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FISH PREDATORS OF THE GOLDEN MUSSEL *Limnoperna fortunei* IN DIFFERENT ENVIRONMENTS IN A SOUTH AMERICAN SUBTROPICAL RIVER

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ABSTRACT

This study aimed to evaluate whether the golden mussel, *Limnoperna fortunei*, identified in the upper Uruguay River for the first time in 2012, has been incorporated into the diet of the ichthyofauna present in different environments of a Neotropical reservoir. To achieve this, we analyzed the digestive tract of fish that were collected seasonally between August 2015 and May 2016. The results showed that 22 fish species had *L. fortunei* in the digestive tract, of which 11 were previously not known to comprise the diet of this mollusk. Furthermore, it was observed that species belonging to the orders Characiformes and Cichliformes were the main consumers of *L. fortunei* in the lentic environment, whereas in the lotic and transition environments, the main consumers belonged to the order Siluriformes. The degree of digestion of *L. fortunei* in the digestive tract of fish indicated that although most fish could digest this food resource, some Siluriformes found it difficult. Thus, it can be concluded that the availability of *L. fortunei* in the upper Uruguay River forms a new food resource for the endemic ichthyofauna.

Key words: biological control; fish feeding; invasive species; neotropical fishes; potential predators; Uruguay River.

PEIXES PREDADORES DO MEXILHÃO-DOURADO *Limnoperna fortunei* EM DIFERENTES AMBIENTES DE UM RIO SUBTROPICAL DA AMÉRICA DO SUL.

RESUMO

O presente estudo teve como objetivo avaliar se o mexilhão-dourado *Limnoperna fortunei*, identificado na região do alto rio Uruguai pela primeira vez em 2012, vem sendo incorporado na dieta da ictiofauna presente nos diferentes compartimentos de um reservatório neotropical. Para isto, foi analisado o trato digestório de peixes através de coletas sazonais realizadas entre agosto de 2015 e maio de 2016. Os resultados mostraram que 22 espécies de peixes apresentaram *L. fortunei* no trato digestório, sendo que o registro de consumo deste molusco era desconhecido para 11 delas. Além disso, foi possível observar que espécies das ordens Characiformes e Cichliformes foram as principais consumidoras de *L. fortunei* no ambiente lêntico, enquanto que nos ambientes lóticos e de transição (lótico/lêntico) os principais consumidores deste mesmo recurso foram espécies pertencentes a ordem Siluriformes. Quando avaliado o grau de digestão de *L. fortunei* encontrado no trato digestório dos peixes, foi observado que a maioria dos peixes consegue digerir esse recurso alimentar, entretanto, merece destaque o fato de que algumas espécies de Siluriformes encontram dificuldade em digerir esse molusco invasor. Diante dessas informações é possível concluir que a disponibilidade de *L. fortunei* no alto rio Uruguai vem proporcionando uma nova oferta de alimento para diferentes espécies de peixes, e que os consumidores variam de acordo com o compartimento do reservatório.

Palavras-chave: alimentação de peixes; controle biológico; espécies invasoras; peixes neotropicais; potenciais predadores; rio Uruguai.

INTRODUCTION

The South American freshwater ichthyofauna are characterized by high feeding plasticity, using a wide variety of food resources present in aquatic (including many species of vertebrates, invertebrates, microorganisms, and primary producers) as well as terrestrial (including leaves, fruits, seeds, and insects) environments (Petry et al., 2011). In addition, trophic opportunism is also a key attribute among these fish, which may benefit from certain unusual food resources in their diet that are widely available in the environment either temporarily or permanently (Oliveira et al., 2010).

A few years ago, the golden mussel *Limnoperna fortunei* (Dunker, 1856), a bivalve from Southeast Asia, was recorded in South America (Pastorino et al., 1993). In the following years, its presence was reported in the Itaipu hydroelectric power plant (Darrigran and Mansur, 2009) and in reservoirs in the state of São Paulo (Avelar et al., 2004). More recently *L. fortunei* was also found in the São Francisco river basin (Barbosa et al., 2016).

Currently, *L. fortunei* is considered the freshwater bivalve responsible for the greatest economic and environmental impacts in South America, similar to *Dreissena polymorpha* (zebra mussel) in North America (Darrigran and Damborenea, 2005).

The high reproductive capacity and absence of natural predators of *L. fortunei* have aided the development of large population clusters of this organism (Darrigran, 2002), which can result in changes in the trophic chain of ecosystems where this species is established (Brugnoli et al., 2005). Fish species with morphological characteristics for a malacophagous diet, or that have the capacity to break the shells of these molluscs tend to have a greater success in the consumption of this food resource (Oliveira et al., 2010).

Previous studies conducted at different sites detected changes in the diet of fish that consumed the golden mussel (Cantanhêde et al., 2008; Oliveira et al., 2010; Lopes and Vieira, 2012). These changes could be motivated only by the presence of the golden mussel or also by the reduction in the local biodiversity, but it demonstrates the ability of some fish species to explore this new source of food.

The presence of the golden mussel was documented by Agudo-Padrón (2012) in the upper Uruguay River. This region has a fish assembly composed of more than 100 species (Zaniboni-Filho et al., 2004). However, there is no record that the introduction of this mollusk caused changes in the diet of these fish.

Considering that *L. fortunei* is found in high densities and can offer an abundant supply of food for fishes, especially those with broad feeding plasticity, this study aimed to (1) assess whether the golden mussel is consumed by the ichthyofauna in the upper Uruguay River, by evaluating the presence of this mollusk in the digestive tract of fish; (2) evaluate the consumption rates of golden mussel for each fish species; and (3) analyze whether there is a difference in *L. fortunei* predation by fish in environments with different hydrological characteristics.

MATERIAL AND METHODS

Study area

Eight sampling sites were located on a stretch of approximately 350 km of the upper Uruguay, located between the municipalities of Piratuba (SC) and Mondaí (SC). Seven of these were located in the area of influence of the Itá Reservoir. Of these, two were located in a lotic environment, upstream of the reservoir (LO1 and LO2); four were inside the reservoir, of which two were in the transition area (semi-lentic) between the lotic and lentic environment (TR1 and TR2) and two in the lentic environment of the reservoir (LE1 and LE2); and one site was located on a lotic stretch, immediately below the Itá Dam (LO3). The eighth sampling site was located on a lotic stretch of the Uruguay River at a distance of 206 km downstream from the Itá Dam and without the direct influence of hydroelectric effects (LO4) (Figure 1).

Fish collection and laboratory analysis

Samples were collected between August 2015 and May 2016, resulting in four samples at each of the eight sampled sites (totaling 32 samples). Diverse sampling equipment was used, such as gillnets with meshes of 1.5, 2.0, 2.5, and 3.0 cm between adjacent nodes, height of 1.6 m, and length of 10, 15, 20, and 30 mm, respectively; crossing nets *i.e.*, gillnets with meshes of 8.0 cm between adjacent nodes, height of 8 m, and length of 60 to 120 m; and trammel nets with meshes of 3.0, 4.0, and 5.0 cm between adjacent nodes, height of 1.8 m, and length of 30 and 40 m. The capture effort was constant over time at all sampling points, allowing the comparison of the data. All the nets were installed at dusk and collected at dawn the next day, remaining in the environment for 12 h. All fishes caught were fixed in 10% formalin and later analyzed in the laboratory. Owing to the high number of fish caught, a sub-sampling strategy was established, wherein a maximum of 20 specimens of each species at each of the eight sampling sites (in each season) was selected for further analysis.

Subsequently, the fixed fish were transferred to 70% alcohol to measure their biometry. In the laboratory, the fishes were identified to the lowest possible taxonomic level. The fish were then dissected and the digestive tract removed, stored individually, and preserved in 70% alcohol. For the analysis, only adult fish were considered, according to Vazzoler (1996), to avoid distortions caused by ontogenetic changes in fish feeding.

Fish diet

The digestive tract of each fish was placed individually in a Petri dish and observed under a binocular stereomicroscope for identification and quantification of food items. The identification of the items was done with the aid of specialized bibliography (McCafferty, 1983; Zaniboni-Filho et al., 2004; Santos et al., 2012) and through consultations with experts. In order to facilitate the interpretation of the trophic groups among the different fish species, the food items were grouped into seven categories: crustaceans (Cladocera, Copepoda, Decapoda, and Ostracoda), detritus/sediment (organic material in different degrees of decomposition from the bottom, mud, and sand), insects (Chironomidae, Coleoptera, Diptera, Ephemeroptera, Hemiptera, Homoptera, Hymenoptera, Isoptera, Lepidoptera, Orthoptera, Trichoptera, and insect remains that could not be identified), golden mussel (only adult individuals with valves were identified), other invertebrates (Acarina, Araneae, Gastropoda, Hirudinea, Nematoda, and Oligochaeta), fishes (Characiformes, Cyprinodontiformes, Cichliformes, Siluriformes, and fish remains that could not be identified), and plants (algae, leaves, fruits, and seeds).

The frequency of occurrence (FO) of a food item was calculated as the percentage of digestive tracts in which a given food

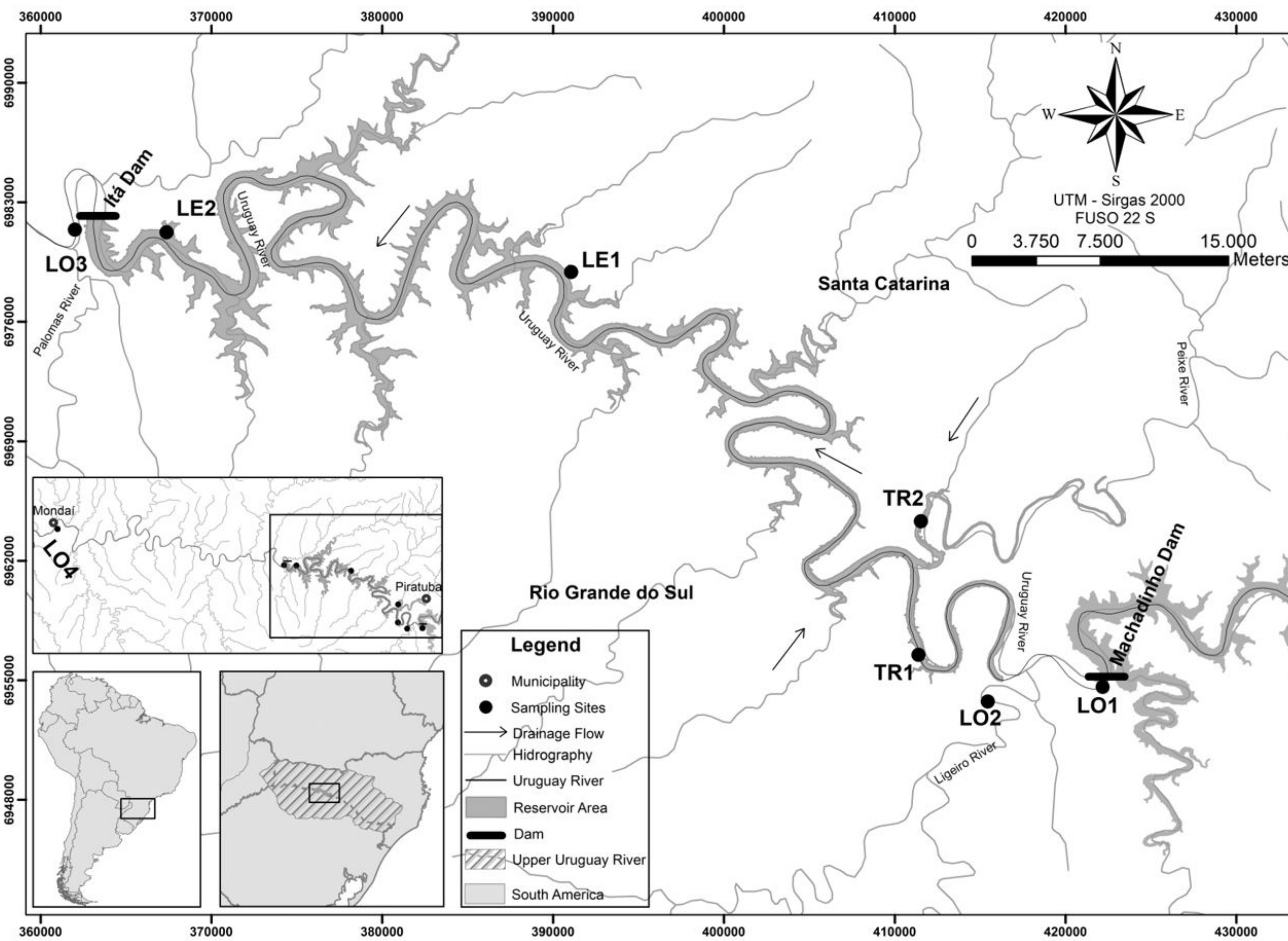

Figure 1. Location of sampling sites in the upper Uruguay River, Brazil. TR: transition, LE: lentic, LO: lotic.

item occurred in relation to the total number of digestive tracts evaluated which contained some type of food. The volumetric frequency (FV), which is the total volume occupied by a given food item in relation to the total volume of all items present in the digestive tract and expressed as a percentage was also calculated (Kawakami and Vazzoler, 1980). These values were then integrated to determine the feeding index (IAi), expressed as a percentage as proposed by Kawakami and Vazzoler (1980), and used in further analysis of the diet.

To evaluate the main fish species that consumed the golden mussel, the IAi (%) was used: $IAi = 100\ (\%FO.\%FV / \sum \%FO.\%FV)$, where FO = frequency of occurrence of a food item in the diet (%); FV = volume of a given item in the diet (%). Any fish which contained even one specimen of the golden mussel in the digestive tract was removed from the analysis to avoid including specimens in which this food resource was ingested unintentionally.

Difference between environments

Sampling sites were classified according to characteristics reported in previous study (Hermes-Silva et al., 2008; Schork and Zaniboni-Filho, 2018). According to these authors, the LE1 and LE2 sites present characteristics of a lentic environment, TR1 and TR2 are environments characteristic of the transition between lotic and lentic stretches, whereas LO1, LO2, and LO4 are lotic environments. Although Hermes-Silva et al. (2008) classified LO3 as a lotic environment, in the present study, this condition was altered by the recent construction of the Foz do Chapecó Dam in 2010, located downstream of this site, which has caused changes in the environment. Hence, to avoid any errors in data interpretation, the LO3 site was not included in the detrended correspondence analysis (DCA).

Degree of digestion of golden mussel

The degree of digestion (DD) of the golden mussel in the digestive tract of fish was analyzed to evaluate their capacity to digest the golden mussel. Following Oliveira et al. (2010), the golden mussels within the digestive tract were classified into four categories according to the level of breakdown: 0 = intact, 1 = almost intact, 2 = valves fragmented, and 3 = muscle digested.

Statistical analysis

The abundance of the species in the different environments was evaluated through the catch per unit effort (CPUE), calculated on the basis of the number of individuals caught. The distribution of the species in the different environments was compared using the Kruskal-Wallis non-parametric test for comparison of means and the chi-square test, using the software STATISTICA 7.0.

To summarize the feeding of fishes in different environments, the ordination method, detrended correspondence analysis (DCA) was used. To minimize the effect of rare species on the ordination, only those species that presented frequency of occurrence (FO) >5% across the entire study period were selected. To evaluate the spatial difference in the composition of the diet and demonstrate the aspects observed in the DCA, the same dataset used for this multivariate analysis was submitted to the multiple response permutation procedure test (MRPP, using the software PC-ORD 5.0). The consistency of MRPP groupings (T), homogeneity between the groups (A), and statistical significance were computed (McCune and Grace, 2002).

RESULTS

In total, 1,655 fish belonging to 55 species, 38 genera, 18 families, and 8 orders were analyzed. The Order Characiformes presented the largest number of species captured (40.7%), followed by Siluriformes (35.2%), Cichliformes (13%), Gymnotiformes (3.7%), and four others with 1.9% (Table 1).

The golden mussel was present in the diet of 40% of the fish species evaluated in this study. The present study showed that 22 fish species consumed the golden mussel (*Acestrorhynchus pantaneiro*, *Astyanax fasciatus*, *A. lacustris*, *Crenicichla celidochilus*, *C. jurubi*, *C. minuano, C. missioneira*, *Cyprinus carpio*, *Geophagus brasiliensis*, *Gymnogeophagus gymnogenys*, *Hypostomus isbrueckeri, H. roseopunctatus*, *H. uruguayensis*, *Iheringichthys labrosus*, *Loricariichthys anus*, *Paraloricaria*

Table 1. Feeding index (IAi%) of the food resources consumed by ichthyofauna in eight sampling sites located in the upper Uruguay River, from August 2015 to May 2016. N total = number of individuals analyzed containing food in their digestive tract, SL = standard length in cm (minimum and maximum values), FO% GM = frequency of occurrence (%) of the golden mussel for each species. Values of IAi of each of the main food items: CR = crustaceans, DS = detritus and / or sediment, FI = fish, IN = insects, GM = golden mussel, OI = other invertebrates, PL = plants.

Taxa	N total	SL	FO%	IAi						
			GM	CR	DS	FI	IN	GM	OI	PL
ACANTHURIFORMES										
Sciaenidae										
Pachyurus bonariensis	30	9.8-16.1	0.0	0.07	5.52	-	93.06	-	0.02	1.33
ATHERINIFORMES										
Atherinopsidae										
Odontesthes aff. *perugiae*	1	17.0	0.0	100	-	-	-	-	-	-
CICHLIFORMES										
Cichlidae										
Crenicichla celidochilus	13	10.8-12.0	61.5	-	19.43	-	6.30	73.91	-	0.36
Crenicichla jurubi	9	10.0-15.2	44.4	-	23.83	-	0.54	72.80	-	2.83
Crenicichla minuano	9	10.0-16.5	66.7	-	12.03	-	0.70	84.75	1.51	1.01
Crenicichla missioneira	1	16.0	100	-	-	-	-	100	-	-
Crenicichla vittata	3	13.2-18.5	0.0	-	95.08	-	3.28	-	-	1.64
Geophagus brasiliensis	17	5.8-12.5	35.3	-	74.26	-	7.60	14.24	0.30	3.60
Gymnogeophagus gymnogenys	3	8.0-10.0	33.3	0.78	66.14	-	2.55	30.33	-	0.20
CHARACIFORMES										
Acestrorhynchidae										
Acestrorhynchus pantaneiro	54	13.8-27.5	1.9	-	*	99.99	-	*	-	-
Anostomidae										
Leporinus amae	1	13.3	0.0	-	-	-	66.80	-	-	33.20
Megaleporinus obtusidens	1	17.7	0.0	-	-	-	90.00	-	10.00	-
Schizodon nasutus	175	11.2 - 30.7	19.4	-	1.88	-	-	2.60	-	95.53
Characidae										
Astyanax fasciatus	201	8.0-13.5	2.5	0.09	0.78	0.21	57.98	0.01	*	40.92
Astyanax gr. *scabripinnis*	4	8.1-10.6	0.0	32.47	0.62	32.95	32.16	-	-	1.82

* indicates that the presence of this resource represented <0.01 of the IAi of the species. -indicates absence of a particular food resource in the digestive tract of fish.

Table 1. Continued...

Taxa	N total	SL	FO%	IAi						
			GM	CR	DS	FI	IN	GM	OI	PL
Astyanax lacustris	23	5.2-11.7	8.7	*	0.97	0.65	56.60	0.61	0.46	40.70
Bryconamericus iheringii	1	7.0	0.0	-	44.72	-	55.28	-	-	-
Cynopotamus kincaidi	10	14.5-26.0	0.0	-	-	100	-	-	-	-
Galeocharax humeralis	59	10.5-26.5	0.0	-	-	99.95	0.05	-	-	-
Oligosarcus jacuhiensis	1	20.0	0.0	-	-	96.00	-	-	-	4.00
Oligosarcus cf. *jenynsii*	35	13.7-24.5	0.0	-	0.03	99.91	0.05	-	-	-
Pygocentrus nattereri	1	23.0	0.0	-	-	100	-	-	-	-
Serrasalmus maculatus	35	13.5 - 14.3	2.9	0.14	-	69.67	3.23	5.00	-	21.96
Curimatidae										
Cyphocharax spilotus	2	13.5-14.3	0.0	-	100	-	-	-	-	-
Steindachnerina biornata	1	8.5	0.0	-	18.71	71.94	9.35	-	-	-
Steindachnerina brevipinna	130	7.5-16.0	0.8	-	99.99	-	-	*	-	-
Erythrinidae										
Hoplias australis	2	31.0-41.0	0.0	-	-	100	-	-	-	-
Hoplias lacerdae	2	23.2-28.0	0.0	-	-	99.75	-	-	-	0.25
Hoplias malabaricus	5	23.0-45.0	0.0	-	-	100	-	-	-	-
Parodontidae										
Apareiodon affinis	82	6.5-15.5	0.0	-	85.24	0.01	0.50	-	-	14.25
Prochilodontidae										
Prochilodus lineatus	4	36.8-59.9	0.0	-	99.61	-	0.17	-	-	0.22
CYPRINIFORMES										
Cyprinidae										
Cyprinus carpio	3	23.5-37.2	100	-	-	-	-	100	-	-
GYMNOTIFORMES										
Gymnotidae										
Gymnotus carapo	2	47.0-56.0	0.0	21.84	2.59	-	-	-	-	75.57
Sternopygidae										
Eigenmannia virescens	10	14.5-31.5	0.0	0.46	53.59	-	22.75	-	0.02	23.17
SILURIFORMES										
Auchenipteridae										
Auchenipterus nuchalis	3	14.0-16.7	0.0	-	-	-	100	-	-	-
Trachelyopterus galeatus	3	13.5-15.5	0.0	-	0.46	0.15	98.32	-	-	1.07
Heptapteridae										
Rhamdella longiuscula	1	10.5	0.0	-	100	-	-	-	-	-
Rhamdia quelen	12	16.5-32.5	0.0	0.38	26.25	56.92	10.24	-	0.41	5.80
Loricariidae										
Ancistrus taunayi	2	7.8-8.5	0.0	-	100	-	-	-	-	-
Hemiancistrus sp.	7	11.0-13.5	0.0	-	100	-	-	-	-	-
Hypostomus commersoni	13	13.5-36.5	0.0	-	100	-	-	-	-	-
Hypostomus isbrueckeri	113	7.9-27.2	1.8	-	99.98	-	-	*	-	0.01
Hypostomus regani	2	18.2-19.5	0.0	-	95.21	-	-	-	-	4.79
Hypostomus roseopunctatus	18	9.2-38.5	11.1	-	99.54	-	-	0.43	-	0.03
Hypostomus uruguayensis	3	16.5-18.0	33.3	-	83.45	-	-	16.55	-	-
Loricariichthys anus	95	16.8-33.0	1.1	-	91.75	-	0.77	*	2.76	4.71

* indicates that the presence of this resource represented <0.01 of the IAi of the species. -indicates absence of a particular food resource in the digestive tract of fish.

Table 1. Continued...

Taxa	N total	SL	FO%	IAi						
			GM	CR	DS	FI	IN	GM	OI	PL
Loricariichthys melanocheilus	78	11.2-28.5	0.0	-	98.59	-	0.30	-	0.14	0.97
Loricariichthys sp.	36	13.8-22.5	0.0	-	94.22	-	0.09	-	0.67	5.02
Paraloricaria vetula	44	16.5-31.0	45.5	-	7.16	*	0.02	71.97	20.80	0.03
Pogonopoma obscurum	3	20.5-24.2	0.0	-	100	-	-	-	-	-
Pimelodidae										
Iheringichthys labrosus	185	9.5-34.0	22.7	0.30	67.40	0.15	14.03	1.94	2.83	13.35
Parapimelodus valenciennis	49	8.6-17.0	4.1	91.49	1.52	-	6.33	0.43	-	0.22
Pimelodus absconditus	6	13.8-21.0	0.0	0.47	98.01	-	0.25	-	0.75	0.52
Pimelodus atrobrunneus	31	10.0-18.0	19.4	0.01	10.53	1.22	52.08	6.72	12.03	17.42
Pimelodus maculatus	20	11.1-35.1	15.0	4.05	68.77	4.20	6.02	0.83	-	16.14
SYNBRANCHIFORMES										
Synbranchidae										
Synbranchus marmoratus	1	69.0	0.0	-	-	100	-	-	-	-

* indicates that the presence of this resource represented <0.01 of the IAi of the species. -indicates absence of a particular food resource in the digestive tract of fish.

vetula, *Parapimelodus valenciennis*, *Pimelodus atrobrunneus*, *P. maculatus*, *Schizodon nasutus*, *Serrasalmus maculatus*, and *Steindachnerina brevipinna*). Values of fish collection and the relative percentage of individuals that recorded golden mussel consumption per sampling site are presented in Appendix A.

Fish diet

Among the species that consumed the golden mussel, at least two individuals of 15 species consumed it (Figure 2). In five species (*C. carpio, C. minuano, C. celidochilus, C. jurubi,* and *P. vetula*), the golden mussel represented >70% of the IAi value. Of these, *C. carpio* fed exclusively on this resource. Of the remaining four species, three belonged to the genus *Crenicichla* (Figure 2), whereas the golden mussel formed the second most consumed food item for *G. brasiliensis* (IAi of 14.24%), the first being detritus/sediment (74.26% of the IAi), which formed the third most consumed item for *P. atrobrunneus* (6.72% of the IAi). For the other fish species, this food resource represented <3% of their IAi values (Figure 2).

Differences between environments

The DCA showed a distinction between fish species that consumed golden mussel in lentic environments and transition and lotic environments (Figure 3). This distinction observed in the DCA was confirmed by MRPP analysis (Table 2). Further, the results showed that species of the orders Characiformes and Cichliformes were the main consumers of the golden mussel in the lentic environment, whereas in transition and lotic environments, the main consumers were species of the order Siluriformes (Figure 4).

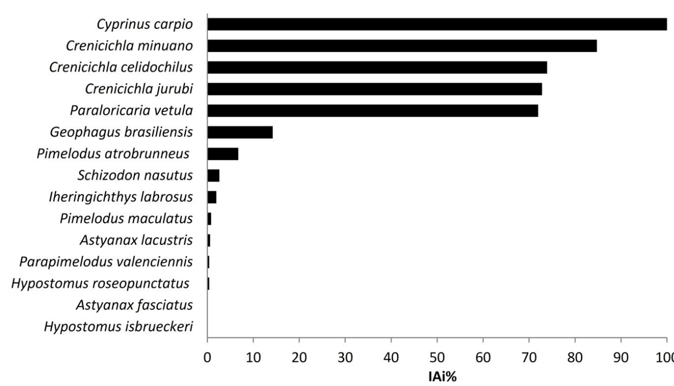

Figure 2. Percentage of golden mussel (given Feeding index IAi) for the 15 fish species that were the main consumers of this resource. Fishes collected between August 2015 and May 2016, on the upper Uruguay River.

Table 2. Diet of fish species in three different environments. LO: lotic environment, LE: lentic environment, and TR: transition environment between lotic and lentic.

Peer Comparison			
Environments	T	A	p
LE X LO	-4.4587	0.0892	0.0038*
LE X TR	-2.8313	0.0756	0.0194*
LO X TR	0.4059	-0.0082	0.5401

*Significant difference between environments (p < 0.05) from the multiple response permutation procedure (MRPP).

The multiple response permutation procedure (MRPP) analysis indicated that there was no significant difference in the diet ($p > 0.05$) between the transition and lotic environments. However, these two environments were significantly different from the lentic environment ($p < 0.05$) (Table 2).

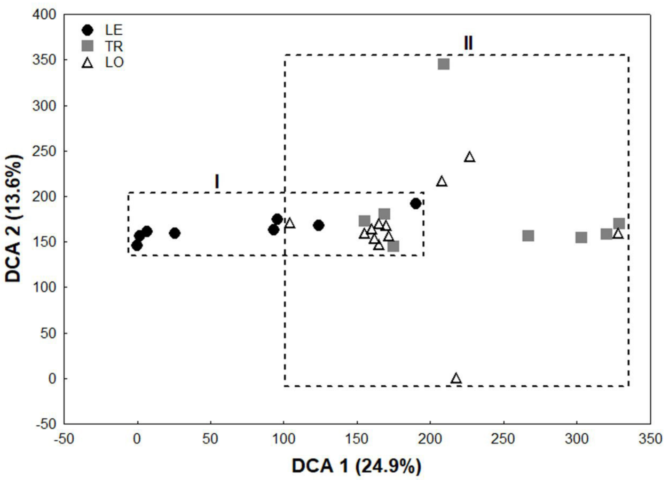

Figure 3. Detrended correspondence analysis (DCA) summarizing the feeding data of the 15 main fish consumers of the golden mussel in the three evaluated environments in the upper Uruguay River. Samples collected between August 2015 and May 2016. LE = Lentic, TR = Transition, and LO = Lotic.

The Kruskal-Wallis test showed that there was a significant difference ($p < 0.05$) in the CPUE values between the three evaluated environments for *C. jurubi*, *G. brasiliensis,* and *H. isbrueckeri* (Figure 5).

Degree of digestion of golden mussel

Among the 15 fish species that consumed the golden mussel, it was observed that *A. lacustris*, *C. carpio*, *C. jurubi*, *C. minuano*, *G. brasiliensis*, *P. maculatus,* and *P. vetula* digested >90% of the mussels ingested. The species *C. celidochilus* and *S. nasutus* also presented high digestion values of this mollusk with 65.9% and 71.6%, respectively. However, *H. isbrueckeri*, *H. roseopunctatus*, *I. labrosus*, and *P. atrobrunneus* showed a lower capacity to digest the golden mussel, presenting more intact or almost intact valves inside the digestive tract (Figure 6).

DISCUSSION

In the present study, 22 fish species from the upper Uruguay River basin were found to be predators of the golden mussel, and for only eleven of these species, ingestion of golden mussel had previously been documented (Cataldo, 2015; Rosa et al., 2015). For the other eleven species (*A. pantaneiro*, *A. lacustris, C. celidochilus, C. jurubi*, *C. minuano, C. missioneira*, *G. gymnogenys*, *H. isbrueckeri, H. roseopunctatus*, *P. atrobrunneus*, and *S. brevipinna*), consumption of this mussel has been recorded for the first time.

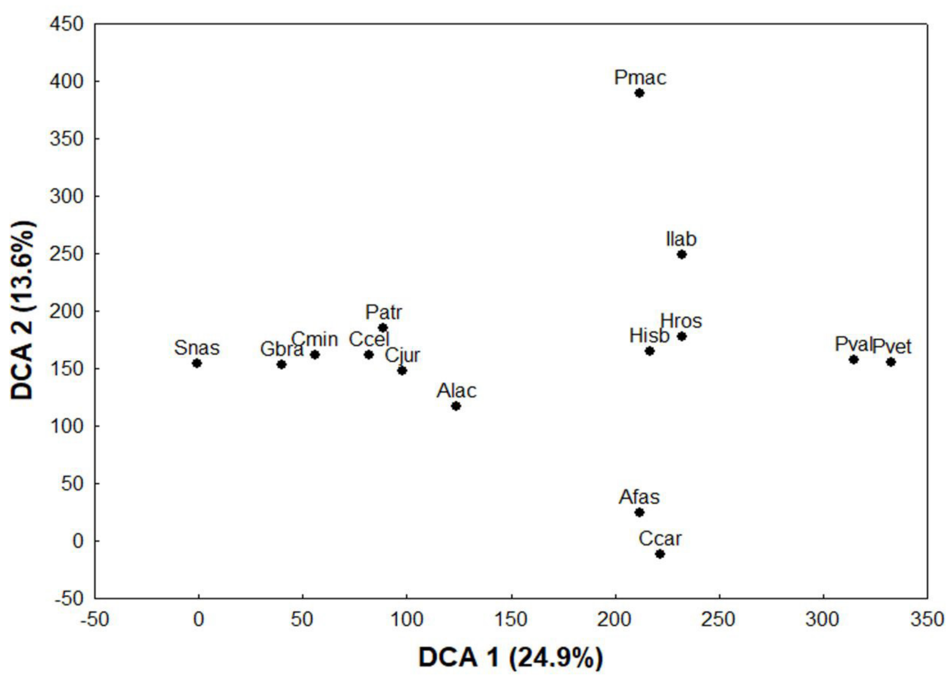

Figure 4. Detrended correspondence analysis (DCA) summarizing the feeding data of the 15 main fish consumers of the golden mussel in the three evaluated environments in the upper Uruguay River. Samples collected between August 2015 and May 2016. Afas = *Astyanax fasciatus*, Alac = *Astyanax lacustris*, Ccel = *Crenicichla celidochilus*, Cjur = *Crenicichla jurubi*, Cmin = *Crenicichla minuano*, Ccar = *Cyprinus carpio*, Gbra = *Geophagus brasiliensis*, Hisb = *Hypostomus isbrueckeri*, Hros = *Hypostomus roseopunctatus*, Ilab = *Iheringichthys labrosus*, Patr = *Pimelodus atrobrunneus*, Pvet = *Paraloricaria vetula*, Pval = *Parapimelodus valenciennis*, Pmac = *Pimelodus maculatus,* and Snas = *Schizodon nasutus*.

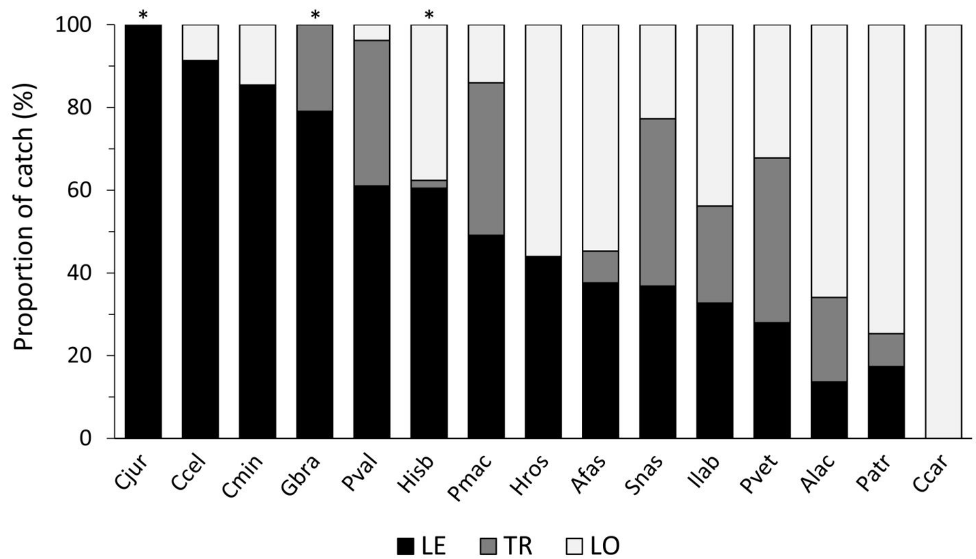

Figure 5. Proportion of catch, based on the CPUE calculated using the number of individuals, in each of the three studied environments presenting different hydrological characteristics (LE = lentic, TR = transition and LO = lotic). Fishes collected between August 2015 and May 2016, on the upper Uruguay River. Afas = *Astyanax fasciatus*, Alac = *Astyanax lacustris*, Ccel = *Crenicichla celidochilus*, Cjur = *Crenicichla jurubi*, Cmin = *Crenicichla minuano*, Ccar = *Cyprinus carpio*, Gbra = *Geophagus brasiliensis*, Hisb = *Hypostomus isbrueckeri*, Hros = *Hypostomus roseopunctatus*, Ilab = *Iheringichthys labrosus*, Patr = *Pimelodus atrobrunneus*, Pvet = *Paraloricaria vetula*, Pval = *Parapimelodus valenciennis*, Pmac = *Pimelodus maculatus,* and Snas = *Schizodon nasutus*.* Significant statistical difference ($p < 0.05$) for the Kruskal-Wallis test.

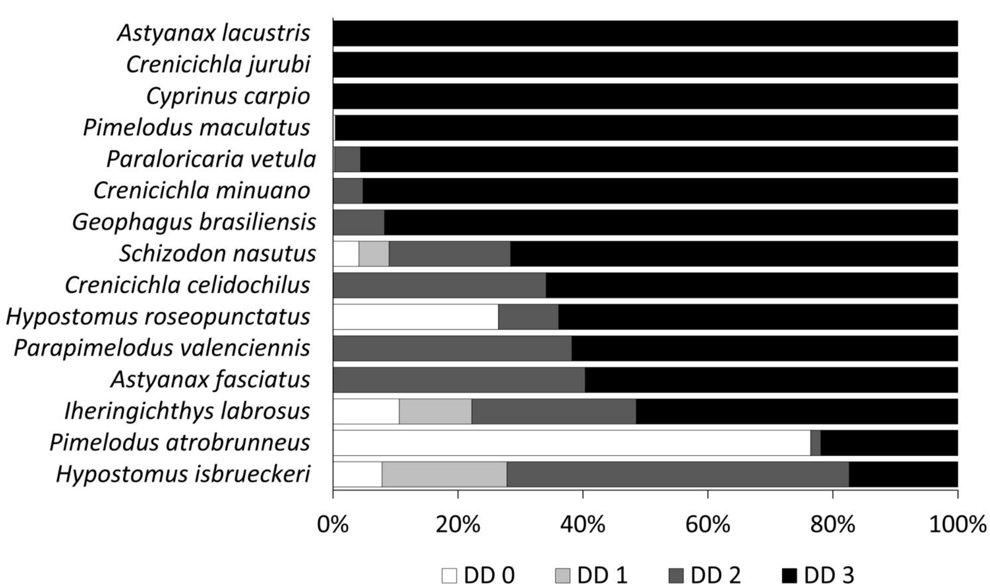

Figure 6. Degrees of digestion (%) of the golden mussel found in the digestive tract of different fish species. DD means degree of digestion. DD 0 = intact, DD 1 = almost intact, DD 2 = valves fragmented, and DD 3 = muscle digested. Fishes collected between August 2015 and May 2016, on the upper Uruguay River.

Paolucci et al. (2007) had already identified the consumption of golden mussel larvae by *P. valenciennis* larvae; however, the present study identified, unprecedentedly, *P. valenciennis* adults consuming adult mussels. The results showed the potential of the genus *Crenicichla* as a predator of the golden mussel in the upper Uruguay River, because five of the fish species captured of this genus, only *C. vittata* did not consume this invasive mollusk.

In five of the fish species (*C. carpio*, *C. minuano*, *C. celidochilus*, *C. jurubi*, and *P. vetula*) that consumed the golden mussel, the feeding index was >70% for this resource. Although consumption of the golden mussel by *C. carpio*, an omnivorous species, has been reported previously by Cataldo (2015) from the mouth of the Paraná River, in the present study, the feeding index showed that in the upper Uruguay River, this species fed exclusively on the golden mussel. Our results also revealed the importance of the golden mussel as a food resource for *P. vetula*, corroborating other previous study (García and Protogino, 2005). Thus, the present study reiterates the importance of some of the earlier reported consumers of the golden mussel, and reinforced their role as potential predators of this invasive species in the upper Uruguay River.

In addition to the ingestion of the golden mussel, studies have also shown that *C. carpio* fed on other invasive mollusk species in aquatic environments in North America and Europe (Bartsch et al., 2005). Similarly, a study on the feeding behavior of species of the genus *Crenicichla* have also reported the presence of *L. fortunei* in their diet (Lopes and Vieira, 2012). *Paraloricaria vetula* has been reported to show preference for another mollusk (*Corbicula fluminea*) in the Paraná River (García and Protogino, 2005).

Thus, in general, it can be observed that the ichthyofauna of the upper Uruguay River exhibits high feeding plasticity owing to the wide use of the available resources in the environment. The trophic opportunism of fish was also confirmed in this study, which revealed that 40.7% of the fish species from the upper Uruguay River have included the golden mussel in their diet.

In the different environments studied, we observed an evident distinction between the species that consume golden mussel in lentic environments and those in the transition and lotic environments. A possible explanation for this segregation is that the composition of fish assemblages in these environments (lentic, lotic, and transition) were distinct (Zaniboni-Filho et al., 2008), allowing different fish species to prey on the golden mussel in each of the analyzed environments. The CPUE values of the 15 species reinforced this hypothesis, since species such as *C. celidochilus*, *C. jurubi*, *C. minuano*, *C. carpio*, *G. brasiliensis,* and *H. roseopunctatus* were not found in all environments.

In the lentic environment, cichlids were the main consumers of *L. fortunei*. Similarly, it has been reported by Lopes and Vieira (2012) in a study carried out in the São Gonçalo Channel (State of Rio Grande do Sul) that among the fish caught here, *Crenicichla punctata* showed the highest frequency of occurrence of *L. fortunei* in its diet. In addition, it is expected that in lentic environments of the upper Uruguay River, which are mostly deeper environments, cichlids occupy the coastal regions not only during the breeding season, as suggested by Reynalte-Tataje and Zaniboni-Filho (2008), but also in the other stages of its life cycle, in search of shelter and food. According to Karatayev et al. (2010), these coastal environments present the greatest abundance of *L. fortunei* in aquatic environments and, consequently, may provide an additional supply of food for fish that inhabit these environments and can ingest these mollusks.

In transitional and lotic environments, most species containing the golden mussel in their digestive tracts belonged to the order Siluriformes. A hypothesis to explain this result is related to the lower depths of these than lentic environments, which can favor the dispersion and development of the golden mussel in the benthic zone, thus providing high availability of this resource to the predominant fish species that inhabit these places, which includes several species of Siluriformes. The availability of the golden mussel in benthic zones may be limited by depth, as indicated by Boltovskoy et al. (2009) in a reservoir in Argentina, where it was observed that 98% of the total capture was found in depths <10 m. Thus, in the upper Uruguay River, the benthic zones of lentic environments may present fewer *L. fortunei* or even the absence of this mollusk, which may justify the minor importance of this item in Siluriformes that inhabit the bottom of lentic environments. Furthermore, in lotic environments, where there is higher water dynamics, these fish could prefer alimentary resources with reduced capacity of evasion and high abundance, reducing the energy expenditure to obtain them. The variation in feeding behavior, with higher consumption of insects and mollusks in lotic environments than that in lentic environments, has already been described previously for a fish species of the order Siluriformes (*Pimelodus maculatus*) in the upper Paraná River (Lolis and Andrian, 1996).

The lower intake of *L. fortunei* by siluriform species in the lentic environment may also be related to variations in the availability of other food items. These lentic environments tend to have a higher sediment deposition in the benthic zones than in lotic environments. Debris and benthic organisms were the main food resource used by Siluriformes in lentic environments in the present study. Other authors also confirmed the importance of debris and benthic organisms as a food resource for Siluriformes fishes (Gomiero and Braga, 2008; Novakowski et al., 2008; Brejão et al., 2013).

In relation to the degree of digestion of the golden mussel in the digestive tract of fishes, similar to that observed in other study (Oliveira et al., 2010), species with greater capacity to digest these mollusks are those with anatomical and morphological characteristics that provide better capacity to break the valves and facilitate the digestion of muscles of *L. fortunei*, for example, species of the Cichlidae family, which have been highlighted in the present study for their high rates of digestion of the golden mussel. The presence of well-developed pharyngeal teeth and buccal musculature in these fish provides a high capacity of manipulation of their prey through the retention of small food resources in the sediment, and also by the crushing of harder organisms, such as snails and bivalve mollusks (Lopes and Vieira, 2012; Burress, 2016). Other species, such as *A. fasciatus*, *A. lacustris*, *C. carpio*, *P. vetula*, *P. maculatus,* and *S. nasutus* also showed high efficiency in digestion of *L. fortunei*. This can be attributed to morphological characteristics of the mouth and pharynx of these species, capable of crushing food resources harder than the golden mussel (Thorp et al., 1998; Salvador Junior et al., 2009), indicating that these species may also be considered as potential predators of *L. fortunei*.

However, it was observed that several species of the order Siluriformes, except *P. maculatus* and *P. vetula*, have a low capacity to digest the golden mussel. One possible explanation for this would be the absence of adequate oral mechanisms to break the shells of the golden mussel. Species of the order Siluriformes usually present feeding habits based on the consumption of less complex resources, such as debris (Novakowski et al., 2008). The difficulty to crush hard organisms, such as the golden mussel may favor *L. fortunei* dispersal, since the undigested food can pass through the digestive tract intact, being eliminated, and returning alive to the aquatic environment (Oliveira et al., 2010). This condition suggests that some Siluriformes species could act as dispersers of *L. fortunei* in the upper Uruguay River.

CONCLUSIONS

In summary, approximately 40% of the fish species evaluated in this study ingested the golden mussel *L. fortunei*, and for 11 of these species, this is a new feeding record. These results indicate that the high abundance of *L. fortunei* in the upper Uruguay River could result in an increase in the consumption of this species by the local ichthyofauna, because *L. fortunei* may be occupying the niche of other native species. In addition, this study suggests that *L. fortunei* is predated by different species according to the hydrodynamics of the environment.

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Appendix A. Values of fish collection at each sampled site and the relative percentage of individuals that recorded golden mussel consumption per sampling site. Sampling sites: lentic environment (LE1 and LE2); lotic environments (LO1, LO2, LO3, and LO4); transition between lotic and lentic stretches (TR1 and TR2). N total: number of individuals captured at each sampling site. % individuals consuming golden mussel: Relative percentage of individuals who presented golden mussel intake record at each sampling site.

Sampling sites	N Total	% individuals consuming golden mussel
LE1	245	20.4
LE2	268	10.1
LO1	172	12.2
LO2	169	0.0
LO3	183	15.3
LO4	204	1.5
TR1	247	2.4
TR2	167	10.2