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Article

Feeding strategy of the introduced *Astronotus crassipinnis* (Cichlidae) in upper Paraná river floodplain

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ABSTRACT. The cichlid *Astronotus crassipinnis* (Heckel, 1840) known as "oscar" or "apaiari" is native to the Amazon basin and presents an omnivorous feeding habit, with a tendency to carnivory. The species was introduced in the upper Paraná River floodplain, where the trophic strategies adopted by the species are not well-known. The objective of this study was to characterize the diet of *A. crassipinnis* in different size classes to identify ontogenetic differences in diet composition and to determine its feeding behavior in the invaded floodplain. In addition, we experimentally compared the feeding behavior of *A. crassipinnis* with *Hoplias* sp. 2, a native piscivorous. We evaluated the predation rate of the two species with different prey (fish and shrimp). *Astronotus crassipinnis* consumed items from several trophic levels in the juvenile stage, characterizing an omnivore feeding. In the adult stage, *A. crassipinnis* displayed a specialist strategy in which fish and mollusks dominated the diet. Under controlled conditions, *A. crassipinnis* consumed more shrimp than *Hoplias* sp. 2. The preference for shrimp during the experiment contrasted to its feeding in natural environments, showing the potential trophic plasticity of *A. crassipinnis*. The piscivorous habit in the invaded environment can be considered a trophic strategy of *A. crassipinnis*, which feeds on an abundant resource in the upper Paraná River floodplain. In conclusion, the ontogenetic diet shifts and the trophic opportunism of the carnivore adults can be the strategies used by the species to invade and settle the floodplain. The piscivorous strategy of *A. crassipinnis* may impact fish biodiversity, altering ecosystem functioning.

KEYWORDS. Ontogenetic variations, diet, freshwater fish, predation behavior, upper Paraná River Floodplain.

RESUMO. Estratégia alimentar do introduzido *Astronotus crassipinnis* na planície de inundação do alto rio Paraná. *Astronotus crassipinnis* (Heckel, 1840), conhecido como "oscar" ou "apaiari", é nativo da bacia Amazônica e apresenta hábito alimentar onívoro, com tendência à carnivoria. A espécie foi introduzida na planície de inundação do alto rio Paraná, onde as estratégias tróficas adotadas pela espécie não são bem conhecidas. O objetivo deste estudo foi caracterizar a dieta de *A. crassipinis* em diferentes classes de comprimento para identificar diferenças ontogenéticas na composição da dieta e determinar seu comportamento alimentar na planície de inundação invadida. Em adição, nós comparamos experimentalmente o comportamento alimentar de *A. crassipinnis* com *Hoplias* sp. 2, um piscívoro nativo. Avaliamos a taxa de predação das duas espécies com presas diferentes (peixes e camarões). *Astronotus crassipinnis* consumiu itens de diferentes níveis tróficos no estágio juvenil, caracterizando uma alimentação onívora. No estágio adulto, *A. crassipinnis* apresentou uma estratégia especialista em que peixes e moluscos dominaram a dieta. Em condições controladas, *A. crassipinnis* consumiu mais camarões que *Hoplias* sp. 2. A preferência por camarão durante o experimento em contraste com sua alimentação em ambientes naturais evidencia a alta plasticidade trófica de *A. crassipinnis*. O hábito piscívoro no ambiente invadido pode ser considerado uma estratégia trófica de *A. crassipinnis*, que se alimenta de um recurso abundante na planície do alto Rio Paraná. Em conclusão, as mudanças ontogenéticas na dieta e o oportunismo trófico dos adultos podem ser as estratégias utilizadas pela espécie para invadir e colonizar a planície de inundação. A estratégia piscívora de *A. crassipinnis* pode impactar a biodiversidade de peixes, alterando o funcionamento do ecossistema.

PALAVRAS-CHAVE. Variação ontogenética, dieta, peixes de água doce, comportamento de predação, planície de inundação do alto Rio Paraná.

The introduction of freshwater fish species is amongst the major threats to aquatic biodiversity (Dudgeon *et al.*, 2006; Olden *et al.*, 2010; Vitule *et al.*, 2017). The success of invasion is commonly determined by the isolated and synergetic effects of several factors, such as low local species richness (Elton, 1958; Fitzgerald *et al.*, 2016), local characteristics of the recipient river basin (Duncan *et al.*, 2003), global changes (Dukes & Mooney, 1999; Hellmann *et al.*, 2008), propagules pressure (Vitule *et al.*, 2009), facilitation for establishment provided by other invasive species (Invasional Meltdown; Simberloff & Von Holle, 1999; Ricciardi, 2001) and the biological traits of the invasive species (Kolar & Lodge, 2002).

The recognition of invasive fish traits allows predicting their potential impacts on the structure and functioning of a native community (Comte *et al.*, 2017). Among such traits are those that facilitate dispersion (*e.g.*, ability to overcome natural barriers, high fecundity, and high survival rates of eggs and larvae) and population growth (*e.g.*, high growth rates, high competitive ability; Catford *et al.*, 2009; Côté *et al.*, 2013). Moreover, the feeding strategy is a key mechanism that facilitates growth and may increase the invasion success of a species (Bohn *et al.*, 2004; Ruesink, 2005; Tonella *et al.*, 2017).

In the invaded environment, invasive species may consume the same food resources that they consumed in their native environment. However, some species can adjust their diet to consume different resources available in the new area (Hahn & Fugi, 2008), using this feeding strategy to establish in the new environment. During invasion processes, trophic generalists are favored over specialists who demonstrate a more limited ability to explore different resources (Hahn & Fugi, 2008). Species with omnivorous feeding habitats have high trophic plasticity and can adjust their diet according to the local availability of food resources (Gerking, 1994).

Piscivorous fish are specialists and generally do not change their diets (Hahn & Fugi, 2008). Specialist feeders are favored only if their primary resources are abundant in the invaded environment (Agostinho *et al.*, 2015; Pereira *et al.*, 2016; Tonella *et al.*, 2017). An additional mechanism for successful invasion is ontogenetic shifts in food preferences, that reduces intraspecific competition as immature individuals eat different food types than adults (Sánchez-Hernándes *et al.* 2019; Alves *et al.*, 2021).

The cichlid *Astronotus crassipinnis* (Heckel, 1840), known as "oscar" or "apaiari", is native to the Amazon basin and its distribution is restricted to the southwestern portion of the basin (Kullander, 2003). The species was introduced in the upper Paraná River floodplain by aquaculture and fish farming (Ortega *et al.*, 2015) in the late 90s (Ota *et al.*, 2018). Previous studies have categorized its feeding strategy as piscivorous in the floodplain (Hahn *et al.*, 2004; Abujanra *et al.*, 2009), but without evaluating its diet. On the other hand, *A. crassipinnis* was categorized as omnivorous with a carnivorous tendency in the Amazon and the São Francisco basins, feeding mainly on small fish and shrimps (Rebelo *et al.*, 2010; Costa *et al.*, 2018). Furthermore, the congeneric *Astronotus ocellatus* (Cuvier, 1829) displays a carnivorous diet, consuming a large amount of fish (Santos *et al.*, 2009; Trindade & Queiroz, 2012).

Given the lack of empirical information on its local diet, this study aimed to characterize the diet of introduced *A. crassipinnis* in the upper Paraná River floodplain and identify potential ontogenetic shifts. We also experimentally compared its feeding behavior with *Hoplias* sp. 2 (*sensu* Ota *et al.*, 2018), a native piscivorous (Pereira *et al.*, 2017a,b). The objective here was to confirm if piscivory is a feeding strategy of *A. crassipinnis* in the invaded environment and to evaluate how plastic the diet of both species could be in front of other prey than fish. In the experiment, we evaluated the predation rates of the two species for different prey (fish and shrimp). We expected that *A. crassipinnis* would be able to consume both types of prey in high amounts, which may contribute to its invasion success in the floodplain.

MATERIAL AND METHODS

Study area. The upper Paraná River floodplain (Fig. 1) is located downstream from the Engenheiro Sérgio Motta dam (locally known as Porto Primavera) and upstream from the Itaipu Reservoir. The study area is 230 km long, covers 5,268 km^2, and represents the last remnant stretch of floodplain along the Brazilian section of the Paraná River (Agostinho *et al.*, 2004). Its waterscape is formed by the main channel of the Paraná River, the channel of two major tributaries (Ivinhema and Baía), and many adjacent lakes, small tributaries, backwaters, and channels, configuring a highly heterogeneous environment (Agostinho *et al.*, 2004).

Fish sampling and diet of *Astronotus crassipinnis*. We sampled individuals of *A. crassipinnis* quarterly from March 2000 to March 2016 in three main rivers (Ivinhema, Baia and Paraná) and adjacent lakes in the upper Paraná River floodplain, as a part of the Long-Term Ecological Research (LTER – research site 6). Fish were sampled with sets of 10 m long gillnets (24, 30, 40, 50, 60, 70, 80, 90, 100, 120, 140, and 160 mm meshes) installed perpendicularly to the margins for 24 h and checked every 8 hours. We measured the standard length (SL; cm) for each captured fish and visually determined their gonadal maturation stage (Vazzoler *et al.*, 1996). Individuals were separated into size classes (Class I = 0 - 10 cm, Class II = 11 - 19 cm, Class III = 20 - 30 cm). Class I corresponds to individuals in the juvenile stage and classes II - III in the adult stage. Stomachs with food contents were preserved in 4% formaldehyde for further laboratory analysis under a stereoscopic microscope. The identification of food items followed specific literature (*e.g.*, McCafferty, 1983; Pes *et al.*, 2005; Graça & Pavanelli, 2007; Trivinho-Strixino, 2011) and experts' opinions for each group, and the items were classified to the lowest possible taxonomic level. For analysis, food items were grouped into the following categories: aquatic insects, terrestrial insects, microcrustaceans, other invertebrates, mollusks, fishes, plants, and detritus.

The diet composition was determined by analyzing stomach contents, and results were expressed following the volumetric percentage of the items (Hyslop, 1980). The volumetric percentage represents the volume of a given item over the total volume of all items recorded in the stomach contents. For smaller food items (*e.g.*, insects, microcrustaceans, detritus) millimeter petri dishes with known depth were used, where the volume was obtained in mm^3 and later converted to ml (Hellawel & Abel, 1971). For larger food items (*e.g.*, fish, shrimp) graduated test tubes with known liquid volume were used. After the insertion of each food item, the difference between the initial volume and the final volume caused by the displacement of the item in the test tubes was verified, indicating the volume in ml of the item.

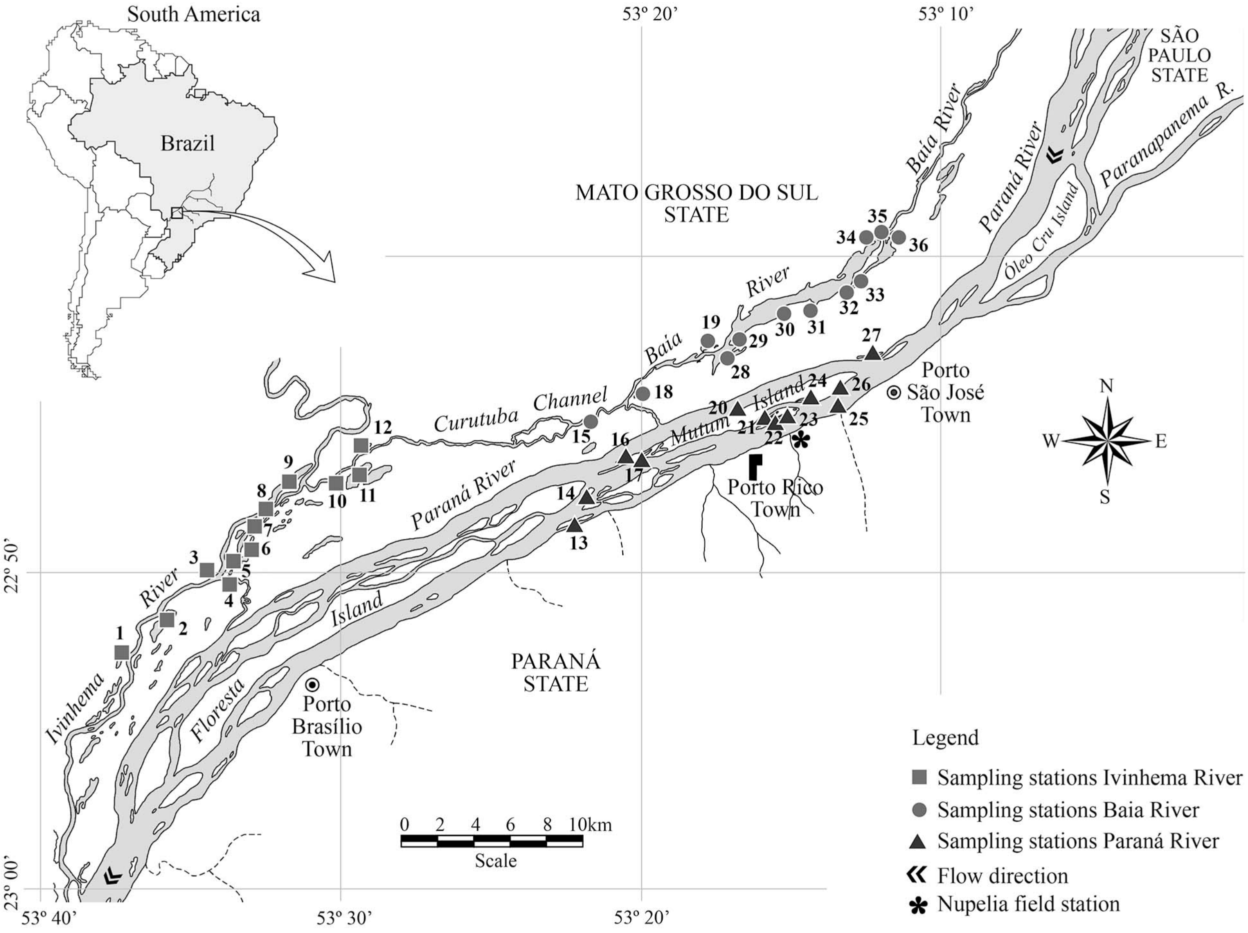

Fig. 1. Upper Paraná River floodplain with Nupelia field laboratory in detail.

To evaluate the differences in diet between size classes (factor) a resemblance matrix was generated based on the volume data matrix of the food items identified in the stomachs, using the Gower similarity coefficient (Gower, 1971). Each individual was considered a replica within the matrix (lines), food items (columns), and the size classes was the factor. The differences were determined using the Permutational Analysis of Variance (PERMANOVA) applied to the resemblance matrix (Anderson *et al.*, 2008). The patterns of similarity in diet composition were summarized for the size classes by a Principal Coordinates Analysis (PCoA; Gower, 1966). Pearson's correlations between each PCoA axis and the original variables (matrix of the food items) were performed to assess the association between food resources and PCoA axes. Correlations with $r > 0.70$ and significant p-value were considered. Significances were conducted using 4.999 Monte Carlo permutations ($p < 0.05$). Analyses were performed in the R environment (R Core Team, 2018) using package vegan (Oksanen *et al.*, 2019).

Laboratory experiment. We conducted an experiment to evaluate the feeding strategy of the introduced *A. crassipinnis* compared to the native *Hoplias* sp. 2 (*sensu* Ota *et al.*, 2018). This native species belongs to the *Hoplias malabaricus* group and it is currently being described since it has a well-defined morphotype (A. G. Bifi, unpubl. data). *Hoplias* sp. 2 is described as primarily piscivorous, with the diet dominated by fish and some consumption of insects, crustaceans, and plants (Pereira *et al.*, 2017a,b).

Adults of *A. crassipinnis* (SL: 20.5 ± 1.09, n = 4) and *Hoplias* sp. 2 (SL: 18.23 cm ± 2.07, n = 4) were sampled using rods in Baía River (22°47'S, 53°22'W). Although both species co-occur in structured environments by macrophytes, they display different predatory behaviors. The introduced species is a diurnal, active predator and stays close to the surface, near or inside the macrophytes patches (Poulin *et al.*, 1987). On the other hand, the native species is a nocturnal sit-and-wait ambush predator that often sits on the bottom facing upwards and waits for a prey to pounce abruptly (Figueiredo *et al.*, 2018).

To perform as prey in the experiment, we used the small native Characidae *Moenkhausia sanctaefilomenae* Benine, Mariguela, Oliveira, 2009 (Total Length – TL: 3.34 ± 0.54 cm) and the introduced shrimp *Macrobrachium amazonicum* (Heller, 1862) (TL: 4.17 ± 0.58 cm), both dip netted from the same habitats as the predators. Both species are abundant in the floodplain and play important roles as prey for several fish. After capture, predators and prey were separately transported into 250 L flow-through tanks to acclimation to laboratory light (12 - 12 h day-light cycle) and temperature (air = 30°C and water = 27ºC) conditions for ten days (*sensu* Petry *et al.*, 2007) before running the experiment. Predators were fed with smaller fish to satiation during the first two days and then were left starving to standardize starvation time, while prey was daily fed with commercial pellets to satiation.

The experiment was performed at the research station "*Base de Pesquisas em Limnologia, Ictiologia e Aquicultura (Nupélia)*" from the State University of Maringá (UEM), municipality of Porto Rico, Paraná State, Brazil. The experiment was conducted in aerated aquariums (100 x 50 x 40 cm) filled with 200 L of river water and submerged macrophytes branches (*Hydrilla verticillata* (L.f.) Royle and *Egeria najas* Planch) to provide shelter and minimize stress. The back and both sides of each aquarium were covered with black fabric to prevent visual disturbance, while the front and right sides were left open to allow observation. Experimental conditions were the same during the acclimatization period.

At the beginning of the experiment, we added six prey species to the aquarium 30 minutes before predators, allowing prey to acclimatize. Each treatment corresponded to a shoal of either *M. sanctaefilomenae* or *M. amazonicum* with the same size class. After the acclimatization, predators were randomly added to the aquariums, and the trials were carried out for 24 h. There were four independent experimental units for each of the two predator treatments, totalizing eight experimental units for each prey species. Each predator was used only in a single experimental unit, and each shoal was exposed only to a single predator.

The number of consumed prey (response variable) was evaluated using generalized linear models fitted with a Binomial negative distribution, considering prey type and predator species (predictor variables). The significance of the deviance captured by the fixed variables was analyzed using a deviance analysis (Type II test). The analysis was performed in the R environment (R Development Core Team, 2018) using packages car (Fox & Weisberg, 2011) and MASS (Venables & Ripley, 2002).

RESULTS

Diet of *Astronotus crassipinnis*. In 16 years of PELD monitoring, we sampled 612 individuals of *A. crassipinnis*, which 50 individuals with stomach contents (Class I = 3.7 – 4.6 cm; Class II = 13.5 – 19.5 cm; Class III = 20.0 – 27.0 cm) (Tab. I). The diet composition expressed by percentage volumetric (V%) suggested that individuals of Class I had their diet mostly based on aquatic insects (V% = 45.01%) and microcrustaceans (V% = 51.58%). Class II and III primarily consumed fish (V% = 40.68% and 35.64%, respectively) and mollusks (V% = 33.23% and 57.31%, respectively) (Tab. I).

Tab. I. Food item consumed by the size classes of *Astronotus crassipinnis* (Heckel, 1840) estimated by the values of volume (V%) of the food items in the upper Paraná River floodplain (N, number of individuals; n.i., not indentified). Values in bold represent the calculated metrics for the food categories.

Items	Class I (N=15)	Class II (N=23)	Class III (N=12)
	V%	V%	V%
Aquatic Insects	**45.01**	–	–
Trichoptera	1.22	–	–
Lepidoptera	0.71	–	–
Ephemeroptera	16.06	–	–
Chironomidae	13.81	–	–
Diptera n.i.	0.28	–	–
Chaoboridae	0.28	–	–
Odonata	8.81	–	–
Coleoptera	0.71	–	–
Collembola	0.28	–	–
Hemiptera	2.13	–	–
Plecoptera	0.65	–	–
Ceratopogonidae	0.06	–	–
Terrestrial insects	**0.31**	–	–
Diptera n.i.	0.14	–	–
Coleoptera	0.17	–	–

Tab. I. Cont.

Items	Class I (N=15)	Class II (N=23)	Class III (N=12)
	V%	V%	V%
Microcrustaceans	**51.58**	–	–
Chidoridae	2.33	–	–
Ostracoda	46.89	–	–
Cyclopoida	0.26	–	–
Cladocera n.i.	1.71	–	–
Amphipoda	0.40	–	–
Other invertebrates	**0.37**	**0.83**	–
Araneae	0.37	–	–
Decapoda	–	0.83	–
Mollusks	**0.09**	**33.23**	**57.31**
Gastropoda	0.09	32.24	12.51
Bivalve	–	0.99	44.80
Fishes	**1.11**	**40.68**	**35.64**
Doradidae	–	–	1.54
Loricariidae	–	0.83	–
Characidae	–	–	32.67
Rhamphichythyidae	–	4.13	–
Fish parts	1.11	35.72	1.44
Plant	**1.53**	**25.25**	**1.89**
Aquatic plant	–	0.26	–
Terrestrial plant	1.53	0.21	0.02
Fruit/Seed	–	24.78	1.87
Detritus	**–**	**0.02**	**5.16**

PERMANOVA indicated a significant difference in the diet composition between size classes of *A. crassipinnis* (Pseudo-F = 6.02, p = 0.001). Class I differed from classes II (t = 8.93, p < 0.001) and III (t = 5.63; p = 0.001), and Class II differed from Class III, but with a lower effect size (t = 2.18, p = 0.002). In the PCoA, Chironomidae larvae (r = -0.80), Ostracoda (r = -0.80) and Ephemeroptera (r = -0.74) were the items that most explained the patterns in Axis 1 (Tab. II). However, there was no clear pattern in Axis 2 (Fig. 2). Differences accounted in the PERMANOVA are shown in PCoA (Fig. 2).

Laboratory experiment. The amount of consumed prey differed for the interaction of predator species and prey type ($\chi^2 = 6.67$, p = 0.01). *Astronotus crassipinnis* predated less fish than *Hoplias* sp. 2 (Z = 2.67, p = 0.037), and the predation of shrimp among predators did not differ (Z = -0.59, p = 0.93). *Astronotus crassipinnis* predated, on average, four individual shrimps more than individual fish, and *Hoplias* sp. 2 predated, on average, three individual fish more than individual shrimps (Fig. 3). All individuals of *Hoplias* sp. 2 consumed fish, while the same did not occur for *A. crassipinnis*.

Tab. II. Values of significant correlation of food items with the Principal Coordinate Analysis (PCoA) axes. *** p-value significant.

Items		Axis	r	p
Chironomidae larvae	***	1	-0.80	0.00
Ostracoda	***	1	-0.80	0.00
Ephemeroptera	***	1	-0.74	0.00
Chidoridae	***	1	-0.50	0.00
Odonata nymph	***	1	-0.45	0.00
Coleoptera larvae	***	1	-0.38	0.00
Trichoptera larvae	***	1	-0.35	0.01
Diptera pupa	***	1	-0.32	0.02
Aquatic vegetable	***	1	0.28	0.05
Ostracoda	***	2	-0.36	0.01
Plecoptera	***	2	-0.36	0.01
Odonata nymph	***	2	-0.34	0.01
Chironomidae larvae	***	2	-0.29	0.04
Cladocera	***	2	-0.28	0.04
Diptera pupa	***	2	0.33	0.02
Coleoptera larvae	***	2	0.41	0.00

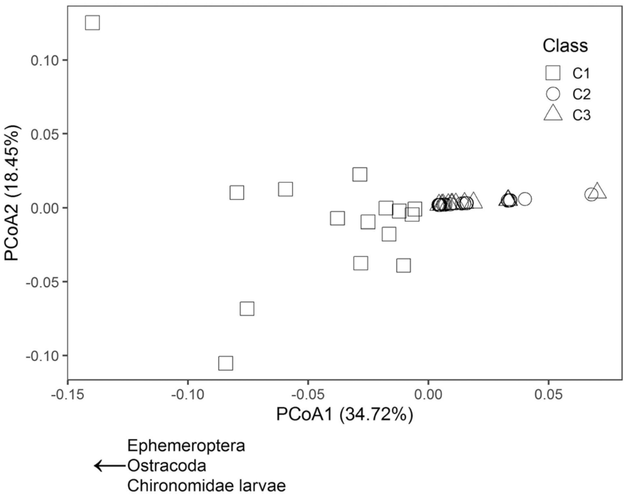

Fig. 2. Ordination by principal coordinate analysis (PCoA) of the food items for the size classes of *Astronotus crassipinnis* (Heckel, 1840) along the upper Paraná River floodplain. Axis 1 separated the diet of Class I (spheres on the right) from the other two classes (square and diamond in the left, with little variability) (Chiro, Chironomidae larvae; Ostra, Ostracoda; Ephe, Ephemeroptera).

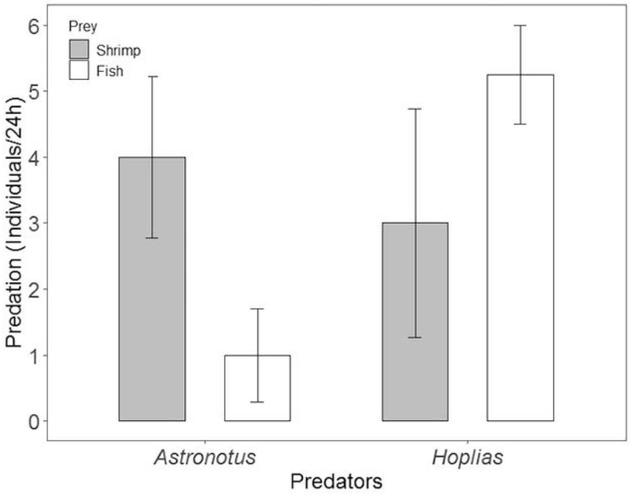

Fig. 3. Boxplot of the predation rate of *Astronotus crassipinnis* (Heckel, 1840) (introduced species) and *Hoplias* sp. 2 (native species) in relation to prey type *Moenkhausia sanctafilomenae* (Steindachner, 1907) (Fish) and *Macrobrachium amazonicum* (Heller, 1862) (Shrimp).

DISCUSSION

The introduced species *A. crassipinnis* shows ontogenetic diet shift, with generalist feeding habit in juvenile stage and specialist habit in the adult stage in the upper Paraná River floodplain. Under experimental conditions, *A. crassipinnis* predated more shrimp than fish compared with the piscivorous native species (*Hoplias* sp. 2). The feeding preference of *A. crassipinnis* in experimental conditions corroborates with its diet in the native basin (Rebelo *et al.*, 2010; Trindade & Queiroz, 2012). The piscivorous habit in the invaded environment can be considered a trophic strategy that facilitates the invasion of *A. crassipinnis*, which feeds on an abundant resource in the upper Paraná River floodplain.

In the juvenile stage (Class I), individuals consumed a wider variety of invertebrates. Ontogenetic diet shifts are well known in fishes (Wootton, 1999; Amundsen *et al.*, 2003;) and may reduce intraspecific competition through diet segregation (Canavero *et al.*, 2013; Alves *et al.*, 2021). The relative proportions of the body and other anatomical characteristics developed during growth are the key factors determining the type and food size that fish predators will prey on (Werner, 1974; Keast, 1985; Scharf *et al.*, 2000; Huskey & Turingan, 2001). Juveniles have limited body size and mouth gape, determining the consumption of only small food (Schmitt & Holbrook, 1984; King, 2005). Also, the small size of the fish at this stage makes them highly vulnerable to predators, which may lead them to forage in smaller or protected areas and consume only the locally available resources as a defense against predators (Sánchez-Hernández *et al.*, 2019). The generalist feeding behavior in the juvenile stage and the tendency to consume low-trophic level prey, is considered a feature that contributes to the successful establishment of some invasive fish species (Koehn, 2004; Gido & Franssen, 2007; Alves *et al.*, 2021) because food resources do not become a limiting factor. Therefore, this characteristic of *A. crassipinnis* may be one that may have favored its establishment in the upper Paraná River floodplain. The same pattern was observed for *Cichla kelberi* Kullander, Ferreira, 2006 (Gomiero *et al.*, 2010) and *Serrasalmus marginatus* (Alves *et al.*, 2021), two other piscivorous fish species introduced in the study area.

In the adult stage, *A. crassipinnis* shifts the intake to other items, such as fish and mollusks. Due to the high percentage of fish in their diet, in this study the species was classified as piscivorous in the upper Paraná River floodplain, just as it was proposed by Hahn *et al.* (2004) and Abujanra *et al.* (2009). Thus, the omnivorous feeding habit of *A. crassipinnis* in the Amazon river basin (native; Rebelo *et al.*, 2010; Trindade & Queiroz, 2012) and São Francisco river basin (invaded; Costa *et al.*, 2018) displayed a shift in the upper Paraná River floodplain. Although we have evaluated large individuals of *A. crassipinnis* (20 to 27 cm in class III), class II individuals correspond to those evaluated in Costa *et al.* (2018), which also have high fish consumption. Many species have trophic plasticity and diet variation between different locations, depending on the abundance of the available resources (Abelha & Goulart, 2004; Loureiro-Crippa & Hahn, 2006; Gomiero & Braga, 2008; Tonella *et al.*, 2017, Malpica-Cruz *et al.*, 2019).

The preference for shrimps displayed by *A. crassipinnis* under experimental conditions was similar to its diet in the native environment, favored by morphological features, such as mouth size and intestine shape (Costa *et al.*, 2018). The behavior of predators and prey may have favored this consumption. The predator *A. crassipinnis* has a benthopelagic habit (Froese & Pauly, 2019), similar to that of prey. Also, its foraging behavior is pursuing, and the shrimp swimming slower compared to the fish *M.*

sanctaefilomenae (Felipe *et al.*, 2009). Then, predators prefer to consume the prey requiring less energy to be captured (MacArthur & Pianka, 1966). In contrast, *Hoplias* sp. 2 has characteristics that may have disadvantages in shrimp predation, as a benthic habit, foraging behavior sit-and-wait (Winemiller, 1989; Pereira *et al.*, 2017b), and the reduced trophic plasticity. Some piscivorous fishes, commonly considered specialists, can exhibit some feeding plasticity by including invertebrates in their diets (Pereira *et al.*, 2017a). The optimal foraging theory postulates that fishes should feed on prey that maximizes their energy gain (Gerking, 1994). Thus, the consumption of invertebrates would be higher when prey fishes are not available or demand a high energetic cost for foraging (Pereira *et al.*, 2017a).

Therefore, the preference for shrimp in the experiment and the omnivory in the native environment (Rebelo *et al.*, 2010; Trindade & Queiroz, 2012) suggests that the piscivory of *A. crassipinnis* adults in the upper Paraná River floodplain is context dependent. In this invaded environment, the species might be adopting a feeding strategy of consuming an abundant resource. In addition, the species lives amid aquatic macrophytes, a place of refuge for small fishes (Lopes *et al.*, 2015) and where it does not have piscivore competitors (Gomes *et al.*, 2012). In this floodplain, the piscivorous habit favored some invasive species even in the presence of native piscivores due to the high abundance of this food resource (Pereira *et al.*, 2015).

In summary, our study combining data obtained from fish in the natural environment and experimental data demonstrated that the introduced species *A. crassipinnis* can use two mechanisms to invade and establish in the upper Paraná River floodplain. The generalist (omnivorous) feeding habit in the juvenile stage associated with the parental care characteristic of this species (Suzuki *et al.*, 2004) can maximize their survival in the initial development stages. In the adult stage, the species has a specialist (piscivorous) but opportunistic behavior, as it may alter their feeding habits to take advantage of an abundant resource (fishes and mollusks) in the invaded area. We encourage further studies of the biology of *A. crassipinnis* and experimental studies to assess its invasiveness, potential impacts on the native community of this region, and the associations with other invasive species.

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