

## Phenotypic variation among silverside populations (Atherinopsidae: *Atherinella brasiliensis*) from distinct environments in Northeastern Brazil

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### ABSTRACT

The successful adaptation of populations to a wide range of environments is a central topic in ecology. Based on the assumption that body shape may affect survival, we evaluated to what extent biotic and abiotic factors are capable of inducing morphological changes in Brazilian silverside populations (*Atherinella brasiliensis*). To reach this goal, we compared 18 morphological traits of specimens from five ecosystems representing three types of environment (estuary, coastal lagoon, reservoir). Populations from estuaries displayed greater anal fin area and greater caudal fin aspect ratio and area. Populations from coastal lagoons had more compressed bodies, larger heads, and slightly broader caudal peduncles. The fish from estuaries and coastal lagoons had longer caudal peduncles, larger pelvic fins and larger eye area. Population from reservoir had more depressed bodies and greater oral protrusion. Food availability explained 31% of the observed ecomorphological patterns. Overall, the morphology of the respective populations was consistent with each type of environment, making it possible to associate phenotypic variation with habitat and feeding patterns, although abiotic factors were more significant than biotic factors. In conclusion, landlocked populations of *A. brasiliensis* are sustainable and add to current knowledge of phenotypical variability in a species widely distributed along the Western Atlantic coast.

### 1. Introduction

Understanding how organisms become successfully established in different environments, considering the selective pressures inherent to each habitat is a major topic in evolutionary ecology (Gomes and Monteiro, 2008; Sutherland et al., 2013; Costa-Pereira et al., 2016; Barros et al., 2019). Establishment in environments with divergent pressures may be explained by phenotypical differentiation (Weissing et al., 2011; Torres-Dowdall et al., 2012; Zamudio et al., 2016), for example, by observing the morphological variation at population level along the ecological scale (Shukla and Bhat, 2017). In fishes, morphological variation is associated with survival through occupation of habitats and foraging strategies (Mittelbach et al., 1992; Gomes and Monteiro, 2008; Senay et al., 2015). Morphological variation involves energy and physiological costs (Liao et al., 2003; Sampaio et al., 2012),

as fish experience resistance acting on the surface of the body depending on the environment in which they are inserted (Costa-Pereira et al., 2016). Since energy costs influence fitness, individual survival can be determined by the environmental selection regime (Helfman et al., 2009; Marques et al., 2020). Thus, assuming morphology is an indicator of function in the environment, phenotypes may be expected to reflect ecological parameters (Casatti and Castro, 2006; Sampaio et al., 2012; Feilich and López-Hernández, 2019).

Individuals of the same species may show minor phenotypical variations and even different swimming styles, depending on the type of habitat (e.g., river vs. lake, Collin and Fumagalli, 2011), structural complexity of the habitat (Costa-Pereira et al., 2016), occurrence of predators (Ghalambor et al., 2004; Langerhans et al., 2004), and availability of food resources (Hegrenes, 2001; Vera-Duarte et al., 2017; Zhang et al., 2020). One would not expect to observe more than one

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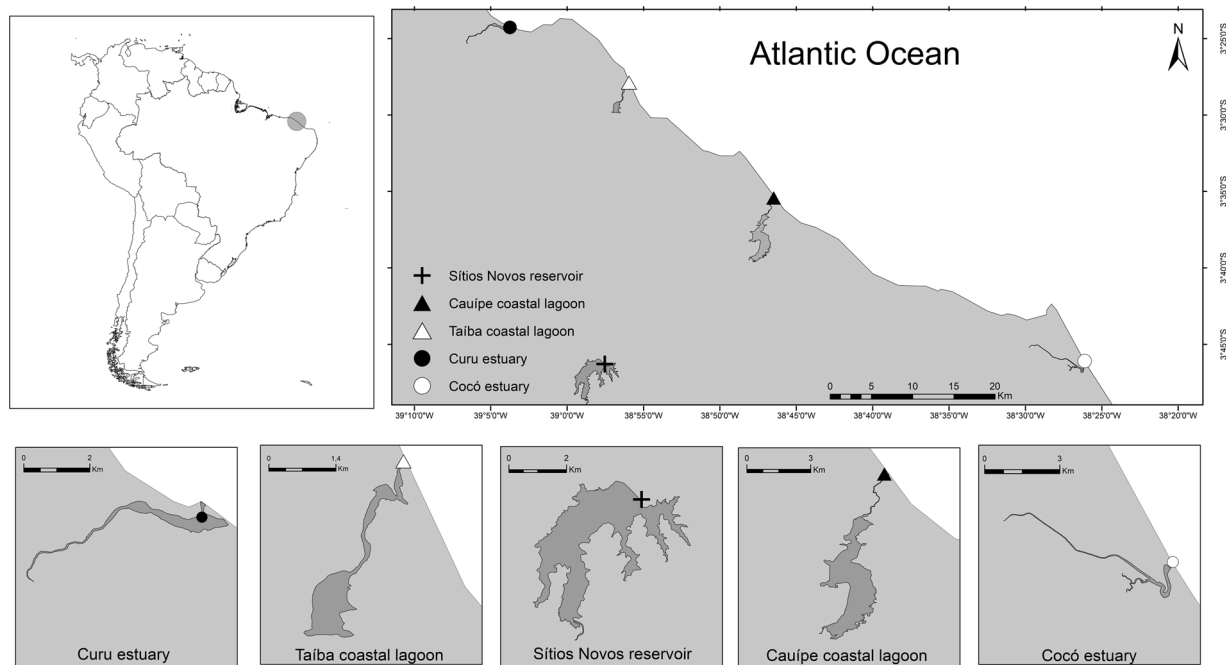
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**Fig. 1.** Locations within the five ecosystems where specimens of *A. brasiliensis* were collected. From west to east: Curu river estuary, Taíba coastal lagoon, Sítios Novos reservoir, Cauípe coastal lagoon, and Cocó river estuary.

swimming style in the same individual, but specimens from widely different habitats may display bodily variations (Langerhans and Reznick, 2010; Senay et al., 2015), including morphological traits like height and body shape, position and size of fins and caudal peduncle, associated with swimming performance, maneuverability, and acceleration (Gatz, 1979; Watson and Balon, 1984; Webb, 1982; Casatti and Castro, 2006; Perazzo et al., 2019).

Freshwater fishes living in slow-flowing waters often have more compressed bodies, broader caudal peduncle, and less stable swimming, while fishes living in fast-flowing waters tend to have more slender or fusiform bodies and narrower caudal peduncle, reflecting continuous and stable swimming patterns (Langerhans et al., 2003; Langerhans, 2008). Likewise, fishes from different coastal environments, where water currents seem to be an important environmental factor, show variation in body shape and size (Perazzo et al., 2019).

The availability of food in the environment also exerts selective pressure on certain traits (Vera-Duarte et al., 2017; Zhang et al., 2020). Fishes with a relatively large head and mouth are likely to feed on accordingly large prey, while increased jaw protrusion may be a morphological variation resulting from reliance on small food items (Winemiller, 1991; Pouilly et al., 2003; Willis et al., 2005). For example, some types of fishes (e.g., cichlids and serranids, Oufiero et al., 2012; Pease et al., 2018) can expand the oral cavity to secure large prey, while others (e.g., atherinopsids and gerreids, Silva et al., 2016; Martínez-Palacios et al., 2019) protract the mouth longitudinally to capture small prey through a minute opening. Even the size and position of the eyes can reflect behavioral aspects related to prey detection or defensive visualization of predators (Pankhurst, 1989; Pouilly et al., 2003). Predation pressure may also explain morphological variation (Glazier and Deptola, 2011; Hammerschlag et al., 2018). In the presence of predators, *Carassius carassius* (Linnaeus, 1758) develops a higher body height (Brönmark and Miner, 1992), and *Lepomis gibbosus* (Linnaeus, 1758) increases body height and dorsal spine length when stimulated by predation cues (Januszkiwicz and Robinson, 2007).

Studies have revealed morphological differences among fish populations that occupy distinct estuarine and coastal environments (Bamber and Henderson, 1988; Fluker et al., 2011; Perazzo et al., 2019; Santos et al., 2019; Colautti et al., 2020). In this study we evaluated to

what extent abiotic and biotic factors affect the morphological structure of Brazilian silverside, *Atherinella brasiliensis* (Quoy & Gaimard, 1825), in two estuaries, two coastal lagoons and a reservoir. The species is a sexually monomorphic member of the family Atherinopsidae distributed along the coast of the Western Atlantic, from the Colombian Caribbean to Uruguay (Froese and Pauly, 2019). An estuarine resident species, it thrives in both seawater and estuaries (Pessanha and Araújo, 2001; Neves et al., 2006) and is capable of colonizing inland waters (Bamber and Henderson, 1988; Bloom et al., 2013; Colautti et al., 2020). It plays an important role in the food web of coastal ecosystems due to its abundance, generalist feeding habits (Contente et al., 2011; Alves et al., 2016; Brito et al., 2019) and its place as prey for larger fish, birds, and mammals (Bordignon, 2006; Lopes et al., 2012).

The abiotic factors (water flow, depth, salinity fluctuations) and biotic factors (food availability) are widely different in estuaries, coastal lagoons and reservoir. We expected these external factors to explain the morphological differences observed between the sampled populations. To test our hypothesis, we compared the morphology of populations of *A. brasiliensis* from five different habitats and quantified the contribution of each abiotic or biotic factor to the observed variation.

## 2. Materials and methods

### 2.1. Study area and description of environments

Monthly samplings (in 2014) of a landlocked population of *A. brasiliensis* were conducted in an artificial freshwater ecosystem in Northeastern Brazil formed by the damming of the São Gonçalo river (Sítios Novos reservoir). The reservoir covers an area of 16.48 km<sup>2</sup>, with an average depth of 7.64 m. The distance to the sea along the river is approximately 38 km. During the rainy season, the reservoir becomes connected to an outlet (R. Gurgel-Lourenço, pers.obs.) leading to marine ecosystem near the Taíba coastal lagoon, in which *A. brasiliensis* occurs naturally and was sampled for the study. In order to rule out possible influences from this connection, we monthly collected *A. brasiliensis* from another coastal lagoon (Cauípe) 23 km from the Taíba lagoon. Bimonthly samples of *A. brasiliensis* from estuaries were also included in the study due to the peculiar characteristics of this type of ecosystem

**Table 1**  
General environmental characteristics of the coastal lagoons, reservoir, and estuaries of this study.

	Coastal lagoons		Reservoir	Estuaries	
	Taíba	Cauípe	Sítios Novos	Curu	Cocó
Average depth	1.03 m	1.90 m	7.64 m	2.20 m	1.43 m
Maximum depth	2.46 m	3.50 m	11.65 m	3.55 m	2.32 m
Depth pattern	shallow	shallow	deep	shallow	shallow
Flow pattern	lentic	lentic	lentic	lotic	lotic
Salinity	seasonal freshwater (0)-brackish (1-25)	seasonal freshwater (0)-brackish (1-28)	Freshwater (0)	seasonal freshwater (0)-brackish (1-29) -saline (30-37) - hypersaline (38-40)	seasonal freshwater (0)- brackish (1-29)- saline (30-35)

when compared to inland reservoirs and coastal lagoons. The sampled estuaries were at different distances from the coastal lagoons and had different annual salinity profiles. Thus, the Curu river estuary is closer to the coastal lagoons and displays high levels of salinity from June to January. The Cocó river estuary is further away from the other ecosystems and receives a greater input of freshwater. At the mouth, the water is euhaline, but salinity quickly decreases upstream, reaching freshwater levels at only 1 km, with no seasonal hypersalinity. The samplings in the estuaries were carried out during ebb and flood tide in waxing crescent or waning crescent moon. In other words, the ecosystems from which specimens of *A. brasiliensis* were collected differed significantly with regard to depth, water flow, food availability, salinity, and (most likely) predator diversity (Fig. 1, Table 1).

## 2.2. Sampling and procedures

The collection method, which was standardized for the five ecosystems, employed a seine net 25 m long and 2 m high with 12-mm knot-to-knot mesh size. The seine net was used three times in each habitat per sampling trip. Following licensing by federal authorities (SISBio/ICMBio #40308, #43014, #57780), sampling was done near the dam (reservoir) or approximately 300 m from the inlet (lagoons) or river mouth (estuaries). The collected fish were euthanized with eugenol and fixed in 10% formaldehyde for 48 hours, followed by preservation in alcohol at 70%. Voucher specimens were deposited in the collection at the Laboratory of Systematic and Evolutionary Ichthyology of the Federal University of Rio Grande do Norte and in the collection of the Federal University of Paraíba. Vouchers: UFPB11967 (Taíba coastal lagoon), UFPB11966 (Cauípe coastal lagoon), UFRN3526 (Sítios Novos reservoir), UFRN4639 (Curu estuary), UFRN4820 (Cocó estuary).

Twenty subsamples of adult individuals from each of the five ecosystems were randomly selected from a set of individuals (more than 100 individuals per environment type), 10 of which from the rainy season and 10 from the dry season in order to minimize confounding from seasonal fluctuations (Burton et al., 2020). Larger individuals (only adults > 59 mm standard length) were selected at random to reduce ontogenetic bias associated with morphology, feeding patterns and habitat use (Polte et al., 2017; Brito et al., 2019). Individual traits were measured after 15 days of preservation in formaldehyde to minimize the effect of the chemical on the morphometry (Martinez et al., 2013; Sotola et al., 2019; Fruciano et al., 2020).

Fifteen linear and six area measurements were taken for each specimen (Fig. S1), following Oliveira et al. (2010). The linear measurements were made with a caliper (accuracy: 0.01 mm) while area measurements were made from photographs using the software AxioVision 4.8. This allowed determination of 18 ecomorphological variables per individual (Table S1) to calculate the mean values for the respective population.

All measured specimens subsequently had the stomach removed for content analysis using the method developed by Kawakami and Vazzoller (1980). Gonadal maturity was confirmed to ensure only adults were included in the analysis. Each type of prey was identified down to the lowest possible taxon and categorized in major groups. The volume of each macroscopic item was determined with the aid of graph paper

**Table 2**  
Classification of matrices predicted by discriminant function analysis (DFA) for the three types of ecosystem.

Environment	Sítios Novos	Cocó	Curu	Taíba	Cauípe	% classification
Sítios Novos reservoir	18	0	0	0	2	90.0
Cocó estuary	0	14	6	0	0	70.0
Curu estuary	0	7	13	0	0	65.0
Taíba lagoon	1	2	0	16	1	80.0
Cauípe lagoon	1	0	1	1	17	85.0

and a ruler, while the volume of microscopic items was determined with a Segdwick-Rafter camera coupled to a light microscope. The diet of specimens from each ecosystem was quantified with the index of Kawakami and Vazzoller (1980) and expressed in percentage ( $I_{ai} = [F_i \times V_i] / \sum [F_i \times V_i]$ , where  $F_i$  is the frequency of occurrence and  $V_i$  is the volumetric frequency of item  $i$ ).

## 2.3. Data analysis

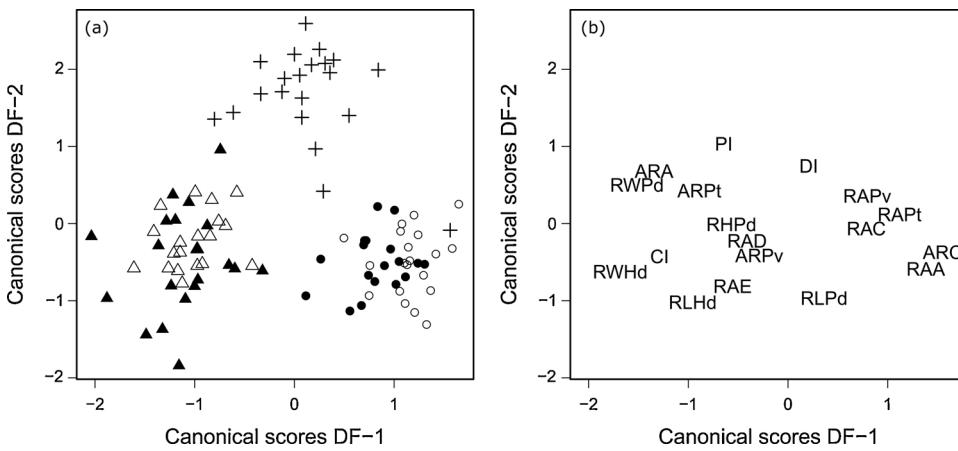
Linear combinations of ecomorphological traits between habitats were identified by Discriminant Function Analysis (DFA) with variable selection in order to separate the main morphological predictors of the five ecosystems. Using Multivariate Analysis of Variance, we then tested for significant ecomorphological differences between the groups identified by DFA. In addition, we verified whether our *a priori* classification of the type of habitat where each individual was collected coincided with the classification generated by DFA, thereby determining the proportion of correct classifications for each type of habitat. High proportions are an indication that the pressure exerted by each type of habitat produced marked morphological differences between the sampled populations.

Finally, we conducted a Redundancy Analysis (RDA) to evaluate the association between diet and ecomorphological variation in each ecosystem. In this analysis we used only the ecomorphological traits selected from the DFA as response variable and the Hellinger-transformed trophic matrix as predictive variable. Habitat type was controlled for in this analysis to evaluate the ability of the trophic component alone to explain the observed ecomorphological patterns. The influence of the predictive matrix on the response matrix was evaluated by running a permutation test with 999 random permutations. Finally, we identified the key trophic items associated with morphological variation using a *forward-selection* procedure with 999 permutations. All analyses were performed with the software R: MASS and vegan packages (Venables and Ripley, 2002; Oksanen et al., 2019).

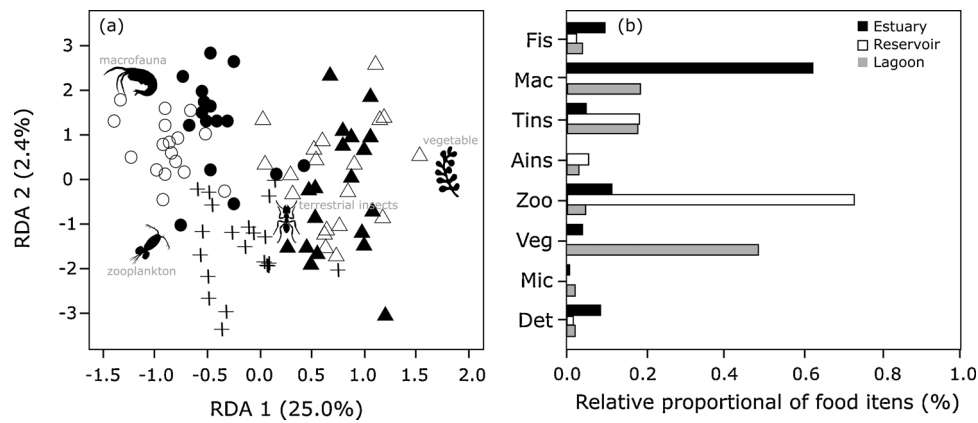
## 3. Results

### 3.1. Intraspecific morphological patterns

A total of 20 specimens from each ecosystem were analyzed, totaling



**Fig. 2.** Discriminant function analysis (DFA) comparing the three types of ecosystem with regard to populational ecomorphology (Wilks'  $\lambda = 0.94$ ,  $F_{05,5} = 20.89$ ;  $P < 0.001$ ). Triangles: coastal lagoons (black: Cauípe, white: Taíba); crosses: Sítios Novos reservoir; circles: estuaries (black: Curu, white: Cocó). Morphological traits: CI (compression index), DI (depression index), PI (protrusion index), RLHd (relative length of head), RWHd (relative width of head), RLPd (relative length of caudal peduncle), RHPd (relative height of caudal peduncle), RWPd (relative width of caudal peduncle), RAE (relative area of eye), ARPt (aspect ratio of pectoral fin), RAPt (relative area of pectoral fin), ARPv (aspect ratio of pelvic fin), RAPv (relative area of pelvic fin), RAD (relative area of dorsal fin), ARA (aspect ratio of anal fin), RAA (relative area of anal fin), ARC (aspect ratio of caudal fin), RAC (relative area of caudal fin).



**Fig. 3.** Redundancy analysis (RDA) of the association between diet and ecomorphological variables (a) and average amounts of food items consumed in the three types of ecosystem (b). Triangles: coastal lagoons (black: Cauípe, white: Taíba); crosses: Sítios Novos reservoir; circles: estuaries (black: Curu, white: Cocó). Fis: fish; Mac: benthic macrofauna; Tins: terrestrial insects and insect fragments; Ains: aquatic insects; Zoo: zooplankton; Veg: vegetable; Mic: microalgae; Det: sediment/detritus.

100 adults. Most of the morphological variables differed between ecosystems (Table S2). The ecomorphological classification of the *A. brasiliensis* populations predicted by DFA revealed a high proportion of correct classifications for each ecosystem (Table 2). The DF-1 axis discriminated the three types of ecosystems. Thus, populations from estuaries displayed greater anal fin area (RAA) and greater caudal fin aspect ratio and area (ARC, RAC), while populations from coastal lagoons had more compressed bodies (CI), larger heads (RLHd, RWHd), and slightly broader caudal peduncles (RHPd). The DF-2 axis segregated the reservoir from the two other types of ecosystem based mainly on the more depressed bodies (DI) and greater oral protrusion (PI). The fish collected in estuaries and coastal lagoons had longer caudal peduncles (RLPd), larger pelvic fins (ARPv) and, to a lesser degree, larger eye area (RAE) (Table S2, Fig. 2).

### 3.2. Diet/ecomorphology relationship

After controlling for habitat type, food availability explained 31% of the observed ecomorphological patterns. In other words, the type of diet was significantly associated with ecomorphological variables ( $F_{92,8} = 5.22$ ;  $P = 0.001$ ). The variables 'benthic macrofauna', 'vegetable matter', 'terrestrial insects' (mainly fragments), and 'zooplankton' were forward-selected ( $p < 0.05$ ). Populations from estuaries were found to feed mostly on benthic macrofauna (Decapoda, Polychaeta) followed by

zooplankton, while the stomachs of lagoon-dwelling fishes contained mostly vegetable matter, followed by insects and benthic fauna (shrimp). The specimens from the reservoir consumed primarily zooplankton (Ostracoda, Calanoida, Cyclopoida), followed by insects (Fig. 3, Table 3).

## 4. Discussion

In this study, morphological variation in *A. brasiliensis* was found to be associated with habitat and diet. Thus, the measured morphological traits depended on whether the specimen was collected in an estuary, coastal lagoon, or reservoir. Most of the variation between ecosystems was consistent with our hypothesis of external factors explaining morphological differences. Twelve traits (habitat use  $n = 3$ , feeding  $n = 4$ , swimming performance  $n = 3$ , fine maneuvering  $n = 2$ ) showed variation from one ecosystem to the other, while other traits remained unchanged. The observed morphological differences allowed to assign a set of ranges of traits to each environment, including the population in the reservoir, despite the small number of generations since their introduction (generation time = 1.3 years; lifespan = 3.4 years, Froese and Pauly, 2019). Therefore, we highlight that abiotic and biotic factors in aquatic habitats are important to understand the phenotypic variation in *A. brasiliensis*.

The Sítios Novos reservoir is the slowest-flowing and deepest water

**Table 3**

Prey consumed by *Atherinella brasiliensis* in the five ecosystems, expressed as index of Kawakami and Vazzoler (1980). \* = forward-selected items. Bold = Items groups and significant values.

Item	Coastal lagoons		Reservoir	Estuaries	
	Taíba	Cauípe	Sítios Novos	Curu	Cocó
<b>Sediment/detritus</b>					
Sediment	1.52	1.65	0.22	<b>8.55</b>	<b>16.04</b>
Detritus	-	-	-	1.64	-
<b>Microalgae</b>					
Diatomaceae	-	-	-	0.43	-
Perifiton	0.03	0.29	-	-	-
<b>Vegetable</b>					
Vegetable matter	<b>31.69</b>	<b>83.04</b>	-	-	2.89
Seed	0.41	-	-	-	-
<b>Zooplankton</b>					
Rotifera	-	-	-	<b>3.06</b>	0.01
Ostracoda	-	-	<b>36.30</b>	0.06	-
Copepodito	-	-	-	-	0.39
Calanoida	-	-	<b>25.44</b>	<b>14.11</b>	0.61
Cyclopoida	-	-	<b>13.81</b>	0.18	0.89
Harpacticoida	-	-	-	<b>2.65</b>	<b>3.63</b>
Cladocera	-	<b>4.13</b>	0.99	0.04	-
Brachyura Megalopa	-	-	-	-	2.05
<b>Benthic macrofauna</b>					
Amphipoda Gammaridae	0.99	-	-	<b>11.95</b>	2.03
Shrimp	<b>32.59</b>	0.34	-	1.81	-
Brachyura	-	-	-	5.14	-
Crustacea non-Brachyura	-	-	-	<b>25.86</b>	0.73
Polychaeta	0.41	-	-	1.80	<b>46.80</b>
Gastropoda	-	-	-	-	<b>17.77</b>
<b>Aquatic insects</b>					
Diptera larvae	0.02	-	2.13	-	-
Ephemeroptera nymph	0.10	-	-	-	-
Odonata nymph	0.07	-	-	-	-
Hemiptera Belostomatidae	0.58	-	-	-	-
<b>Terrestrial insects</b>					
Diptera adult	-	0.01	-	-	0.10
Hymenoptera	0.54	0.04	0.04	-	0.79
<b>Insect fragments</b>					
Insect fragments	<b>28.08</b>	<b>10.37</b>	<b>20.29</b>	0.34	2.09
<b>Other terrestrial invertebrates</b>					
Aranae	0.01	-	-	-	-
<b>Fish scale/fish</b>					
Fish scale	0.86	0.10	0.75	0.02	<b>2.80</b>
Fish	<b>2.09</b>	-	0.02	<b>7.61</b>	0.38
<b>Not identified</b>					
	-	0.03	-	14.74	-
	Taíba	Cauípe	Sítios Novos	Curu	Cocó
Sediment/detritus	1.52	1.65	0.22	<b>10.19</b>	<b>16.04</b>
Microalgae	<b>0.03</b>	0.29	-	0.43	-
Vegetable (*)	<b>32.10</b>	<b>83.04</b>	-	-	2.89
Zooplankton (*)	-	4.13	<b>76.54</b>	<b>20.11</b>	7.58
Aquatic insects	0.77	0.01	<b>2.13</b>	-	-
Terrestrial insects	0.54	0.05	0.04	-	0.89
Insect fragments (*)	<b>28.08</b>	<b>10.37</b>	<b>20.29</b>	0.34	2.09
Benthic macrofauna (*)	<b>33.99</b>	0.34	-	<b>46.56</b>	<b>67.33</b>
Other terrestrial invertebrates	0.01	-	-	-	-
Fish scale/fish	<b>2.95</b>	0.10	0.77	<b>7.63</b>	<b>3.18</b>
Not identified	-	0.03	-	14.74	-

body included in the study. The body depression index was highest in this environment, indicating pelagic habits (Costa-Pereira et al., 2016; Malato et al., 2017; Barros et al., 2019), and specimens collected in the reservoir had no benthic prey in the stomach. Such prey is scarce or hard to forage due to hypoxia at greater depths in this habitat (Bezerra et al., 2014; Bezerra et al., 2018). The pectoral fins aspect ratio and relative width of caudal peduncle were larger in specimens from the reservoir and coastal lagoons, indicating habits of continuous swimming and a preference for the pelagic zone (Winemiller, 1991; Wainwright et al., 2002). This was borne out by the predominance of zooplankton in the diet.

Specimens collected in coastal lagoons had more compressed bodies in association with slow-flowing shallow waters and greater structural complexity due to the presence of aquatic vegetation (Neves and Monteiro, 2003; Thomaz and Cunha, 2010; Kovalenko et al., 2012). These characteristics also allowed to predict the mixed benthic/zooplankton diet observed for specimens from coastal lagoons (Pérez-Ruzafa et al., 2011; Brito et al., 2019). Area of the anal fin (added stability in fast-flowing waters) was larger in estuarine populations. On the other hand, the ability to make swift forward and backward movements (aspect ratio of the anal fin, Breda et al., 2005) was greater in lagoon and reservoir specimens, reflecting adaptation to structurally complex environments and/or slow-flowing waters.

The oral protrusion index revealed a morphological gradient between the different types of environment. Thus, the index was greatest in specimens from the reservoir, as a result of the reliance on tiny prey and zooplankton (Gatz, 1979; Motta, 1984; Winemiller, 1991), followed by specimens from coastal lagoons and specimens from estuaries, matching the increasing size of the consumed prey. However, head size was largest in lagoon specimens; this was contrary to our expectations (Winemiller, 1991; Pouilly et al., 2003; Willis et al., 2005; Martínez-Palacios et al., 2019), considering the predominance of large macrobenthic prey in the diet of specimens from estuaries.

A benthic-pelagic species like *A. brasiliensis* can occupy most of the water column, from surface to bottom (Gibran, 2010), ensuring successful adaptation to a variety of ecosystems. For example, a well-established landlocked population of an opportunistic species like *A. brasiliensis* should explore the ecological opportunities (Stroud and Losos, 2016; Levis et al., 2017) provided by artificial ecosystems with low faunal diversity (Agostinho et al., 2008). Directed studies are necessary to evaluate the predation pressure *A. brasiliensis* is exposed to in these environments (a species may have no predators in recently colonized ecosystems, Moyle and Marchetti, 2006). In estuaries silversides have many natural predators (Whitfield, 2015), such as needlefish, snooks and barracudas (Garcia and Vendel, 2016). In the Taíba coastal lagoon, in addition to the possible occurrence of these predators, peacock bass (*Cichla* sp.) were observed during snorkeling. When introduced, this non-native predator is capable of decimating populations of small fish (Pelicice and Agostinho, 2009). Non-native species such as *Cichla* spp., *Arapaima* sp. and *Plagioscion* spp. (potential predators of *A. brasiliensis*, Pelicice and Agostinho, 2009; Barros et al., 2012; Carvalho et al., 2018) have also been reported from the reservoir at Sítios Novos, and stomachs of peacock bass captured in this reservoir contained silversides (Bezerra et al., 2018). The hypothesized high predation pressure in all three types of ecosystems may explain the small variation observed in eye size, a trait associated with predator detection (Glazier and Deptola, 2011; Hammerschlag et al., 2018).

Salinity exerts a selective pressure on fish through metabolism, leading to the growth or loss of body structures (Bamber and Henderson, 1988; Weaver et al., 2016). Despite the difference in salinity patterns (hypersaline vs. brackish), populations from estuaries formed a cluster of similar morphotypes. More specific investigations are needed to determine the influence of salinity on intraspecific variability in *A. brasiliensis*, as observed for other atherinopsids (Bamber and Henderson, 1988; Berasain et al., 2015; González-Castro et al., 2019) using microgeographic sampling designs (Maciejewski et al., 2020). Such studies should also include physiological (metabolic rate and post-hypoxia oxygen consumption) and life history variables (Moresco and Bemvenuti, 2006; Rius et al., 2019; Pang et al., 2020).

Most studies on functional ecology assume intraspecific variability is small compared to interspecific variability (Villéger et al., 2017). This perception is changing in light of evidence of high levels of variability between populations or individuals (Villéger et al., 2017; Raffard et al., 2019; Blanchet et al., 2020), making it possible to effectively predict the response of species to changes in the environment (Violle et al., 2012; Raffard et al., 2019; Blanchet et al., 2020). A high intraspecific variability allows a single species to occupy different functional niches,

reflecting sexual, ontogenetic and adaptative differences (Villéger et al., 2017). As a result of this variability, populations of the same species may experience different levels of predator pressure or explore different resources depending on the type of environment (Bolnick et al., 2011). The present study shows that phenotypes of *A. brasiliensis* depend on the type of ecosystem where the population is found, and suggests that these phenotypes represent different functional entities (Villéger et al., 2017), with different magnitudes of influence on ecosystemic processes (Bolnick et al., 2011; Blanchet et al., 2020).

## 5. Conclusion

The morphometric profile of the specimens of *A. brasiliensis* sampled for this study was generally consistent with habitat type, abiotic variables and feeding strategies. Our results support the notion that landlocked populations of *A. brasiliensis* are sustainable and add to current knowledge of phenotypical variability in a species widely distributed along the coast of South America, with emphasis on the diversity and structure of lineages in Northeastern Brazil (Baggio et al., 2017). Future studies might attempt to determine whether this variability is the result of phenotypical plasticity or *a priori* genetic differences (Svanbäck and Eklöv, 2006; Elmer et al., 2010; Zamudio et al., 2016; González-Castro et al., 2019; Seymour et al., 2019; Colautti et al., 2020), possibly by focusing on specimens with restricted natural distribution.

## Declaration of Competing Interest

All authors declare no conflict of interest.

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