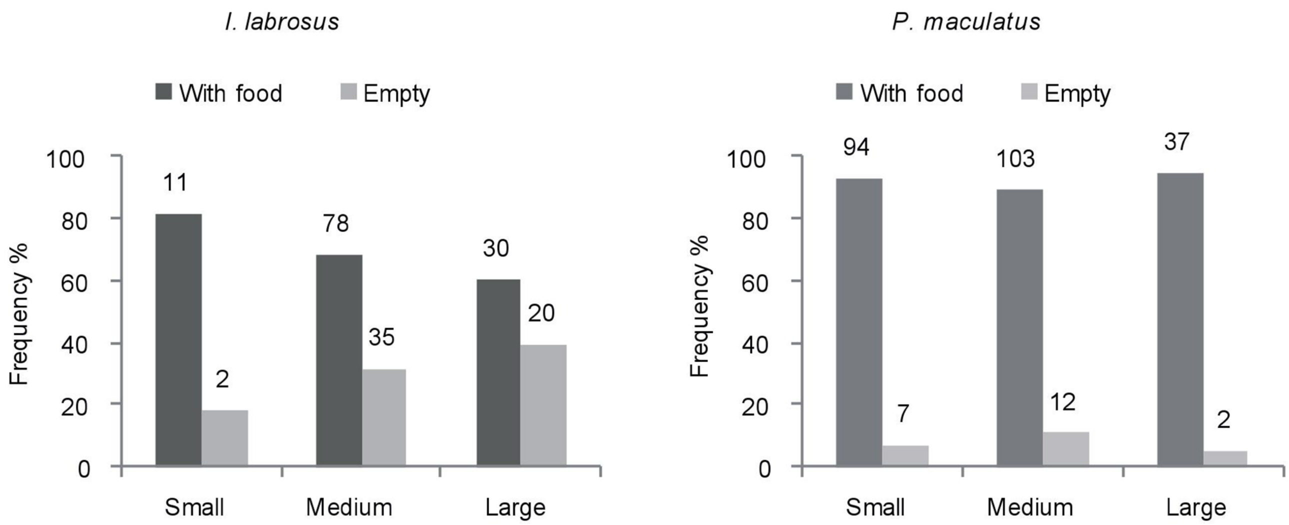

Figure 3. Percentage and number of stomachs with and without content in the three size classes of *I. labrosus* and *P. maculatus* at Camargos reservoir, MG, Brazil

Table 2. List of Identified taxa in the diet of *I. labrosus* and *P. maculatus* and their contribution in the frequency of occurrence (FO%) and volume (V%) at Camargos reservoir, MG, Brazil

Dietary categories/items	***Iheringichthys labrosus***		***Pimelodus maculatus***	
	FO%	**V%**	**FO%**	**V%**
ALGAE				
Actinotaenium sp.	0.84	< 0.001	1.71	< 0.001
Closterium sp.	2.52	< 0.001	0.85	< 0.001
Cosmarium sp.	1.68	< 0.001	2.56	< 0.001
Desmidium sp.	4.20	< 0.001	2.14	<0.001
Elakatotrix sp.	-	-	0.85	< 0.001
Hyalotheca sp.	8.40	0.36	16.24	0.57
Spirogyra sp.	10.08	0.62	8.12	0.50
Staurastrum sp.	1.68	< 0.001	1.28	< 0.001
Micrasterias sp.	1.68	0.002	1.28	< 0.001
Surirella sp.	-	-	2.14	< 0.001
TERRESTRIAL PLANTAE				
Echinolaena inflexa (seeds, leaf, stalk fragments)	48.74	6.12	37.18	6.94
Psidium guajava (seeds)	-	-	1.71	0.01
AQUATIC PLANTAE				
Cyperaceae, Apiaceae, Lentibulariaceae, Onagraceae (Petioles and leaf fragments)	8.4	0.81	53.85	8.86
PROTOZOA				
Difflugia sp.	38.66	0.46	2.56	0.08
ROTIFERA				
Keratella sp.	4.20	0.002	2.14	0.15
Notholca sp.	-	-	1.71	0.10
NEMATOIDA				
Nematoda (Ordem Dorylaimida)	44.53	1.04	33.76	1.14
Nematomorpha	0.84	0.42	2.14	0.29

Continuation Table 2.

Dietary categories/items	*Iheringichthys labrosus*		*Pimelodus maculatus*	
	FO%	V%	FO%	V%
ANNELIDA				
Tubificidae	2.53	0.29	1.71	0.63
Lumbriculidae	4.20	0.47	1.28	0.55
ACARINA				
Hydrachnellidae	21.01	0.28	12.82	0.27
Unsonicolidae	5.88	0.12	5.98	0.21
COPEPODA				
Mesocyclops sp.	41.17	5.78	22.22	2.83
Termocyclops sp.	21.01	4.49	32.48	4.84
Argyrodiaptomus sp.	4.20	0.40	2.14	0.17
CLADOCERA				
Daphnia sp.	16.83	1.83	12.39	0.53
Cariodaphnia sp.	3.36	0.90	5.56	0.12
Bosmina sp.	26.05	3.22	2.99	0.35
OSTRACODA	31.09	1.01	10.69	0.43
INSECTA				
Chaoboridae (larvae)	64.70	30.05	29.99	9.32
Chironomidae (larvae)	96.64	30.97	73.94	22.24
Other aquatic insect				
Ephemeroptera (larvae)	5.88	1.33	5.98	2.23
Odonata (larvae)	-	-	2.56	0.87
Neuroptera (larvae)	3.36	0.88	5.13	3.94
Tricoptera (larvae)	3.36	0.38	5.56	2.46
Ceratopogonidae (larvae)	30.25	4.68	19.66	3.40
Culicidae (larvae)	7.56	2.37	11.11	1.95
TERRESTRIAL ARTHROPODS				
Gryllidae	-	-	1.28	0.35
Isoptera	-	-	1.71	0.32
Hemiptera	-	-	1.71	0.59
Scarabaeidae	-	-	2.99	0.60
Elateridae	-	-	1.71	0.33
Tenebrionidae	-	-	0.43	0.17
Formicidae	-	-	2.14	0.43
Chaoboridae (adult)	3.36	0.36	0.85	0.33
Chironomidae (adult)	1.68	0.20	1.28	0.39
Phoridae	0.84	0.09	0.43	0.43
Aranae	-	-	2.14	0.32
FISH (Characiformes)	-	-	26.07	19.10
SCALE (isolated)				
scale cycloid	2.52	0.06	4.70	0.53
scale ctenoid	0.42	0.02	1.71	0.18

Table 3. Result of PERMANOVA analysis for use of food resources by *I. labrosus* and *P. maculatus* at Camargos reservoir, MG, Brazil

Sources	d.f.	SS	Pseudo-F	P (perm)	Uniq perms
Se	3	26298	2.458	0.006*	997
Sit (Se)	8	30356	0.562	0.981	997
Sp (Sit (Se))	11	78070	2.583	0.001*	999
Siz (Sp (Sit (Se)))	34	1.0876ES	1.646	0.001*	998
Res	296	5.7535ES			
Total	352	8.7055ES			

Sources: Se- Season; Sit: Site; Sp- Species; Siz- Size class; d.f.-degrees of freedom; SS- sum of squares; P (perm) -probabilility; uniq perms- permutations performed; * significant results.

Considering the Alimentary Index (AI - Table 4), it can be observed the dominance of invertebrate animal categories in the diet of *I. labrosus*, whereas in *P. maculatus* animal and vegetal categories presented a more even importance. Among the categories shared by the species, some variations relating to size classes and season can be highlighted. Both terrestrial and aquatic plants were important resources in the diet of smaller individuals of *P. maculatus* and also important for all size classes in the autumn and summer seasons. The microcrustaceans were more important in the diet of the smaller individuals for both species and in the seasons of winter and spring. With regards to insects, Chironomidae were more consumed by the smaller individuals of both species. Conversely, Chaoboridae were consumed in greater quantity by the larger individuals of both species, besides being the category of greater representation during the summer for *I. labrosus*.

The intraspecific and interspecific diet similarities were evidenced through the size classes, with the former presenting higher values (Table 5). Between the two species, diet similarities were observed in three of the four seasons, with higher values in winter. The differentiation among the species diet appears only during the summer. The food categories that most contributed to the differences among the species were Fish, Chaoboridae, Other aquatic insect, Chironomidae and Copepoda (Fig. 4).

Discussion

The Camargos reservoir has low fish productivity, even when compared to other Brazilian reservoirs (Agostinho et al. 2007). Our results allow the classification of *I. labrosus* and *P. maculatus* as invertivorous and omnivorous species, respectively. The largest population of *I. labrosus*, a invertivorous fish species in the Camargos reservoir, also differs from other Brazilian reservoirs (Agostinho et al. 2007), where the success of generalist species such as *P. maculatus* is widely reported in the literature (Agostinho et al. 2008) due to their greater colonization capacity (Sá-Oliveira et al. 2014).

The proportion of empty stomachs can also give information about the autoecology of the fish species (Vinson & Angradi 2011). In this way, the diet diversification of *P. maculatus* including the consumption of food with nondigestible fractions, such as vegetation (Vitule et al. 2008), reduces the proportion of empty stomachs in this species. In contrast, *I. labrosus* showed an increase in empty stomachs through ontogenetic development, since larger individuals seem to feed less frequently on larger prey (Vinson & Angradi 2011), as observed for Annelida and

Table 4. Dietary categories and their Alimentary Index (AI) for species, size class and season at Camargos reservoir, MG, Brazil. Values higher than 5% presented in bold, except sand not considered as food item.

Dietary categories	Alimentary Index (AI) for *I. labrosus*								Alimentary Index (AI) for *P. maculatus*							
	General	Small	Medium	Large	Summer	Autumn	Winter	Spring	General	Small	Medium	Large	Summer	Autumn	Winter	Spring
ALG	0.42	2.20	2.54	0.42	0.09	0.01	1.42	0.71	0.87	0.94	0.96	0.18	0.11	0.20	2.33	1.51
TPL	4.16	0.54	0.46	0.48	1.09	**10.17**	2.41	2.94	**5.92**	**5.56**	**6.54**	2.84	**9.64**	**9.95**	2.10	3.00
APL	0.10	0.05	0.04	0.08	0.32	0.15	0.03	<0.001	**10.11**	**10.26**	**9.85**	**7.04**	**15.37**	**8.28**	**10.27**	**5.97**
PRO	0.25	0.90	0.48	0.02	0.02	0.002	1.00	0.51	0.004	0.005	0.005	0.006	0.002	0.003	0.005	-
ROT	<0.001	<0.001	<0.001	-	-	<0.001	-	<0.001	0.02	0.01	0.05	0.08	0.002	0.02	0.04	0.03
NEM	0.93	3.28	2.57	0.18	1.41	0.15	0.25	1.12	1.19	0.94	1.70	0.19	1.34	0.68	2.66	0.40
ANN	0.07	0.008	0.79	**12.14**	0.12	-	0.20	0.08	0.08	0.01	0.02	1.66	0.02	-	0.16	0.17
ACA	0.15	0.35	0.48	0.005	0.03	0.06	0.42	0.17	0.20	0.39	0.14	-	0.09	0.21	0.17	0.33
COP	**9.88**	**32.37**	**11.44**	**5.05**	1.37	**6.37**	**17.06**	**20.13**	**9.78**	**13.34**	**9.63**	0.45	**7.21**	2.49	**14.09**	**21.91**
CLA	3.84	**16.95**	**5.29**	2.02	0.10	4.79	**9.49**	2.81	0.46	0.88	0.29	0.007	0.12	0.24	1.24	0.13
OST	0.44	0.07	0.12	0.02	0.10	0.38	0.91	0.41	0.10	0.27	0.03	0.01	0.15	0.06	0.15	0.03
CHA	**27.13**	**14.85**	**56.74**	**60.25**	**67.00**	**21.93**	4.90	**17.53**	**5.90**	4.89	**6.69**	4.43	**6.61**	2.82	3.07	**17.97**
CHI	**41.76**	**21.78**	**13.78**	**13.65**	**17.84**	**44.64**	**51.52**	**44.84**	**34.48**	**36.25**	**38.88**	**6.90**	**30.40**	**40.53**	**39.70**	**13.70**
OAI	2.61	0.28	0.95	2.03	2.26	3.76	3.11	0.70	**15.84**	**11.38**	**16.54**	**25.27**	**19.75**	**15.25**	**8.69**	**22.47**
TAR	0.02	<0.001	<0.001	0.02	0.009	0.01	0.09	-	1.55	0.75	1.60	**5.14**	0.74	1.92	0.64	3.03
FIS	-	-	-	-	-	-	-	-	**10.90**	**11.39**	4.53	**44.86**	**5.22**	**15.22**	**11.89**	**7.74**
SCL	0.002	0.06	<0.001	<0.001	-	0.01	-	<0.001	0.12	0.29	0.04	0.02	0.28	0.15	0.03	0.09
SAN	8.25	6.30	4.33	3.61	8.23	7.56	7.20	8.07	2.44	2.44	2.49	0.91	2.95	1.98	2.78	1.53

Codes: ALG: Algae; TPL: Terrestrial plantae; APL: Aquatic plantae; PRO: Protozoa; ROT: Rotifera; NEM: Nematoida; ANN: Annelida; ACA: Acarina; COP: Copepoda; CLA: Cladocera; OST: Ostracoda; CHA: Chaoboridae; CHI: Chironomidae; OAI: Other aquatic insect; TAR: Terrestrial arthropod; FIS: Fish; SCL: Scale and SAN: Sand.

Table 5. Pianka's Index of diet similarity to species, size class and season at Camargos reservoir, MG, Brazil

	***I. labrosus*- Small**	***I. labrosus*- Medium**	***I. labrosus*- Large**	***P. maculatus*- Small**	***P. maculatus*- Medium**
I. labrosus- Small					
I. labrosus- Medium	**0.61**				
I. labrosus- Large	0.44	**0.97**			
P. maculatus- Small	**0.66**	0.37	0.32		
P. maculatus- Medium	**0.62**	0.39	0.35	**0.97**	
P. maculatus- Large	0.09	0.12	0.13	0.50	0.42
I. labrosus and *P. maculatus*	Summer	Autumn	Winter	Spring	
	0.37	**0.82**	**0.91**	**0.66**	

High significant overlaping > 0,6 (Novakowski et al., 2008) in bold.

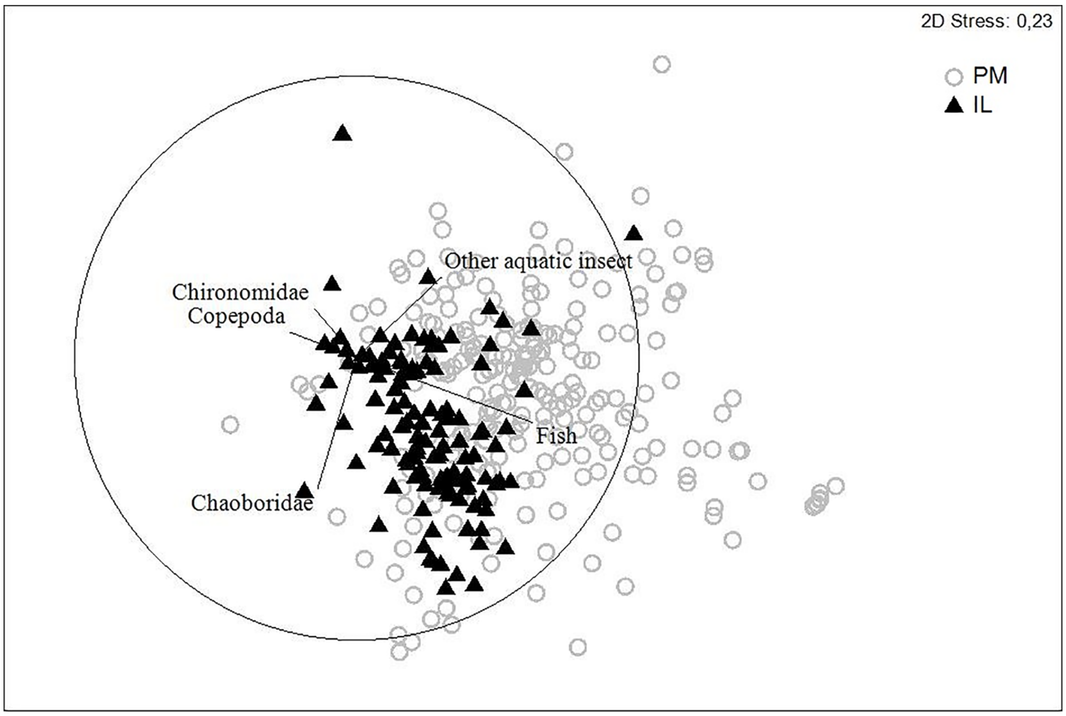

Figure 4. Non-metric multidimensional scaling (NMDS) showing the food resources responsible for the difference between the species *I. labrosus* and *P. maculatus* at Camargos reservoir, MG, Brazil

Chaoboridae. Arrington et al. (2002) also observed a greater number of empty stomachs in invertivorous than omnivorous fish.

The spatial scale considered in this study may be responsible for the higher values of biotic factors in the difference between diets, since large-scale studies are more effective in emphasising the regulation of abiotic factors in fish communities (Jackson et al. 2001). Changes in the diet during ontogenetic development reinforce the statement of Vitule et al. (2008) that species may not be an adequate analysis unit per se and ontogeny also need to be evaluated when food habits are compared among species that live in the same area. As for the abiotic factors, the ability to change seasonally the digestive morphology such the intestinal length, intestine weight, and liver weight has already been reported in *I. labrosus* (D'Anatro et al. 2013). In some species, these changes are reversible and reached in a few days in response to nutritional variations (Gaucher et al. 2012).

In the present study, *I. labrosus* and *P. maculatus* showed a diversified diet based on benthic items that corroborate other studies (Basile-Martins et al. 1986, Abes et al. 2001, Fugi et al. 2001, Andrade & Braga 2005, Ribeiro et al. 2014). The categories Sand and Scale (isolated) should not be considered as part of the diet, but rather as an involuntary intake and confirmation of feeding in the benthic zone as occurred in other fish species that search prey near the bottom (Atobatele & Ugwumba 2011). Despite this, it is important to note that not only benthic items were found in the stomachs of the studied species. The ingestion of microcrustaceans, Chaoboridae and allochthonous resources indicates the use of the limnetic zone (Câmara et al. 2012) and marginal areas of the reservoir (Agostinho et al. 2008). Feeding habitat expansion was also observed by Dill (1983) and justify by food limitation. Among the studied species, *I. labrosus* was more associated to the benthic environment in feeding (Abes et al. 2001) and ecomorphology (Teixeira & Bennemann 2007, Masdeau et al. 2011) studies than *P. maculatus*, which has already been associated with different trophic levels (Lobón-Cerviá & Bennemann 2000).

Our results demonstrated less resource sharing among the species in period of greater trophic abundance**,** as in the studies of Prejs & Prejs (1987) and Meschiatti (1995). However, we emphasize that this occurred exclusively in the summer and not during the entire rainy season. The reason for this may be the lack of correspondence between natural periods of drought and rainfall with the low and high levels in reservoirs (Silva et al. 2008), as shown in Fig. 1. The greater richness and abundance values of aquatic insects in reservoir in the rainy-warm season (Câmara et al. 2012) was associated with the increase in water levels, greater external material input and greater habitat heterogeneity (Santana et al. 2015). This occurred in the summer, but not in the spring, which is the season with lowest level of the Camargos reservoir. In addition, the two dry seasons of autumn (where the level of the reservoir is at its highest) and winter had lowest presence of Chaoboridae and Other aquatic insect. This caused the higher intake of common prey such as Chironomidae and Copepoda and greater similarity between diets. The pressure of similar diet in three out of four seasons was reduced by the interspecific diet difference, which was found along the ontogeny. This phenomenon has already been recorded in fish by Frehse et al. (2015) and described as part of a strategy to reduce competition and allow coexistence among related species.

Contextualizing the studied environment during the collection period, which began forty years after its construction, the characteristics of few macrophytes and oxygenated hypolimnion help to explain the relative importance (AI) of the Chaoboridae found, which differs from studies that show greater presence and importance of Chironomidae in reservoirs (Abes et al. 2001, Callisto et al. 2002, Costa et al. 2006, Silva et al. 2015). As the Camargos reservoir ages, *I. labrosus*, a species with a less diversified and invertivorous diet, is shown to be successful and competitive (Mérona et al. 2003). This may be related to the fact that *I. labrosus* has a lower body mass and uses less allochthonous resources than *P. maculatus*, a relevant fact in a reservoir with scarce marginal vegetation. Thus, the long period of diet overlap between two of the most fished species and the low fish productivity may indicate the limitation of resources in this reservoir and should be considered from an ecological perspective for future plans of new upstream reservoir construction. In addition, the autochthonous and allochthonous food categories with high common use or low values are supporting information to optimize management and best use of this reservoir.

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Author Contributions

Zoraia Silva: performed data collection, data analysis and interpretation and writing of the manuscript;

Patrícia Elaine Cunha do Nascimento: data collection and analysis and manuscript preparation.

Jean Ricardo Simões Vitule: data analysis, critical revision and adding intellectual content.

Fabrício de Andrade Frehse: data analysis, critical revision and adding intellectual content.

Mayara Silva Oliveira Ferraz: data analysis and interpretation and manuscript preparation.

Lea Rosa Mourgués-Schurter: contribution in the concept, design of the study and data collection.

Conflicts of interest

The authors declare that they have no conflict of interest related to the publication of this manuscript.

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