



Morphological differences between an artificial lentic and adjacent lotic environments in a characid species

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Abstract Dam constructions cause fundamental changes in the natural landscape, creating new ecological and evolutionary challenges for aquatic organisms. In some cases, such water impoundments have been related with morphological changes in organisms. Understanding how populations respond to rapid environmental changes imposed by dams is the first step to elucidate the consequences that disturbed habitats may have on species evolution. In this work, we analyzed shape and size variation in *Bryconamericus iheringii* Boulenger 1887 from the Chasqueiro stream basin, south of Brazil, which was recently dammed. We used linear measurements and geometric morphometrics to identify morphological differences among specimens from the reservoir (lentic habitat) compared to the habitat upstream and downstream of the dam (lotic habitats). We also tested for size- and shape-related sexual dimorphism to

determine whether variations observed were the same for both sexes. We found that *B. iheringii* from the artificial reservoir were distinct in shape and size to those from their natural habitat in the stream. The size variation between environments was the same for both sexes, but the shape variation differed between males and females. Regarding the linear measurements, lotic populations were larger (greater body length, width, pectoral fin base length and caudal peduncle length), probably in response to increased swimming activity. Regarding body shape, we found that both sexes have a more fusiform body in lotic habitats than in the reservoir. In addition, females showed an altered mouth position that was distinct between these environments. This work indicates that the water reservoir seems to be an important factor influencing morphological variation in *B. iheringii*, a species with sexual shape dimorphism.

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Introduction

The demand for fresh water has more than tripled since 1950, leading to an increase in human interventions in water resources such as modifications of the flow regime of rivers and streams (Goudie 2018). Reservoir

operating regimes, determined to best use reservoirs for their intended purposes, may substantially change their physical and chemical characteristics as well as the biology of organisms living within their confines (Schmutz and Moog 2018). Organisms inhabiting these types of altered habitats are exposed to different environmental conditions compared to those inhabiting native environments, which can lead to members of the same species eventually exhibiting different phenotypes, depending on the type of environmental conditions they are exposed to. Intraspecific morphological divergence in fishes has been recorded in response to anthropogenic disturbances such as impoundments (Haas et al. 2010; Franssen 2011; Franssen et al. 2013; Grabowski et al. 2018). Impoundment causes the interruption of the continuity of a river, affecting both the migration of fishes and the transport of sediments and nutrients. In addition, impoundments create a completely new environment, characterized by homogenization of habitats and the alteration of the flow regime of the river, which can in turn affect water quality and downstream flow conditions. A first attempt to understand how populations respond to such rapid and extensive environmental changes should be to predict the consequences of habitat disturbance on species evolution (Franssen et al. 2013), beyond the immediate ecological effects that such disturbances have on native species (such as the possibility of loss of species diversity and the creation of conditions for exotic invasion). The response of organisms to rapid environmental disturbances as mediated by the creation of a water reservoir is often manifested in distinctive morphological features.

Alterations, such as those caused by dams, lead to fundamental changes in natural landscapes, creating new ecological and evolutionary challenges related to water flow regime in aquatic organisms (Haas et al. 2010). Therefore, analyzing species in these altered environments and comparing them to the source populations may serve as a study system to investigate responses to environmental disturbances (Franssen et al. 2013). In general, fish species that inhabit lotic and lentic environments may show morphological differentiation related to swimming performance, which can be altered according to water current changes (Lauder 2014). Individuals from lentic environments, or from areas with very slow water current, tend to have a deeper body (larger dorsal–ventral axis

and smaller anterior–posterior axis) when compared with populations from rivers and streams with faster currents (Theis et al. 2014). Fish usually are characterized by a more fusiform body shape (Haas et al. 2010) with longer, wider and deeper caudal peduncles (Gaston and Lauer 2015) (but see Franssen 2011). However, the construction of reservoirs does not only alter the water current, but also the entire ecology of the area, potentially creating different selective pressures, such as those related to feeding, predator evasion, maneuverability, microhabitats and refuge availability, reproduction, etc. The ability to escape from predators and the availability of food items and predator efficiency between altered and natural environments may vary, affecting fish fitness and promoting the expression of morphological plasticity, which have already been noted for many fish species (Langerhans and DeWitt 2004; Langerhans et al. 2004; Gomes and Monteiro 2008).

In the present work, we analyzed morphological variation of a characid fish species from a recently-dammed, subtropical stream in the Neotropical region. Specifically, we described shape and size differences between both sexes of *Bryconamericus iheringii* Boulenger 1887 from lentic and lotic habitats present in the Chasqueiro Stream basin, Southern Brazil. We choose *B. iheringii* because it is an abundant species along the basin (Corrêa et al. 2015). *B. iheringii* is thought to be a generalist with opportunist dietary habits, and shows a high degree of trophic plasticity (Kokubun et al. 2018). The species shows no sexual dimorphism, except with respect to small fin-ray hooks apparent in mature males (Lampert et al. 2004). These characteristics make *B. iheringii* from the Chasqueiro Stream a good model to investigate two hypotheses: (1) alteration of the water current is an environmental factor affecting fish morphology in this recently dammed subtropical stream, and (2) both sexes show the same differentiation across water regimes.

Methods

Study area

Sampling sites were at the hydrographic basin of the Chasqueiro Stream, which belongs to Mirim Lagoon system, in the city Arroio Grande, south of Brazil

(31°6'51"S and 50°5'17"W) (Fig. 1a). In general, this region presents a subtropical climate with an average annual rainfall ranging from 1200 to 1450 mm and an average temperature that varies between 11 and 25 °C. The Chasqueiro Stream basin is formed by two main streams (Chasqueiro and Chasqueirinho) that unite to form a single stream (also called Chasqueiro), with a total area of approximately 248 km². During the 1980s, the stream was dammed with the aim of constructing a water reservoir to meet the agricultural demand for water in the area, predominantly to sustain rice production. The impoundment has altered the natural watercourse, creating an artificial lentic environment with an area of 1800 ha between the upstream and downstream natural lotic environments (Fig. 1b).

Beyond distinctions related to current, these lentic (reservoir) and lotic (downstream and upstream) environments also are different with respect to geomorphological features, vegetation composition and aquatic fauna (Corrêa et al. 2015).

Sampling and data acquisition

We sampled the reservoir and upstream and downstream sections of the Chasqueiro stream between May and September of 2016, using a beam trawl and hand nets. Ninety-four adult specimens with a mean of 43.6 mm of standard length (SL) were sampled, of which, 42 were females (32.3–60.3 mm SL) and 52 were males (28.3–61.8 mm SL) (Table 1). We

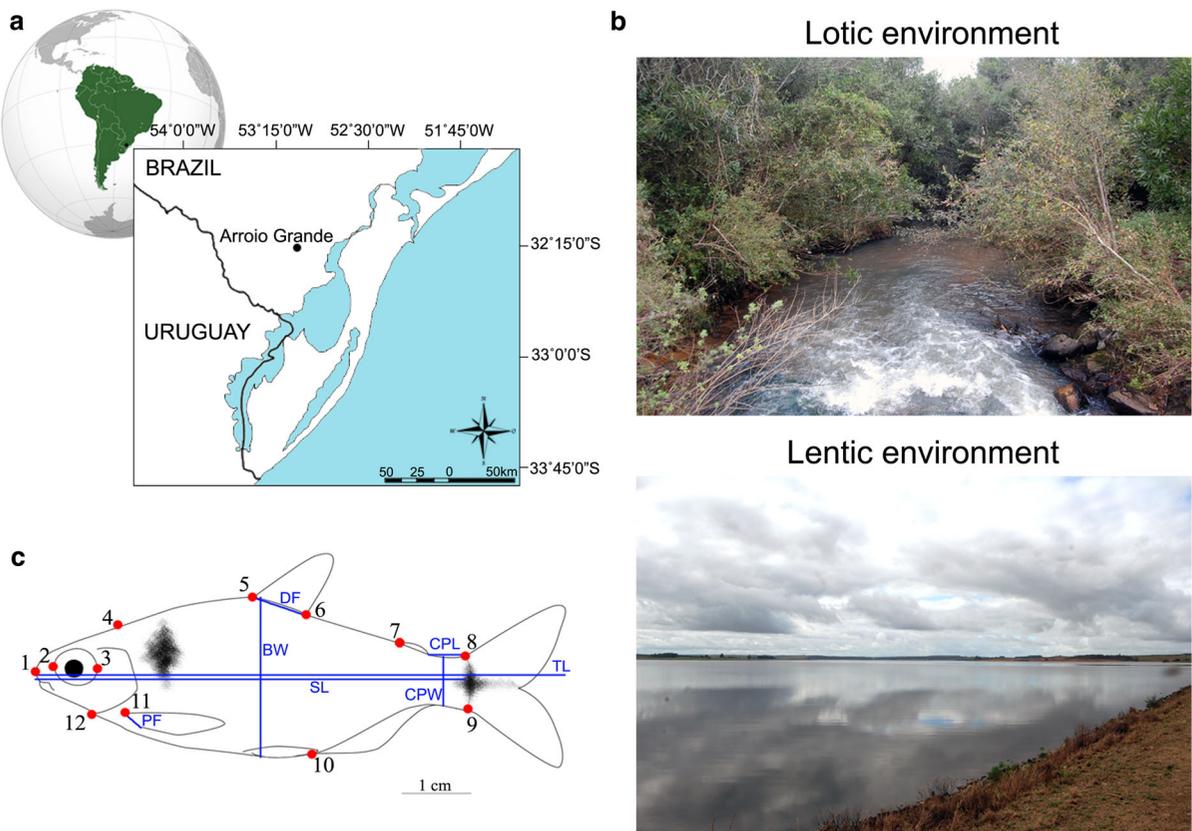


Fig. 1 Sampling site map (a), illustrative images from lotic environments (both upstream and downstream of the reservoir) and lentic environments (reservoir) (b) and landmarks plus linear measurements of *Bryconamericus iheringii* at left (c). Landmarks are marked by red dots: 1-snout anterior margin upper jaw; 2-eye anterior most margin; 3-posterior most eye margin; 4-supraoccipital process posterior margin; 5-dorsal fin base origin; 6-dorsal fin base posterior margin; 7-adipose fin

base origin; 8-caudal fin base dorsal margin; 9-caudal fin base ventral margin; 10-anal fin origin; 11-pectoral fin base anterior margin; 12-ventral margin of gill opening. Linear measurements are indicated with blue lines and include: Total length (TL), standard length (SL), dorsal fin base length (DF), body width (BW), pectoral fin base length (PF), caudal peduncle length (CPL) and caudal peduncle width (CPW)

Table 1 Number of specimens per sex per site of sampling

Sex	Upstream	Dam	Downstream	Total
Males	10	19	13	42
Females	13	14	25	52
Total	23	33	38	94

considered adult specimens with SL > 20 mm to be in reproductive state, according to the relationship between gonadal maturation and SL for this species (see Lampert et al. 2004). In the laboratory, individuals were anesthetized by immersion in clove oil solution and digital images were taken in a standardized way. Specifically, photographs of the lateral left side of each specimen were taken using a digital camera (Nikon® D90) mounted at approximately 50 cm. The specimens were positioned on a graph paper, their fins were extended, and the dorsal and anal fins were pinned. Soon after the photographs were taken, sex identification was performed by observing the gonads using a microscope. Prior to morphometric analyses, digital images were converted into .tps files, using tpsUtil 1.64 software (Rohlf 2013). For each specimen, 12 landmarks were recorded using tpsDIG2 2.30 software (Rohlf 2015) (Fig. 1c). We used the same software to get the following linear measurements: total length (TL), standard length (SL), dorsal fin base length (DF), body width (BW), pectoral fin base length (PF), caudal peduncle length (CPL) and caudal peduncle width (CPW) (Fig. 1c). To avoid bias related to the acquisition of landmarks and linear measurements, the same person performed all processes (GXP).

Data analysis

Linear morphometry Standardized relative measures (RM) were used for linear morphometric analyses, which were obtained by dividing each measure by the individual standard length, according to Shukla and Bhat (2017) and Perazzo et al. (2019). To accomplish this, we first tested the linearity between standard length and each variable using a regression analysis. Normal distribution and homogeneity of variances for relative distances were examined by Shapiro–Wilk and Levene’s tests, respectively. The variation between sites and sexes for each relative measurement

was analyzed through two-way Analysis of Variance (ANOVA) followed by a pairwise Tukey test and visualized using boxplots.

Geometric morphometrics Geometric morphometric analyses were performed with shape coordinates obtained from Generalized Procrustes Analyses (GPA) (Rohlf and Slice 1990), which minimizes the differences of translation, scaling, and rotation between landmarks (Zelditch et al. 2012). We also obtained the centroid size values from GPA, characterized as the square root of the sum of the squares of the distance of each landmark from the centroid (mean of all coordinates) of the configuration (Bookstein 1991). Assumptions of normality and homogeneity of variances of centroid size values were evaluated by Shapiro–Wilk and Levene’s tests, respectively. We tested centroid size differences between sexes and habitats using two-way Analysis of Variance (ANOVA). Possible allometric effects, caused by different size classes among adult specimens, were removed by regressing Procrustes coordinates (shape variable) into centroid size (size variable). Regression residuals were added back to the mean shape of all specimens and multivariate analyses were performed based on a co-variance matrix calculated from the allometry-free shape values (Drake and Klingenberg 2008). Principal Component Analysis (PCA) was used to identify the axes of maximal shape variance among all specimens and the patterns associated with this variance, as well as to identify the grouping of variance among specimens. Multivariate Analysis of Variance (MANOVA), followed by pairwise comparisons, was performed to analyze shape statistical differences using the scores of informative principal components (based on a Broken-Stick distribution) as dependent variables and habitat as the independent variable. The MANOVA was followed by Wilks’ λ test to identify the proportion of the variance that is explained by the independent variable (population). We used the Canonical Variates Analysis (CVA) to describe the differences among groups (habitats) and to form mathematical functions, which were used to assign specimens to groups through jackknife cross-validation analyses (Zelditch et al. 2012).

Sexual size dimorphism (SSD) and sexual shape dimorphism (SShD) We used the results of linear and geometric morphometric analyses to evaluate sexual size and shape dimorphism. We tested SShD through Procrustes ANOVA, using Procrustes coordinates as

response variable and sex and site as factors. An estimation of SSD was obtained using an SSD index (Tamagnini et al. 2018), described as the following:

$$SSD\ index = \frac{[female\ mean\ CS] - [males\ mean\ CS]}{[female\ mean\ CS]},$$

where the SSD index was calculated separately for each site, considering all specimens. For SSD, a value of zero indicates that no sexual dimorphism was observed (Tamagnini et al. 2018).

Analyses were performed in the RStudio environment (RStudio Team 2018). We used the *Geomorph* package (Adams and Otárola-Castillo 2013; Adams et al. 2017) for GPA and PCA, and the *Morpho* package (Schlager 2017) for CVA. Other statistical tests were performed with *stats* package (RStudio Team 2018). Graphs were edited using the software Inkscape v0.92. Differences were considered significant when $p < 0.01$.

Results

The mean average fish standard length was 42.6 ± 7.30 mm, without statistical differences between sexes ($p = 0.0249$) but between different sites ($p < 0.0001$). Specimens from the lentic environment are larger than those from lotic habitats (Fig. 2). We also analyzed linear measurements that could be related to different habitats (lotic versus lentic environments). We found that total length, body width, dorsal fin base length, pectoral fin base length and caudal peduncle length are statistically distinct when fish measurements from lotic and lentic environments were compared ($p < 0.01$). Only body width was different between sexes ($p = 0.0024$). Despite the largest standard length of lentic specimens, standardized measurements revealed that lotic specimens have the greatest total length, body width, caudal peduncle length and dorsal and pectoral base lengths. We also observed that specimens from upstream and downstream (lotic environments) were all similar with respect to the aforementioned measurements (Fig. 3).

Bryconamericus iheringii was statistically different regarding to centroid size in both site and sex comparisons ($p < 0.01$), with the site variation being more important than sex variation (Table 2, Fig. 4). Table 2 also shows that site and sex do not interact,

regardless of linear or geometric shape measurements; and, therefore, either site or sex are sufficient to explain shape variation. These results correspond with the relatively low SSD indices (Table 3). Also, the interaction between habitat and sex was not significant ($p = 0.898$), which indicates that degree of SSD does not differ between lotic and lentic environments.

We found allometric effects on shape, which were different for males and females ($p = 0.001$) and between environments ($p = 0.006$). Because of this, shape analyses were performed with allometry-free shapes. A Broken-Stick model with PCA components revealed the first five PCs are most important and scores were used for MANOVA to compare shape variation between sex and among environments. We found statistical differences between sexes ($F_{1,88} = 2.4815$, Wilk's $\lambda = 0.58165$, $p = 0.0028$) and environments ($F_{2,88} = 2.8045$, Wilk's $\lambda = 0.30426$, $p = < 0.0001$). PC1 and PC2 explained 20.4 and 18.1% of total variation, respectively, with the landmarks 5, 9, 8, 10 and 12 as main PC loadings, which correspond with the variation of caudal peduncle. Exploring the morphospace generated by PCA, the main body shape of females and males occupy distinct distributions (females: negative PC1 and positive PC2 axis; males: positive PC1 and negative PC2 axis), besides many specimens are overlapping in PC1-PC2 shape space (Fig. 5). Such a distinction with respect to body morphology between sexes was then related to fish shape attributes associated with the position of anal fin and body width and length, since these features are represented by landmarks with higher loading values. These findings were corroborated by the CVA, with a correct classification of 71.1% for females and 62% for males. Taken together, these results support that *B. iheringii* shows sexual shape dimorphism, and habitat-related shape alterations were subsequently analyzed separately for males and females.

Females

Females differed with respect to shape when comparing fish living in different environments ($F_{2,47} = 3.4346$, Wilk's $\lambda = 0.5807$, $p = 0.0017$), specifically between upstream and the dam ($p = 0.0011$) and between upstream and downstream ($p = 0.0005$). Centroid size was also different between females from dam and downstream environments

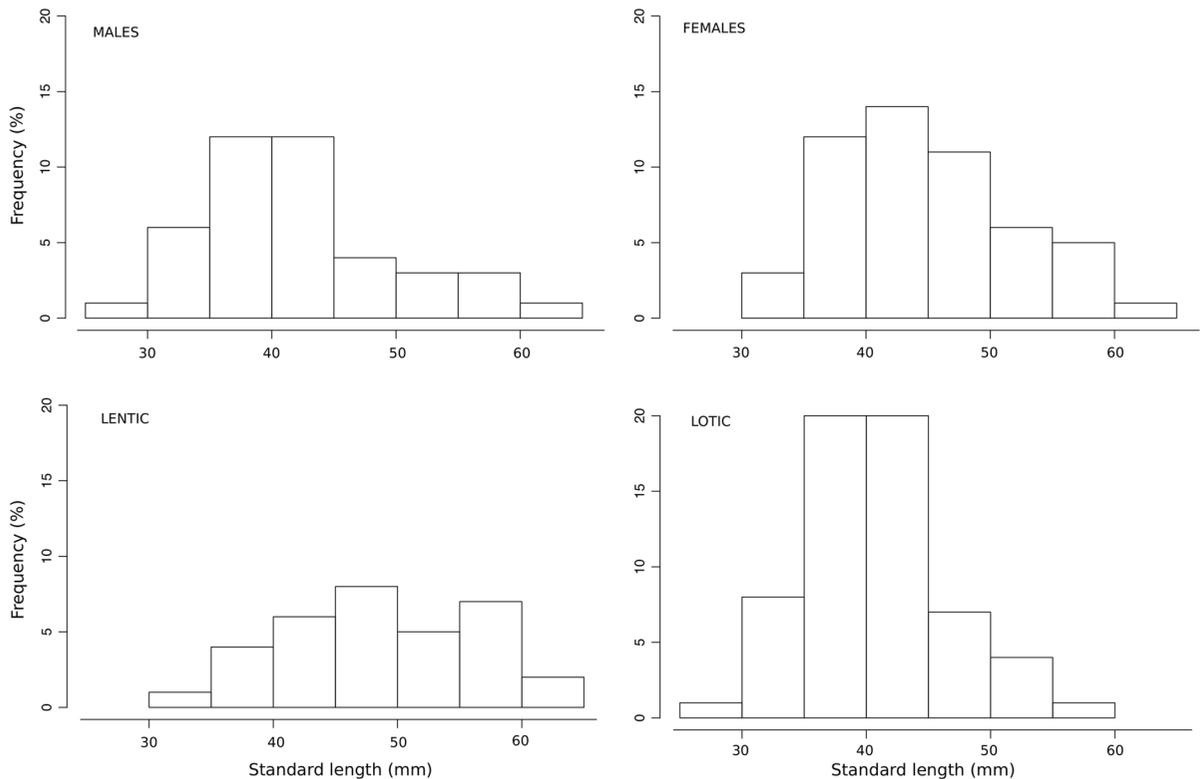


Fig. 2 Standard length frequency distribution of *Bryconamericus iheringii* showing comparisons between sexes and environments

($p = 0.0005$), but not for the remaining comparisons. Through the PCA it is possible to observe groupings related to environmental differences along the PC1, which encompass 22.3% of the total variation. Upstream females occupy the positive end of the PC1, whereas females from the dam occupy the opposite position, with females from downstream occupying a central position. The main loadings for PC1 were the landmarks 10, 5, 1 and 12, which are primarily related to body width and mouth position. Therefore, females from lentic environments had body shapes that were less slim than upstream females. We also observed variation related to mouth position, with females from the dam having a more ventral mouth position than females from upstream (Fig. 6). This grouping was confirmed by CVA, accounted for approximately 65% of total variation in the first CV (Fig. 7). At the CV1 it was possible to visualize the distinction between females from upstream + downstream environments and females from dam environment, with the main variation related to mouth position (Fig. 8). The overall classification accuracy

was 88% (dam = 85.7%, downstream = 92%, upstream = 81.8%).

Males

In contrast to females, males did not show shape variation between environments ($F_{2,37} = 1.499$, Wilk's $\lambda = 0.6641$, $p = 0.1597$), despite significant centroid size differences observed between specimens from downstream and the dam ($F_{2,37} = 5.679$, $p = 0.005$). PCA revealed the first two PCs with 22.3 and 20.4% of total variance, respectively, with landmarks 10, 4, 5 and 7 as main loadings (Fig. 6). As observed in females, these landmarks were related to body width and caudal peduncle shape. In addition, MANOVA showed no statistical differences in fish shape between environments. CVA was able to classify groups with an overall classification accuracy of 95%, meaning that variation between groups is higher than within groups. The first CV accounted almost 80% of total variation, with upstream and dam specimens occupying the negative and positive CV1

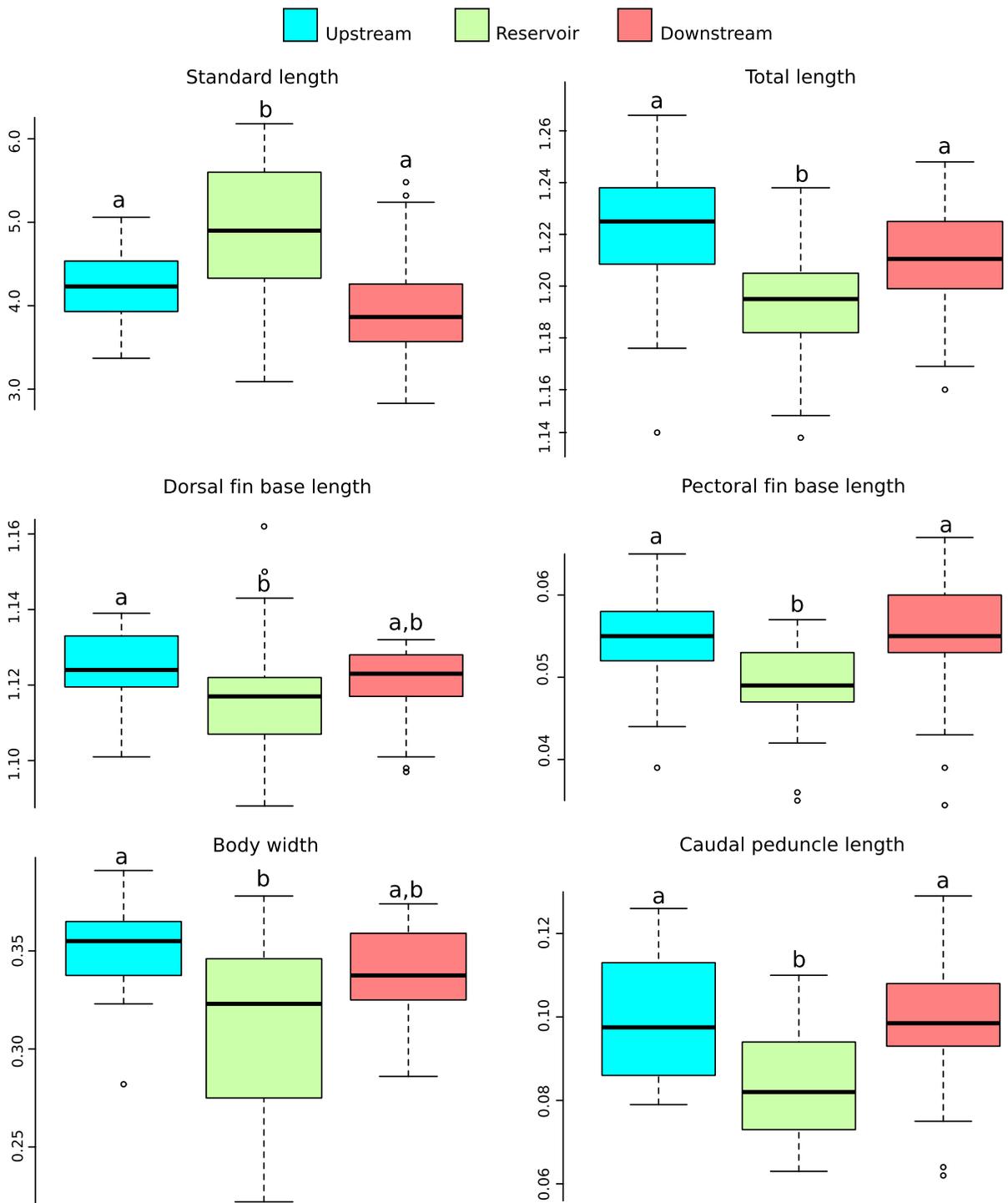


Fig. 3 Boxplot showing comparisons of linear measurements between the three compared environments. Different letters represent the statistical differences for each comparison

Table 2 ANOVA-two way results for size comparisons (centroid size + linear measurements) and Procrustes ANOVA results for shape comparisons (Procrustes coordinates), respectively testing for SSD and SShD between environments

			Df	SS	MS	F	p value
Size	Centroid size	Sex	1	0.1579	0.1579	7.242	0.0085
		Site	2	0.5957	0.2978	13.659	< 0.0001
		Sex:Habitat	2	0.0071	0.0035	0.162	0.8508
		Residuals	88	1.9188	0.0218		
	Standard length	Sex	1	2.05	2.051	5.211	0.0249
		Site	2	16.85	8.423	21.404	< 0.0001
		Sex:Site	2	0.04	0.019	0.048	0.9532
		Residuals	88	34.63	0.394		
	Total length	Sex	1	0.0005	0.0005	0.955	0.3310
		Site	2	0.0111	0.0055	10.500	< 0.0001
		Sex:Site	2	0.0019	0.0009	1.794	0.1720
		Residuals	88	0.0464	0.0005		
	Body width	Sex	1	0.0002	0.0002	11.061	0.0013
		Site	2	0.0003	0.0001	8.795	0.0003
		Sex:Site	2	< 0.0001	< 0.0001	0.232	0.7931
		Residuals	88	0.0015	< 0.0001		
	Peduncle width	Sex	1	< 0.0001	< 0.0001	0.076	0.7838
		Site	2	< 0.0001	< 0.0001	3.108	0.0496
		Sex:Site	2	< 0.0001	< 0.0001	0.489	0.6151
		Residuals	88	< 0.0001	< 0.0001		
Dorsal fin base length	Sex	1	< 0.0001	< 0.0001	0.059	0.8079	
	Site	2	0.0016	0.0008	5.334	0.0065	
	Sex:Site	2	0.0003	0.0001	1.083	0.3432	
	Residuals	88	0.0129	0.0001			
Pectoral fin base length	Sex	1	< 0.0001	< 0.0001	1.082	0.3012	
	Site	2	0.0008	0.0004	9.811	0.0001	
	Sex:Site	2	< 0.0001	< 0.0001	0.656	0.5216	
	Residuals	88	0.0034	< 0.0001			
Caudal peduncle length	Sex	1	< 0.0001	< 0.0001	0.375	0.542	
	Site	2	0.0054	0.0027	13.870	< 0.0001	
	Sex:Site	2	0.0017	< 0.0001	0.447	0.641	
	Residuals	87	0.0170	0.0002			
Shape	Procrustes coordinates	Sex	1	0.0044	0.0044	5.641	0.0001
		Site	2	0.0060	0.0030	4.000	0.0001
		Sex:Site	2	0.0020	0.0010	1.330	0.0788
		Residuals	90	0.0700	0.0008		
		Total	93	0.0781			

ends, respectively (Fig. 7). This variation was related to the displacement of landmark 8, indicating that shorter caudal peduncles occur in males from the dam compared with males from upstream (Fig. 8).

Discussion

Bryconamericus iheringii from the Chasqueiro basin exhibits morphological variation between stream and reservoir specimens, corroborating our first hypothesis. These observations have been reported for other species in distinct aquatic ecosystems altered by the

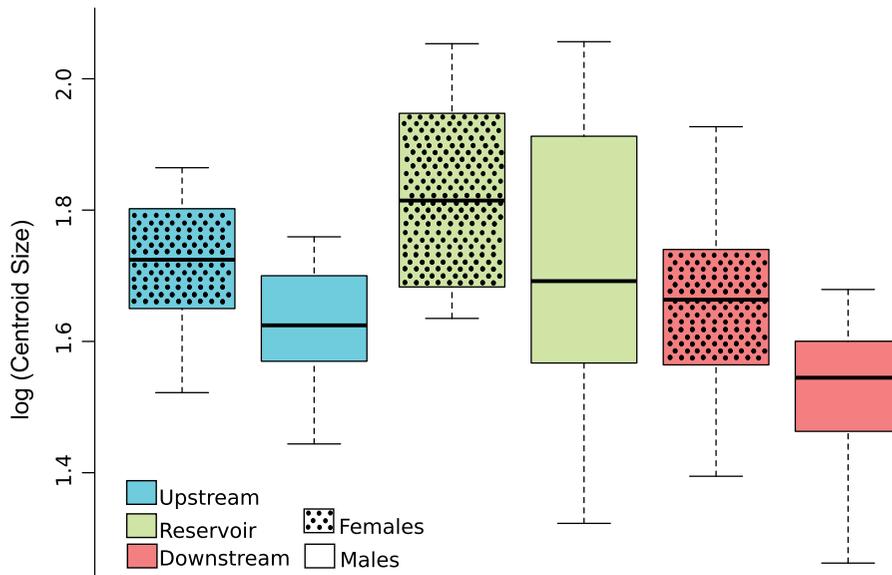


Fig. 4 Boxplot showing comparisons of centroid size between environments and sex. No significant difference between sexes was shown. However, statistical difference between males and females occurred in both downstream and reservoir areas

Table 3 SSD index analysis. The mean value of centroid size (log) for each sex was used to estimate the sexual size dimorphism in *Bryconamericus iheringii* from lentic and lotic habitats

	All habitats	Dam	Downstream	Upstream
Mean females log(CS)	0.7449	0.7933	0.7172	0.7457
Mean males log(CS)	0.7091	0.7467	0.6575	0.7044
SSD index	0.0480	0.0590	0.083	0.055
% of size difference between sexes	4.81	5.87	8.33	5.54

construction of water impoundments (Haas et al. 2010; Franssen 2011; de Assumpção et al. 2012; Franssen et al. 2013; Cureton and Broughton 2014; Gaston and Lauer 2015; Santos and Araújo 2015; Jacquemin and Pyron 2016). Environmental alterations caused by dam construction seem to be a factor that is promoting phenotypical divergence along this stream basin. Specimens from upstream and downstream were similar in most of our comparisons, whereas specimens from the reservoir were diverged. A previous analysis of body shape and size variation of *B. iheringii* did not show differences between populations from 22 streams along the Campos Sulinos ecosystem (geographically near to our sampling area) (Kokubun et al. 2018), but no lentic populations were analyzed in that work.

Linear measurements, together with geometric morphometrics data analyses, clearly indicate differences among individuals from different environments, with the main distinction observable between specimens from upstream and the reservoir. The new lentic environment (reservoir) seems to select specimens with shorter body lengths and widths, smaller dorsal and pectoral fin bases, and shorter caudal peduncle lengths. Note that the linear measurements did not differ between sexes, which means that *B. iheringii* does not present sexual size dimorphism (SSD). However, sex was an important factor when we analyzed the body shape, indicating that *B. iheringii* does exhibit sexual shape dimorphism (SShD). Males and females did not respond equally to the habitat alteration, rejecting our second hypothesis in which we stated that both sexes of species without

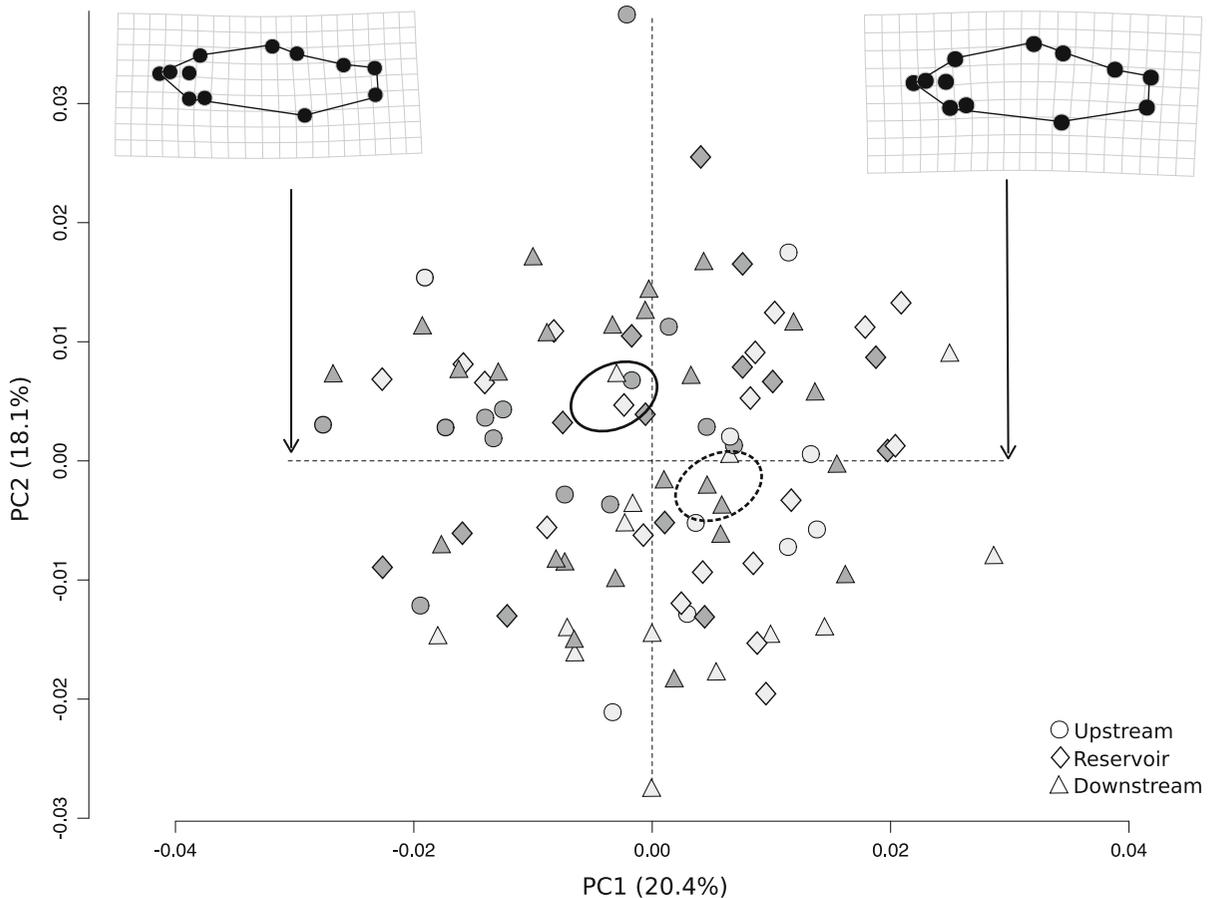


Fig. 5 PCA of all samples. Females are indicated in dark grey, and males are indicated in light grey. Circles represent the mean shape for each sex (a continuous line for females and a dotted

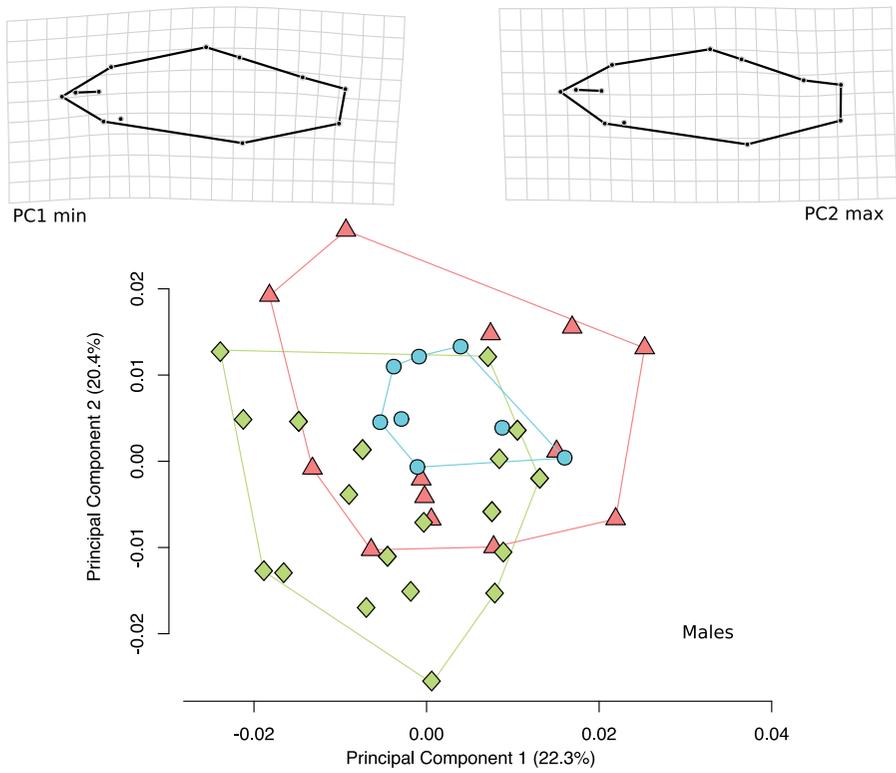
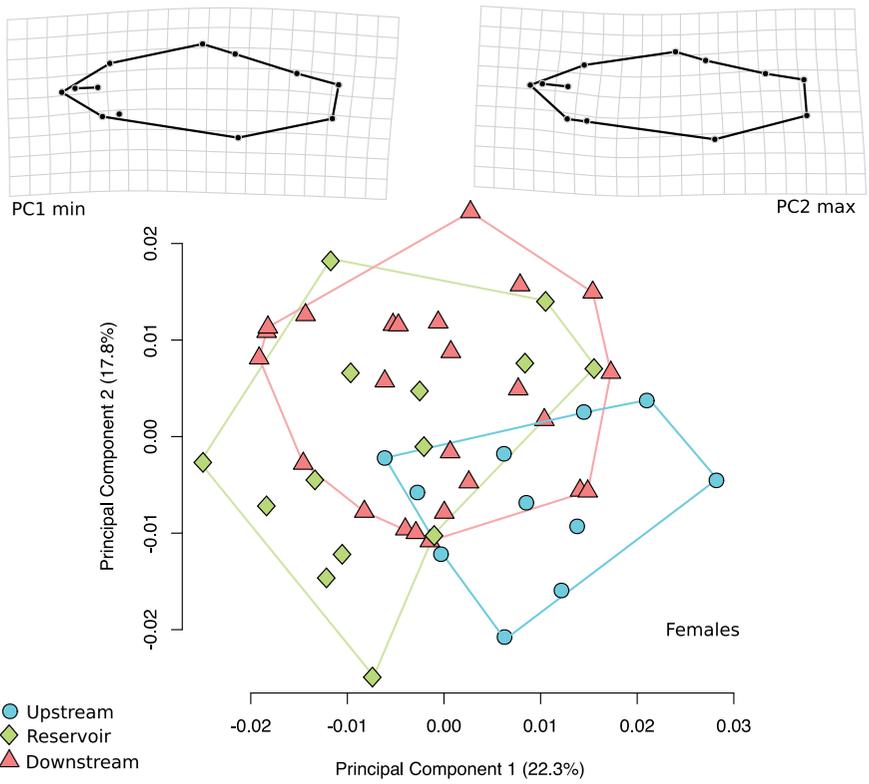
lines for males). Above PCA shapes were plotted through warped drawings on a grid of deformation to show the maximum and minimum PC1

remarkable sexual dimorphism exhibit similar morphological variation in response to exposure to different environments.

Differential morphological variation between sexes in fish exposed to different environmental conditions was also observed in *Jenynsia lineata* (Jenyns, 1842) which, in contrast to *B. iheringii*, has remarkable sexual dimorphism and internal fertilization (Perazzo et al. 2019). Although there are differences regarding the degree of sexual dimorphism between these two species, it is possible that males and females of *B. iheringii* occupy distinct ecological niches as a result of competition for resources, and consequently are responding differently for selective pressures, as was proposed for *J. lineata* (Perazzo et al. 2019). Another general explanation for the sex-specific sensitivity to environmental variation (lentic/lotic environment)

could be sex differences in reproductive roles, with females holding eggs. These are hypotheses that require further testing to better understand the process of sexual shape dimorphism and its influence on the local adaptation of species.

In general, intraspecific morphological variation in fishes other than sexual dimorphism is related to two main factors: locomotion (Langerhans 2008; Haas et al. 2010; Franssen 2011; Franssen et al. 2013; Cureton and Broughton 2014; Lauder 2014; Theis et al. 2014; Gaston and Lauer 2015; Perazzo et al. 2019) and feeding (Langerhans et al. 2004; Gomes and Monteiro 2008; Heinen-Kay and Langerhans 2013; Araújo et al. 2014; Zanella et al. 2015; Ingley et al. 2016; Ronco et al. 2019), which are features directly affected by changing environmental conditions. Regarding locomotion, a general pattern has been



◀ **Fig. 6** PCA performed for females and males separately. The shape of each PCA graph above was plotted through warped drawings on a grid of deformation for the maximum and minimum PC1

observed in which fishes from lotic habitats often display fusiform morphologies, a shape conducive to reducing drag and facilitating sustained swimming. Fishes from lentic habitats, in comparison, generally

have shallower anterior regions and increased caudal peduncle areas, facilitating faster burst speeds and increasing maneuverability (Langerhans and DeWitt 2004; Langerhans 2008; Franssen et al. 2013). In relation to feeding, the main morphological variations are associated with head morphology, specifically mouth position (Franssen et al. 2013). Although these patterns are not universal, we also observed that both sexes of *B. iheringii* from lentic habitats had less fusiform bodies than in those from lotic habitats.

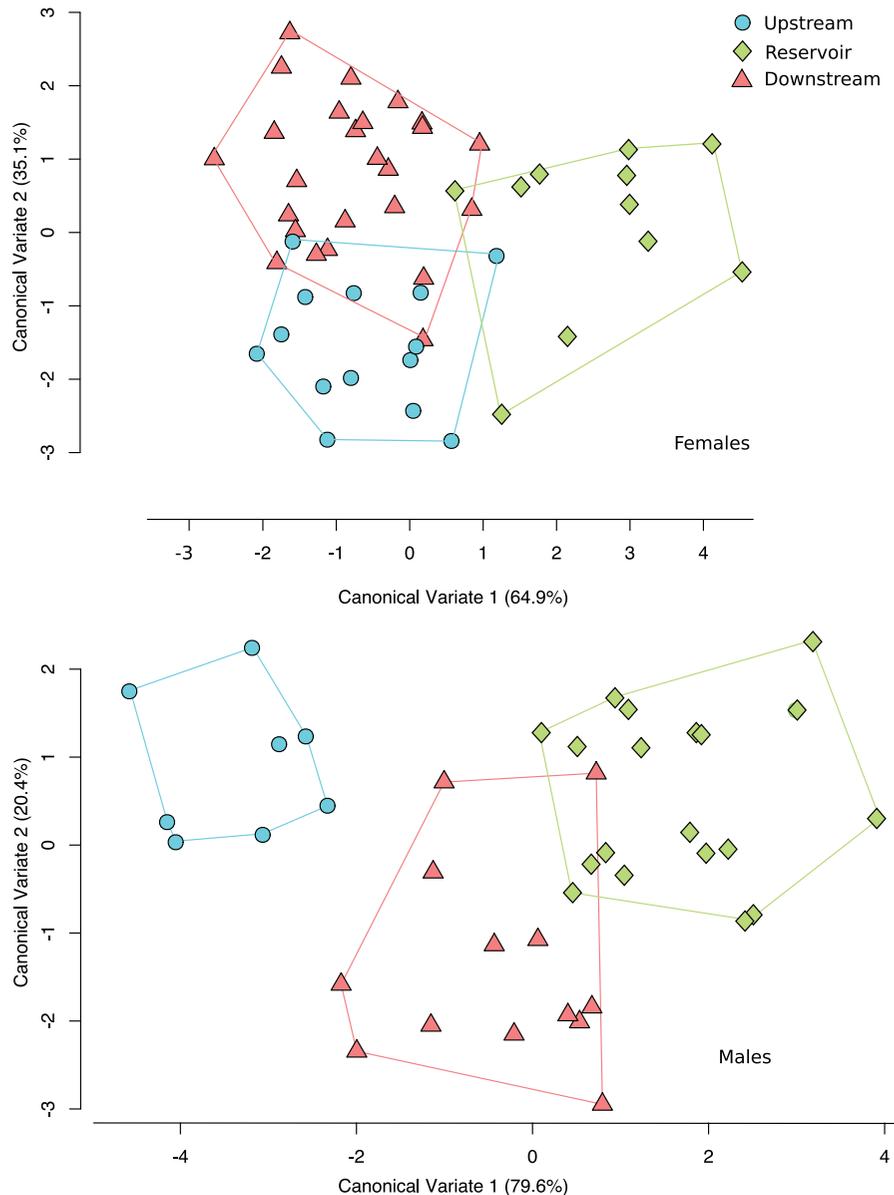


Fig. 7 CVA was performed for both females and males to explore differences observed among the environments examined

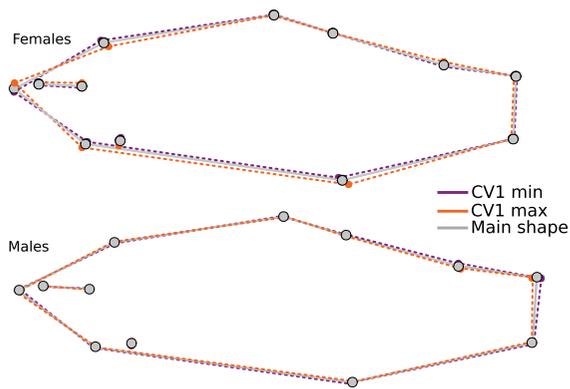


Fig. 8 Representation of shape variation along the first canonical variate for females and males

However, lentic females were increasingly fusiform compared with females from lotic habitats. The mouth position of females (actually, the anterior end of head, according to our landmarks positions; see Fig. 1) also was an important morphological feature distinguishing *B. iheringii* from reservoir and stream environments. CVA revealed that females from the reservoir had snouts that were positioned anterior when compared with females from stream environments. *Bryconamericus iheringii* is a generalist species, capable of prey switching based on the availability of resources (Kokubun et al. 2018). Environmental changes caused by the alteration of lotic to lentic habitats in the reservoir may include the alteration of food resources for *B. iheringii*, at least for females. It is expected that the reservoir operation creates a completely altered environment, affecting both abiotic and biotic factors (Schmutz and Moog 2018).

The size variation was the same for both sexes of *B. iheringii*, but shape variation was distinct for males and females, with shape variation being more prominent in females. Linear measurements of specimens from lotic populations showed larger average measurements (body length and width, dorsal and pectoral fins base length, and caudal peduncle length) than those living in lentic environments, which can facilitate sustained swimming. Regarding body shape, we observed that both sexes have a more fusiform body in the lotic habitats than in the reservoir, but females, in contrast to males, also showed a distinct mouth position between these environments. These results indicate that the water reservoir seems to be an important factor influencing the morphological variation of *B. iheringii*, a species with sexual shape

dimorphism described in the present work. This sexual shape distinction should be considered in future morphological studies of *B. iheringii*. Future studies should also consider the effects of dam construction on the fish community, specifically in relation to those species with co-occurrence along streams and reservoirs, to analyze if the variation observed in *B. iheringii* also occurs in other species. Such comparative analyses would provide the existence of a morphological reservoir-induced modification rule. It would also be interesting to evaluate whether there is genetic variation and structuring among such populations, to understand the genetic basis of these differences. A common garden experiment using *B. iheringii* would help determine if differences observed here are due to phenotypic plasticity or based on genetic differences.

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