



GRAZING UNWORRIED: ENVIRONMENTAL CHANGES IN A DAMMED RIVER FAVOR THE DIET OF THE INVASIVE *METYNNIS LIPPINCOTTIANUS* (CHARACIFORMES, SERRASALMIDAE)

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Abstract: We evaluate the natural diet of the invasive silver dollar *Metynnis lippincottianus* in the Lower São Francisco River, Brazil. The species' diet was composed almost exclusively of Zygnemataceae algae, a food item consumed by almost all individuals (Frequency of Occurrence (FO) = 99.80%). The remaining consumed items were plant fragments (FO = 3.57%), mites (FO = 2.38%), gastropods (FO = 1.19%), thalloid algae (FO = 1.19%), ants (FO = 1.09%), and invertebrate eggs (FO = 1.09%). The high alimentary importance of Zygnemataceae algae (Alimentary Index = 99.992%) highlights the lack of a great intraspecific variation in the diet of *M. lippincottianus* and a high trophic specialization. The herbivorous diet, with a tendency to consume algae, is supported by high values of intestinal coefficient (4.71 ± 1.45) that favor the digestion of these items and are commonly related to low trophic levels. The specialized diet of *M. lippincottianus* is supported by the proliferation of algae following the damming of the river. In addition, the diet composition of the species changed between the rainy and the dry season (PERMANOVA, $p < 0.001$), displaying a broader niche by the consumption of alternative items (e.g., thalloid algae, gastropods) in the rainy season. The species had an herbivorous diet, with a predominance of filamentous algae, throughout the study, with small variations between seasons.

Keywords: biological invasion; establishment; São Francisco River basin; trophic ecology.

Freshwater ecosystems are among the most affected ecosystems by different sources of habitat alteration, including urbanization, mining, deforestation of riparian forest, silting, transformation of the environment into

agroecosystems, and river impoundment (Zeni *et al.* 2017, Reid *et al.* 2019). These alterations modify the river flow and structure of streams and rivers (Lobato *et al.* 2015, Winemiller *et al.* 2016) and might reduce the nutrient deposition in inundation fields

and marginal lagoons (Zahar *et al.* 2008). Also, it reduces waterscape connectivity and promotes numerous negative impacts on the community and ecosystem (Grill *et al.* 2019). These changes primarily affect rheophilic fishes, decreasing their abundance or even leading to their local extinction (Agostinho *et al.* 2008, Nunes *et al.* 2015). Habitat homogenization directly affects fish populations (Torgersen & Close 2004) and communities (Snyder *et al.* 2006, Schneider & Winemiller 2008, Casatti *et al.* 2012), favoring the presence of sedentary and generalist species (Havel *et al.* 2005, Casatti *et al.* 2009) and creating the potential for biological invasions (Agostinho *et al.* 2015, Assis *et al.* 2017). In addition, the homogenized environment offers less variability of resources and microhabitats, which may favor an increase in competition, in which less adapted species may disappear.

In the middle of the 1990s, a dam in the final stretch of the São Francisco River in Brazil was built for electricity production and inundation control (Medeiros *et al.* 2011). The river flow decreased significantly after the start of the plant operations, and inundation pulses became rare (Holanda *et al.* 2009, Assis *et al.* 2017, Brito & Magalhães 2017). These changes in the hydric dynamics provoked the decline of the stocks of migratory fishes (Holanda *et al.* 2009, Medeiros *et al.* 2011, D'avilla *et al.* 2021), the proliferation of algae and macrophytes (Assis *et al.* 2017, Gonçalves-Silva *et al.* 2020), and the establishment of non-native fishes, such as the silver dollar *Metynnis lippincottianus* (Cope 1870) (Holanda *et al.* 2009, Assis *et al.* 2017).

The silver dollar is a medium-sized Serrasalminidae (about 16 cm) native to the Amazon basin (Buckup *et al.* 2007) with a preference for lentic habitats (Beltrão *et al.* 2009, Paiva *et al.* 2014). This species is one of the most abundant fishes in the Lower São Francisco River (D'avilla *et al.* 2021). Its establishment is associated with a small length of reproductive maturity (about 5 cm), continuous reproduction, availability of reproductive sites, and lack of native predators (Assis *et al.* 2017, Brito & Magalhães 2017). Nonetheless, the impacts of the silver dollar in the São Francisco River basin are still unknown. Several impacts of invasive species occur by the disruption of natural food webs, whereas invasive species achieve high abundances and keep strong interactions with some food

resources, negatively affecting the entire food web through trophic cascades (Walsh *et al.* 2016, Franco *et al.* 2021, Wainright *et al.* 2021).

The structure of food webs change in face of spatial and temporal variation (Woodward *et al.* 2010, Fragoso-Moura *et al.* 2016, Yu *et al.* 2019). Rainfall seasonality is one of the primary factors structuring aquatic food webs and the diet of fishes in tropical freshwaters by changing the input of allochthonous resources to aquatic systems and habitat structure (Barbosa *et al.* 2018, Pease *et al.* 2020, Leal *et al.* 2023). Rainfall usually increases the input of allochthonous resources, such as insects and fruits, and these items become more important in the diet of generalist fishes in these systems (Soares *et al.* 2017, Pereira & Godinho 2019, Benone *et al.* 2020).

Therefore, this study describes the diet of *M. lippincottianus* in the Lower São Francisco River in order to contribute to the knowledge of the biology of this invasive species. Further, we address the seasonal variation in the diet of the species, given that rainfall is a significant factor in structuring the input of allochthonous nutrients in Neotropical lotic systems and the diet of fishes (*e.g.*, Barbosa *et al.* 2018, Bartolette *et al.* 2018, Heuvel *et al.* 2019). We expected that the diet of *M. lippincottianus* will include a higher volume and number of allochthonous items carried into the river in the rainy season.

The São Francisco River basin covers a drainage area of approximately 645,067 km² encompassing six Brazilian states (Alagoas, Bahia, Goiás, Minas Gerais, Pernambuco, and Sergipe) and part of Brazil's Federal District. The São Francisco River is the largest river entirely within Brazilian territory, extending 2,700 km from its headwaters in Minas Gerais to its mouth between Sergipe and Alagoas states (Kohler 2003, CBHSF 2021). The basin is divided into Upper, Middle, Sub-Middle, and Lower São Francisco River (MMA 2006).

The Lower São Francisco River is the smallest area, covering approximately 32,013 km² (CBHSF 2017). The area is composed mainly of sub-basins of small-sized rivers dependent on the precipitation regime and with strong influences on the Hydroelectric Plant of Xingó and the marine dynamics (Godinho & Godinho 2003). The prevailing climate is subhumid temperate, with annual averages of 25°C and annual rainfall between 350 and 1,500 mm (MMA 2006). The

construction of the dam, between 1987 and 1994 (CHESF 2023), changed the river flow dynamics, stabilizing the flow and homogenizing the structure of the river channel, leading to the formation of siltation islands and the proliferation of algae and aquatic macrophytes (Figure 1).

We sampled fish bimonthly from May 2015 to March 2016 in a single stretch of the Lower São Francisco River between the municipalities of Propriá (state of Sergipe), and Porto Real do Colégio (state of Alagoas). The captures were duly authorized by Chico Mendes Institute for Biodiversity Conservation (ICMBIO; research permits # 45700-1, 45700-2). Sampling was carried out using gill nets (with mesh sizes from 3 to 12 cm between knots) set at sunset and retrieved at sunrise (14 hours of exposition). Sampled fish were euthanized with a eugenol solution. The rainy season occurred from May 2015 to July 2015, and the dry season occurred from August 2015 to March 2016 (INMET 2022).

For each specimen, we measured the standard length (SL; 0.01 cm), extracted their guts, weighted their stomach (SW; 0.01 g), and measured the length of the intestine (IL; 0.01 cm). Then, we analyzed the stomach contents under a stereoscopic

microscope and identified the food items to the lowest taxonomic level possible using specialized literature (Streble & Krauter 1987). We measured the volume of each food item by the volumetric method described in Albrecht & Caramaschi (2003), where the total volume of each food item per gut content was measured on a 1-mm-high transparent dish with a 1x1 mm grid beneath.

Based on the morphometric data, we calculated the Intestinal Index (Ii) according to the equation: IL / SL , where herbivores and detritivores have higher index values, and carnivores the smaller ones (Zavala-Camin 1996). The importance of food items was assigned by the Alimentary Index (AI) as described in Kawakami & Vazzoler (1980), using the following equation:

$$AI = (F_i * V_i) / (\sum F_i * V_i) * 100,$$

where i is the n food items, F_i is the frequency of occurrence of item i , V_i is the volumetric proportion of item i . Afterward, we applied a Permutational Analysis of Variance (PERMANOVA) and a test of homogeneity of dispersion (PERMDISP) to evaluate differences in diet composition and trophic niche width, respectively, between dry

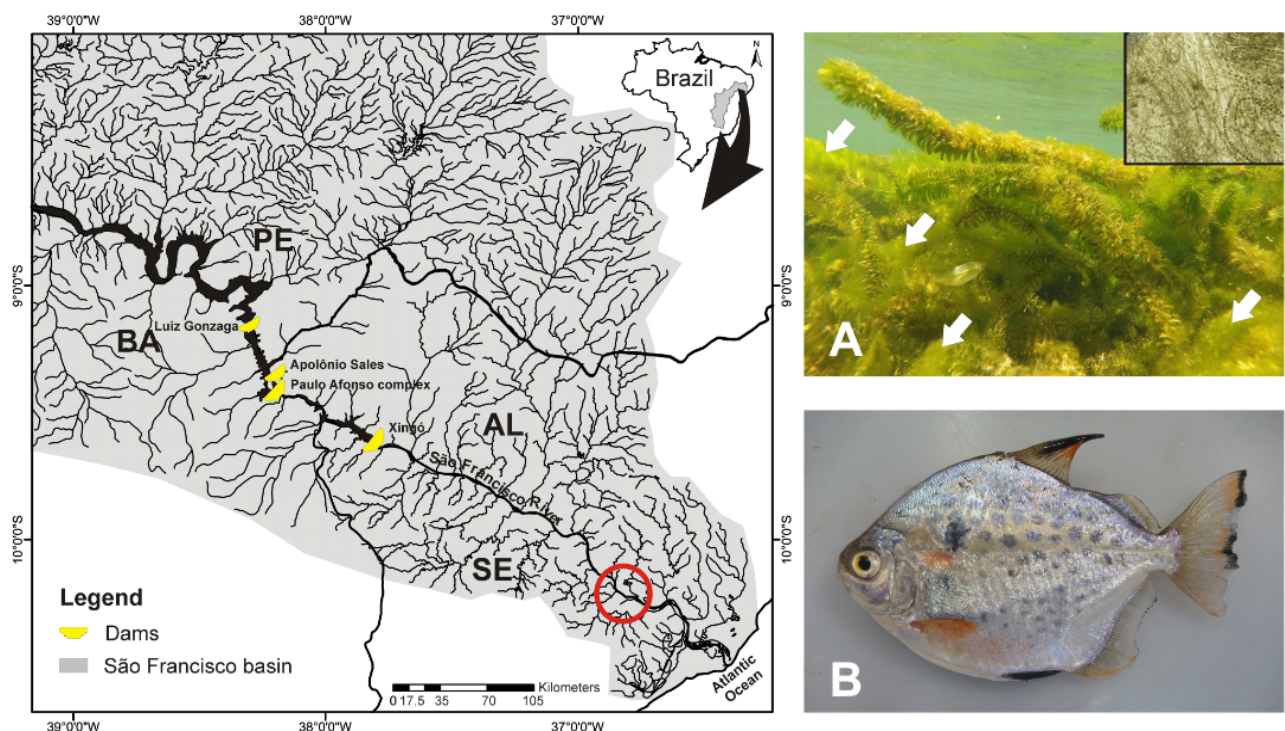


Figure 1. The final stretch of the São Francisco River basin. The study area is highlighted with a red circle. The littoral zone of the Lower São Francisco River harbors a proliferation of filamentous algae (arrows and card) and aquatic macrophytes (A) used as food items by *Metynnis lippincottianus* (B).

and wet seasons. PERMANOVA evaluated if individuals from the same season exhibited more similar diet composition than pairs of individuals from different seasons. PERMDISP evaluated if the average distances to the centroid of a multivariate space representing differences in diet composition were different between wet and dry seasons. We conducted these analyses considering individuals as samples and season (dry or rainy) as independent variable. Individuals were characterized by the volumetric proportion of each food item in their stomach contents. Alimentary Index was calculated using the R function provided in Soares *et al.* (2020). Analyses were performed using the Bray-Curtis dissimilarity coefficient and were conducted in the *vegan* package (Oksanen *et al.* 2022) in R environment (R Core Team 2021).

We analyzed 84 specimens of *M. lippincottianus*, from which 32 were sampled in the dry season and 52 in the rainy season. Specimens exhibited standard lengths ranging from 5.1 cm to 13 cm and an average intestinal quotient of 4.71 (\pm 1.45). *Metynnis lippincottianus* fed predominantly on filamentous algae from the Zygnemataceae family, and the remaining food items exhibit negligible importance in stomach contents (Table 1). Despite this, there are slight differences in the diet composition between individuals captured in the rainy and the dry season (PERMANOVA, $R^2 = 0.21$, $p < 0.001$). These differences are primarily related to a few individuals that consumed alternative items (thalloid algae, gastropoda, invertebrate eggs, and hymenoptera), expanding the niche width of the

population during the rainy season (PERMDISP, $F = 4.48$, $p = 0.04$, Drainy = 0.33, Ddry = 0.25).

The non-native silver dollar *M. lippincottianus* displayed an herbivorous diet in the Lower São Francisco River, with a larger niche width in the rainy season by some individuals' consumption of rare items. The herbivory feeding of the silver dollar is consonant with its intestinal morphology, given that the structure and length of the intestine are adapted to different feeding behaviors (Karachle & Stergiou 2010). The average intestinal quotient of *M. lippincottianus* was high, reaching about five times the standard length of the individual. This reinforces the herbivorous diet since other herbivorous fishes display similar intestinal lengths (Gurgel *et al.* 1994, Cañan *et al.* 1997, Smith *et al.* 2003) and, in general, the lowest the trophic level of fishes, the longer their intestinal lengths (Karachle & Stergiou 2010).

Nonetheless, *M. lippincottianus* is known to display both an herbivorous and an omnivorous diet (Ramos *et al.* 2021), facilitated by a complex set of incisiform and molariform teeth (Regasso 2016). In the Lower São Francisco River, this set of teeth was primarily used for cutting filamentous algae, which was the most important food item. This high importance might be related to trophic opportunism, common in Neotropical freshwater fish (*e.g.*, Lopes *et al.* 2017, Fernandes *et al.* 2020). Indeed, Zygnemataceae algae are highly abundant in the study site because of the reduced river flow, which according to Rodrigues *et al.* (2018), favors the proliferation of filamentous

Table 1. Food items recorded in the stomach contents of the silver dollar *Metynnis lippincottianus* in the Lower São Francisco River. Frequency of Occurrence (FO%), Volume (VO%) overall Alimentary Index (AI), and the Alimentary Index for the rainy season (AI_r) and dry season (AI_d).

Food items	FO (%)	VO (%)	AI	AI_r	AI_d
Filamentous algae (Zygnemataceae)	99.80	99.52	99.9924	99.9813	99.9916
Thalloid algae	1.19	0.04	0.0005	0.0022	0.0000
Plant fragments	3.57	0.18	0.0067	0.0049	0.0068
Gastropoda	1.19	0.01	0.0002	0.0008	0.0000
Invertebrate eggs	1.19	0.01	0.0001	0.0005	0.0000
Acari	2.38	0.02	0.0004	0.0000	0.0016
Hymenoptera: Formicidae	1.19	0.01	0.0001	0.0004	0.0000

algae. In addition to the lentic flow, the proximity of the study area to urban areas can generate an increase in nutrients in the river, mainly nitrogen and phosphorus, which according to Von Sperling (2014) and Tapolczai *et al.* (2015), favor the metabolism of algae. Also, algae display a high nutrient quality for freshwater organisms compared to other basal food sources, such as the leaf matter of vascular plants (Guo *et al.* 2016). Therefore, the environmental changes promoted by the damming of the Lower São Francisco River favored the establishment of the silver dollar by providing a highly abundant food resource with a high nutritional value. In addition to the high abundance of algae, the construction of the Xingó Dam also resulted in the reduction/absence of large migratory native predators (Holanda *et al.* 2009), such as *Salminus franciscanus* (Lima & Britski 2007) and *Pseudoplatystoma corruscans* (Spix & Agassiz 1829) and also in the high availability of macrophytes, especially *Elodea* sp., which serves *M. lippincottianus* as a shelter, feeding area and breeding ground (Assis *et al.* 2017).

Filamentous algae were the most important food item in the rainy and dry seasons, but we observed some individuals' consumption of rare items in the wet season. Some studies consider that rare items are accidentally consumed when associated with the preferred food item (Box *et al.* 2009, Pereira *et al.* 2010). This is because algae banks, often associated with aquatic macrophytes, serve as a refuge for organisms that can be consumed together with the algae (Pereira *et al.* 2010). Nonetheless, other rare items might reflect their low abundances in the environment (Bartolette *et al.* 2018) or intra-population variation related to other sources of variation, such as sex (Soares *et al.* 2016) or size (Heuvel *et al.* 2019). Herein, rare items' consumption was primarily associated with the rainy season. Seasonal variation in the diet of Neotropical freshwater fishes is expected, given the increased input of allochthonous items during the rainy season (Prudente *et al.* 2016, Soares *et al.* 2017, Benone *et al.* 2020). The mild effects of seasonality in the diet of the silver dollar in the Lower São Francisco River might be related to the low variation in the river flow provoked by the damming.

The environmental changes in the face of the damming of the Lower São Francisco River

increase the invasibility of the system and the establishment of potential non-native species (Kolar & Lodge 2000, Shea & Chesson 2002). The invasion success, estimated to be eight times higher in dammed environments (Johnson *et al.* 2008), is facilitated by the high food availability (Mérona & Vigouroux 2012), lack of natural predators (Souza *et al.* 2009), and specific biological attributes that favor colonization (Assis *et al.* 2017). All these factors seem to be important to the establishment of *M. lippincottianus* in the study site.

In conclusion, in the present study *M. lippincottianus* presented an herbivorous diet tending towards algivory, feeding on items generally associated with algae banks on a smaller quantity. Its feeding behavior might generate trophic overlap with native herbivores, such as *Schizodon knerii* (Steindachner 1875) and *Myleus micans* (Lütken 1875) (Pompeu & Godinho 2003), depending on other spatio-temporal factors that might promote food partitioning in fishes (Silva *et al.* 2016, Farago *et al.* 2020). Future efforts for monitoring and quantifying the impacts of the silver dollar in the Lower São Francisco River are essential to control and reduce negative impacts on the ecosystem and native fauna.

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