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RESEARCH ARTICLE

Diet and foraging behavior of *Ageneiosus inermis* (Teleostei, Auchenipteridae)

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Abstract

Ageneiosus inermis is the largest species of the family Auchenipteridae (Siluriformes) and has a primarily piscivorous diet, although no comprehensive data are available on the habitat use of this species. Given this, the present study describes the diet of *A. inermis*, and provides inferences on its habitat use, based on the known behavior of its prey species. We analyzed the stomach contents of 14 specimens collected in the middle of Xingu River in the Brazilian state of Pará, which we complemented with data on 47 other specimens obtained from two published studies. Most of the ingested items were fish associated with the bottom substrate and riverbanks. Although *A. inermis* is considered a pelagic species, we conclude it forages by exploring the river's bottom and margins. Furthermore, as *A. inermis* is presumed to be diurnal, we assume that it does not pursue its prey actively, given that most of the prey species are nocturnal, but rather searches actively during the daytime for prey hidden in the bottom substrate. This hypothesis on the feeding strategy of *A. inermis* can only be confirmed by underwater observations, either in the wild or under captive conditions.

Resumo

Ageneiosus inermis é a maior espécie da família Auchenipteridae (Siluriformes), com um hábito primariamente piscívoro. Porém, nenhum estudo focou no uso do hábitat com essa espécie. Em vista dessa lacuna no conhecimento, o presente estudo objetivou descrever a dieta e inferir sobre o uso do hábitat do *A. inermis* baseado no comportamento de suas presas. Avaliamos 61 estômagos com conteúdo de indivíduos capturados no médio Rio Xingu (Estado do Pará), e outras duas literaturas publicadas. A maioria dos itens consumidos vive associado ao substrato e margens de rios. Considerando que *A. inermis* é um peixe pelágico, supomos que os indivíduos realizem um movimento lateral e vertical para forragear nas margens e fundo, respectivamente. Além disso, *A. inermis* é descrito como uma espécie diurna, porém se alimenta preferencialmente de presas de hábitos noturnos. Isso nos leva a presumir que o *A. inermis* não realiza perseguição das presas, e sim realizaria busca ativa no substrato ou margem dos rios, pois as mesmas estariam abrigadas no período diurno. Para testar essa hipótese de estratégia alimentar, encorajamos estudos complementares com observações subaquáticas no seu hábitat natural ou até mesmo em estudos comportamentais em cativeiro.

Keywords

Amazon, behavior, feeding, fish, habitat use, trophic ecology

Palavras-chave

peixe, ecologia trófica, comportamento, uso do hábitat

Introduction

The mandubé catfish *Ageneiosus inermis* (Linnaeus, 1766) is one of the most widely distributed fish of the family Auchenipteridae found in South American freshwater systems (Ribeiro et al. 2017). Most auchenipterids are quite small, predominantly omnivorous, nocturnal, and can be seen swimming actively just below the water surface (Ferraris 2003; Freitas et al. 2011). The catfish genus *Ageneiosus* is a distinct group, however, being the largest auchenipterids, with a primarily piscivorous diet (Mérona et al. 2001; Sá-Oliveira et al. 2014) and diurnal activity cycle (Ferraris 2003). These species are also assumed to inhabit the pelagic zone (Santos et al. 1984; Birindelli 2014).

Given the complexity of the food chains of tropical freshwater systems (Lowe-McConnell 1987), trophic studies can provide valuable insights into the relationships between species and the environment in which they live (Brejão et al. 2013). Considering the vast diversity of fish in the tropics, especially in the Amazon region (Dagosta and De Pinna 2019), the existing data on species interactions and autecology is far from satisfactory. Accurate data on fish diets and foraging behavior is essential for adequate fishery management and species conservation, as well as the understanding of the ecological services provided by these species, such as the control of the populations of their prey species (Ballesteros et al. 2009; Freitas et al. 2011). The analysis of stomach contents is a reliable method for the collection of detailed data on the feeding ecology (e.g., habitat use, foraging behavior) of fish species (Baker et al. 2014).

While the feeding behavior of some *Ageneiosus* species has already been studied (Tobías-Arias et al. 2006; Sá-Oliveira et al. 2014), there is no comprehensive investigation of habitat use. Given this knowledge gap on foraging strategies, we describe the diet of *Ageneiosus inermis* and infer the habitat use of this fish from the known behavior of the prey species identified in its diet. We based our study on data from the middle Xingu River, in the Amazon basin, complemented with information from two published studies, one conducted in the Orinoco basin (Barbarino-Duque and Winemiller 2003) and the other, in the basin of the Madeira River (Cella-Ribeiro et al. 2016). As the construction of hydroelectric dams – the Belo Monte dam on the Xingu and the Santo Antônio dam on the Madeira – has recently impacted two of these rivers, this overview of the feeding ecology of *A. inermis*, a top predator, provides essential insights, not only into the feeding ecology of this fish but also on the ecology of its prey species.

Methods

We collected the primary data on the middle of the Xingu River (approximately 3°12'52"S, 52°11'23"W; Fig. 1) in the Brazilian state of Pará (eastern Amazonia), at three-month intervals between April 2012 and January 2014. Sampling was conducted by permit #057/2012 and #4681-1 granted by the Brazilian Institute for the Environment and Renewable Natural Resources (IBAMA) and System Authorization and Biodiversity Information (SISBIO), respectively.

We caught specimens of *A. inermis* (Fig. 2) using gillnets with meshes of different sizes (see Barbosa et al. 2015 and 2018 for details of the sampling methods). Live specimens were anesthetized using eugenol solution following the recommendations of the American Veterinary Medical Association (AVMA 2013) and the guidelines of the National Council for Control of Animal Experimentation (CONCEA 2013). Voucher specimens are deposited at the Laboratório de Ictiologia de Altamira (LIA; Laboratory of Ichthyology), Altamira, Pará state, Brazil, under the code LIA 728. After capture, specimens were measured for standard length (S_L in centimeters) and had their stomachs removed and preserved in a mixed solution of 70% alcohol and 10% formalin to prevent the digestion of the food items. We identified the stomach contents to the lowest possible taxonomic level. We calculated the Alimentary index (Ai%; modified from Kawakami and Vazzoler 1980) for each food item, which determines the relative importance of items in the diet.

For comparison proposes, we used two complementary data: (1) Barbarino-Duque and Winemiller (2003), which presented the diet of *A. inermis* from the Apure and Arauca Rivers, Venezuela. In this study, the authors provided the information on the abundance of prey; and (2) Cella-Ribeiro et al. (2016), which presented the diet of *A. inermis* from the Madeira River, and provides the Alimentary index (Ai%).

To infer the habitat use of *A. inermis*, we compiled published data on the position in the water column and circadian activity of the prey species identified in the stomach contents (see Table 1 for references). We classified the habitat use of each

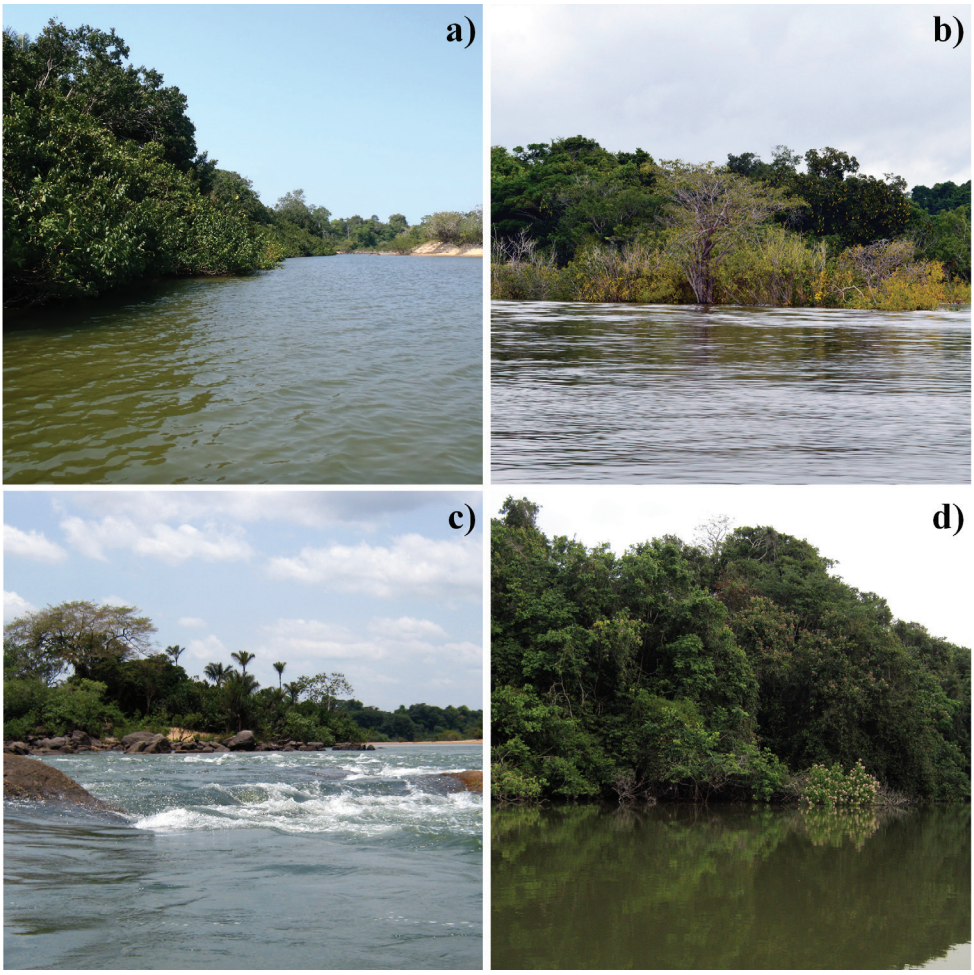

Figure 1. Examples of microhabitats sampled in the Xingu River (state of Pará, Brazil) between April 2012 and January 2014. **a**) flooded vegetation; **b**) main channel; **c**) small rapids; **d**) marginal lakes.

Figure 2. Specimen of *Ageneiosus inermis* (Linnaeus, 1766) (female; 43 cm S_L) collected in the Xingu River (state of Pará, Brazil). Photo by Leandro Souza.

Table 1. Preys consumed by the catfish *Ageneiosus inermis* from three sources, and their respective information on habitat use and circadian activity.

Source	Order	Family	Species	Method	Value	Habitat use	Circadian activity	References*
Primary data (Xingu River)	Characiformes	Characidae	*Brycon* sp.	Ai%	6.2	PL, RB	D	2**
	Characiformes	Characidae	*Moenkhausia xinguensis*	Ai%	14.8	PL, RB	D	3**
	Characiformes	Characidae	n.i	Ai%	6.6	–	–	–
	Characiformes	Erythrinidae	*Erythrinus erythrinus*	Ai%	11.4	BO	N	
	Gymnotiformes	Gymnotidae	*Gymnotus* sp.	Ai%	10.0	RB, BO	N	3**
	Siluriformes	Auchenipteridae	*Tatia musaica*	Ai%	1.2	PL, RB, BO	N	1**, 3**
	Siluriformes	Auchenipteridae	n.i	Ai%	1.7	–	–	–
	Siluriformes	Callichthyidae	*Callichthys callichthys*	Ai%	22.4	BO	N	3
	Siluriformes	Trichomycteridae	*Ituglanis amazonicus*	Ai%	15.1	BO	N	2**
	Siluriformes	n.i.	n.i.	Ai%	0.3	–	–	–
	Synbranchiformes	Synbranchidae	*Synbranchus marmoratus*	Ai%	5.1	RB, BO	N	2
	Fish remains	n.i.	n.i.	Ai%	6.7	–	–	–
	Decapoda	Palemonidae	n.i.	Ai%	0.2	RB, BO	N	4**
	Isopoda	n.i.	n.i.	Ai%	<0.1	–	–	–
Barbarino-Duque & Winimiller (2003)	Characiformes	Anostomidae	*Schizodon* sp.	Abundance	1	PL, RB	D	11*
	Characiformes	Serrasalmidae	*Mylossoma duriventre*	Abundance	2	PL, RB	D	11**
	Characiformes	Serrasalmidae	*Pygocentrus cariba*	Abundance	2	PL, RB	D	11
	Siluriformes	Doradidae	n.i	Abundance	1	BO, DC	N	8**
	Siluriformes	Loricariidae	n.i	Abundance	2	BO, DC	N	11**
	Siluriformes	Loricariidae	*Pterygoplichthys multiradiatus*	Abundance	4	BO, DC	N	11*
	Siluriformes	Pimelodidae	*Pimelodus* sp.	Abundance	2	BO, DC	N	9**
	Fish remains	n.i.	n.i.	Abundance	13	–	–	–
Cella-Ribeiro et al. (2016)	Characiformes	n.i.	n.i.	Ai%	6.6	–	–	–
	Siluriformes	Callichthyidae	*Hoplosternum littorale*	Ai%	1.7	BO	N	3
	Siluriformes	Doradidae	*Nemadoras humeralis*	Ai%	6.6	BO	N	6, 8**
	Siluriformes	Doradidae	*Nemadoras* sp.	Ai%	1.1	BO	N	6**, 8**
	Siluriformes	Doradidae	*Pterodoras granulosus*	Ai%	1.7	BO, DC	N	7, 8**
	Siluriformes	Doradidae	n.i	Ai%	70.5	BO, DC	N	8**
	Siluriformes	Loricariidae	*Loricaria cataphracta*	Ai%	1.7	BO, DC	N	10**
	Siluriformes	n.i.	n.i.	Ai%	0.6	–	–	–
	Fish remains	n.i.	n.i.	Ai%	8.0	–	–	–

Ai% – Alimentary index; n.i. – not identified); habitat use: bottom-oriented (BO), deep-channel (DC), pelagic (PL), and riverbanks (RB); circadian activity: diurnal (D) or and nocturnal (N). *1) Sabino and Zuanon (1998); 2) Oyakawa et al. (2006); 3) Brejão et al. (2013); 4) Melo (2003); 5) Brusca et al. (2016); 6) Sabaj et al. (2014); 7) Agostinho et al. (2009); 8) Sabaj and Ferraris Jr. (2003); 9) Lundberg and Littmann (2003); 10) Thomas and Sabaj (2010); 11) Arrington et al. (2002). ** Information based on species of the same genera or higher taxa.

prey species as bottom-oriented (BO), deep-channel (DC), pelagic (PL) or riverbank (RB), with species being assigned to more than one category in some cases. According to the circadian activity, we classified the preys as diurnal (D) and nocturnal (N). When no information was available for a given prey species, we considered the data for the nearest taxonomic level (e.g., genus, family) that we deemed reliable.

Results

We analyzed the contents of 61 stomachs, including 14 from specimens collected on the Xingu River in the present study, 27 from the Apure and Arauca rivers in the Orinoco basin (collected by Barbarino-Duque and Winemiller 2003), and 20 from the Madeira River (Cella-Ribeiro et al. 2016).

The 14 stomachs evaluated for the Xingu River were obtained from specimens that ranged from 21.1 to 48.0 cm (standard length – S_L). We identified 13 different food items in the stomach contents of *A. inermis* from the Xingu River. The most important of these items was *Callichthys callichthys* (Callichthyidae) with an Ai of 22.4%, followed by *Ituglanis amazonicus* (Trichomycteridae; Ai = 15.1%), *Moenkhausia xinguensis* (Characidae; Ai = 14.8%), *Erythrinus erythrinus* (Erythrinidae; Ai = 11.4%), and *Gymnotus* sp. (Gymnotidae; Ai = 10%).

Barbarino-Duque and Winemiller (2003) examined the stomachs from 503 specimens that ranged between 25 and 50 cm (S_L). However, only 27 stomachs presented some content. The authors identified 27 prey items (all fishes: five characiforms, nine siluriforms, and 13 unidentified fish). Of the siluriforms, the loricariid *Pterygoplichthys multiradiatus* was the most abundant prey, with four records.

Cella-Ribeiro et al. (2016) examined 20 stomachs with content from specimens ranging between 12.7 and 45.0 cm (S_L). The diet of these individuals was entirely composed of fishes. Nine food items were recorded: eight siluriforms (Ai = 85.4%), one unidentified characiform (Ai = 6.6%), and unidentified fish (Ai = 8.0%). Of the siluriforms, doradid catfishes were the most important food items (Ai = 70.5%).

We were able to compile reliable information on the ecology of 22 of the prey species consumed by *A. inermis* (see Table 1). Most (77%) of these species were identified as bottom-oriented (n = 17), followed by species that inhabit riverbanks (41%, n = 9), deep channels (32%, n = 7), and the pelagic zone (27%, n = 6). Regarding the circadian activity, the majority of these prey species were identified as being nocturnal (77%, n = 17), with only five (23%) being classified as diurnal. Due to the small sample size, we were unable to evaluate seasonal variation in the composition of the *A. inermis* diet.

Discussion

The primary data from the Xingu River indicated that *A. inermis* is a predator that feeds mostly on fish. Overall, the *A. inermis* diet was composed primarily of nocturnal siluriforms that inhabit riverbanks and the bottom substrate. In addition to the data from Barbarino-Duque and Winemiller (2003) and Cella-Ribeiro et al. (2016),

which we included here, two previous studies (Lasso et al. 1995; Mérona et al. 2001) had also confirmed the piscivorous behavior of *A. inermis*.

Ageneiosus inermis is a pelagic species that predominantly inhabits river channels (Santos et al. 1984; Birindelli 2014). This behavior is consistent with the morphological features of the species, such as its subterminal mouth and the absence of mental barbels, which would be located in the ventral portion of the head and help to investigate bottom substrates (Jayaram 1978). However, as most of the food items identified in the present study are associated with this type of substrate, we can assume that *A. inermis* forages by exploring bottom and riverbank habitats. Barbarino-Duque and Winemiller (2003) and Cella-Ribeiro et al. (2016) also found that most of the prey exploited by *A. inermis* were bottom-oriented catfishes of the families Loricariidae and Doradidae (Burgess 1989), respectively.

Ageneiosus catfishes are considered to be diurnal (Ferraris 2003). Given this, *A. inermis* might not pursue its prey in the water column since most prey species are nocturnal, and will typically rest during the day. It implies that *A. inermis* searches actively for its prey in bottom substrates or riverbanks, which demands a considerable investment of energy. Additionally, we can also assume that the feeding activity also occurs during the twilight time, when diurnal and nocturnal preys are active and available. However, direct observations would be needed to confirm these assumptions. Torrente-Vilara et al. (2008) reached similar assumptions based on the diet, morphology, and feeding behavior of the piscivorous characiform *Roestes molossus* (Kner, 1858). They concluded that, despite not presenting morphological features for this niche, this fish feeds on prey in the bottom substrate during the night and the crepuscular period. Considering our findings on *A. inermis*, underwater observations in its natural habitat (Brejão et al. 2013), or even behavioral studies in captivity (Volpato 2007), it would be necessary to confirm our hypothesis on the foraging strategy of this species.

Despite the relatively small size of the available dataset (stomachs with contents), we considered the data appropriate for the description of the feeding habit of *A. inermis*, and to provide inferences on its foraging strategies. Previous studies that have described the diet of *A. inermis* have also been based on samples of limited size. Mérona et al. (2001), for example, analyzed the contents of the stomachs of 40 individuals caught on the Tocantins River during five years of fieldwork (1980–1982 and 1984–1987), while Lasso et al. (1995) reported on the contents of only a single stomach.

Overall, then, we believe that our findings provide a more detailed insight into the diet, life history strategies, and habitat requirements of one of the most widely-distributed top predator fish found in the major river basins of South America. The next challenge will be to evaluate the seasonal shifts in the composition of the *A. inermis* diet, related to the natural cycle of the region's fluvial environments, and their food chains. It will require further, more comprehensive studies that collect a more significant number of specimens over a longer period. In addition, as dams are known to have a considerable impact on the diets of predatory fish and other aspects of their life cycle (Mérona et al. 2001; Winemiller et al. 2016), the results of the present study provide important reference data for the evaluation of the effects

of these projects on the biology of the aquatic fauna, which can help to develop effective conservation strategies and management measures for fishery stocks.

Conclusions

The present study results indicate that the mandubé catfish, *Ageneiosus inermis*, have a piscivorous diet and feed primarily on nocturnal, bottom-oriented prey species, despite being described in the literature until now as a diurnal pelagic fish. Based on this, we infer that *A. inermis* forages by exploring the bottom substrate to locate prey sheltering during the daytime or at twilight.

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