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**Environmental Biology of Fishes**

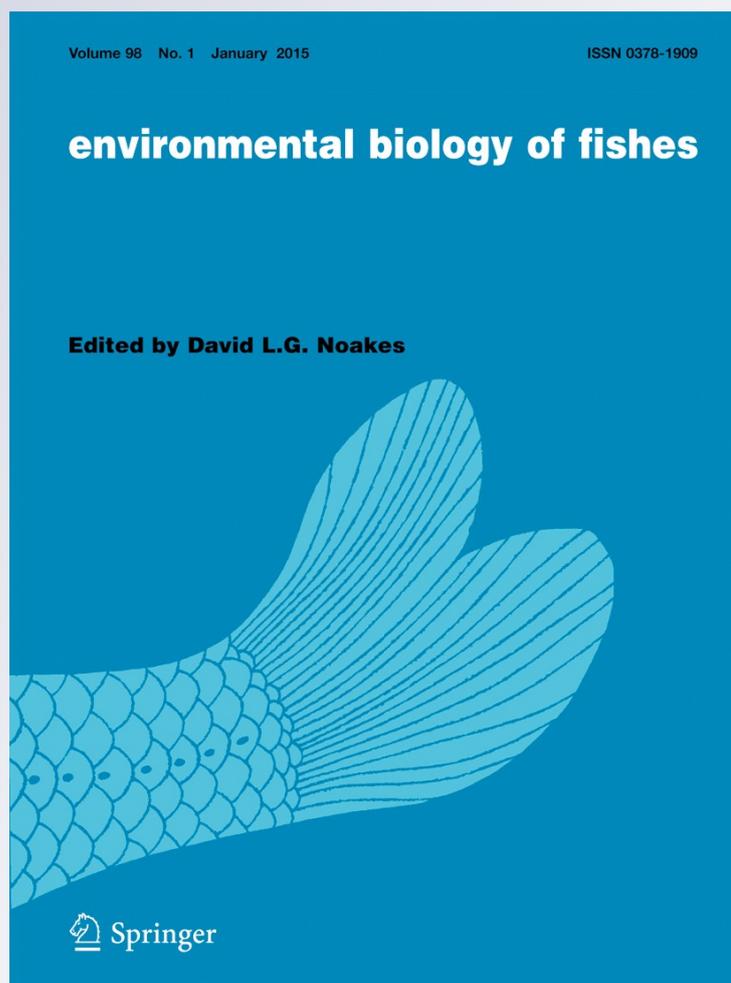
ISSN 0378-1909

Volume 98

Number 1

Environ Biol Fish (2015) 98:183-191

DOI 10.1007/s10641-014-0248-5



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# Evidence of morphological differences between *Astyanax bimaculatus* (Actinopterygii: Characidae) from reaches above and below dams on a tropical river

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Received: 10 August 2013 / Accepted: 18 February 2014 / Published online: 8 March 2014  
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**Abstract** Environmental alterations following river damming can cause body shape changes in freshwater fish species. However, little information is available on morphological responses of fishes to new environments after dam construction. We examined morphological differentiation of a small bodied characin fish collected from three pairs of reservoir and river habitats with distinct hydrological connectivity level (i.e., the degree to which fish movement is facilitated or impaired across reservoir and downriver habitats): (i) without, (ii) intermittent, and (iii) permanent connectivity. We predicted that river damming causes shape changes in fish species and share a common pattern of morphological differentiation, with individuals from lotic habitats having a more hydrodynamic body shape and being poorly adapted for maneuverability compared with those from lentic habitats. Geometric morphometric analysis of the body shape revealed that individuals inhabiting reservoirs were deeper-bodied and had longer dorsal and anal-fin bases compared with individuals from the rivers, features associated with body shape adaptation to lentic environments. We also showed that connectivity between reservoir and river habitats appears to have constrained morphological differentiation, presumably due to population mixing rates. Local characteristics associated with each impoundment (e.g., migration routes and environmental homogeneity) seem to play a

critical role in *Astyanax bimaculatus* body shape differentiation. The observed patterns were consistent with functional morphological principles suggesting adaptive divergence.

**Keywords** Dam · Shape divergence · Geometric morphometrics · Fragmentation · Fish

## Introduction

River damming is a major factor of habitat alteration in aquatic ecosystems. Over half of the world's large river systems are fragmented by impoundments (Nilsson et al. 2005), threatening many freshwater organisms (Dudgeon et al. 2006; Vörösmarty et al. 2010). The end result is that almost a quarter of the freshwater fishes are imperiled worldwide (Vié et al. 2009). Although reservoirs have deleterious impacts on fish faunas, native species that persist in these altered systems may serve as model organisms to investigate population responses to rapid environmental disturbances (Franssen 2011).

It is expected that fish species able to persist in impounded areas are those pre-adapted to cope with novel environment created by dams (Poff et al. 1997; Rosenberg et al. 2000; Nilsson et al. 2005; Agostinho et al. 2008). However, little information is available on morphological responses of fishes to new environments following dam construction. Generally, when rivers are dammed, they rapidly change from lotic to lentic conditions, their physical habitats and landscape are

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profoundly altered, higher densities of non-native piscivorous fishes are facilitated by newly formed lentic habitats and stocking of game fish, and fish movements are restricted. These novel biotic and abiotic selective pressures may modify functional traits by genetic differentiation, phenotypic plasticity or both (Haas et al. 2010; Franssen 2012; Hudman and Gido 2013). In the first process, construction of dams affects fish movements, may restrict gene flow and lead to differentiation of populations (Meldegaard et al. 2003; Yamamoto et al. 2004; Collin and Fumagalli 2011). In the second, a single genotype is able to produce more than one alternative shape in response to different environmental conditions (Keeley et al. 2007; Fischer-Rousseau et al. 2010).

Habitat-associated morphological divergence is well known in fishes inhabiting natural environments, with individuals having hydrodynamic body shapes in lotic habitats and increased capacity of maneuverability in lentic waters (Brinsmead and Fox 2002; Langerhans et al. 2003; Langerhans 2008; Tobler and Carson 2010; Collin and Fumagalli 2011). Only recently, morphological divergence has been identified as a consequence of impoundments (Esguícero and Arcifa 2010; Haas et al. 2010; AvanniFar et al. 2011; Franssen 2011). These studies showed that river damming causes body shape changes and share a common pattern of morphological differentiation, with phenotypic differences representing potentially adaptive responses to divergent selection between lentic and lotic environments. However, there is a lack of information on morphological responses of tropical fish species to impoundments. Here we intend to extend the geographical and taxonomical knowledge of how reservoirs alter fish morphology, and this is the first study considering the effects of different types of dams on fish body shape of a tropical fish species.

Paraíba do Sul River is one of the Brazil's largest rivers and is strongly affected by impoundments. Presently, there are seven dams along its course (Araújo et al. 2009). We restricted our research to the middle-lower reaches of the river to reduce the confounding effects of natural environmental variability. In this reach there are three impoundments with distinct hydrological connectivity level: (i) without connectivity—lacking fish passage system and with all the water flowing through the hydroelectric turbines; (ii) intermittent connectivity—with a fish ladder which works only during the peak of wet season (January and February);

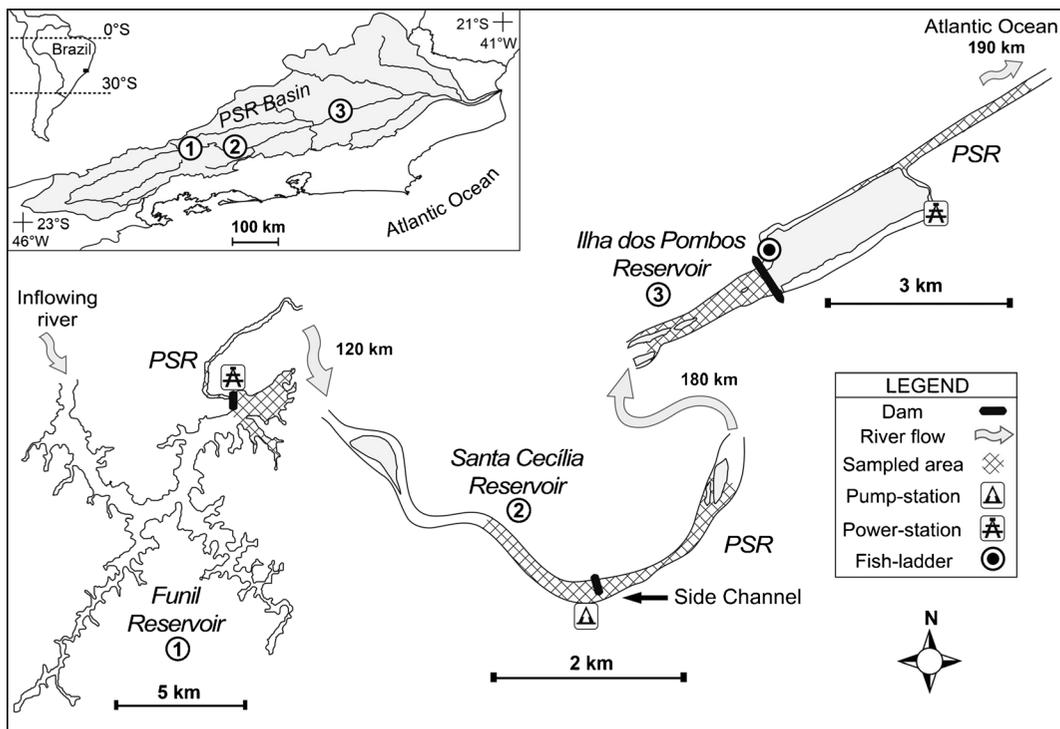
(iii) permanent connectivity—with reservoir and river permanently connected by a side channel (3.5 m height×6 m width). We believe that these different hydrological connectivities, presumably result in different population mixing rates, and may have an important effect on morphological differentiation.

*Astyanax* species are among the most resistant to the negative effects of impoundments because they possess a wide feeding spectrum, early first maturity (0.7 year old), small eggs with rapid development, short generation time (18 months) and an ability to thrive in many different environments, such as headwater streams, large rivers and lagoons (Agostinho et al. 1984; Dias et al. 2005). Considering these features and that *Astyanax bimaculatus* (Linnaeus, 1758) is an abundant and widely distributed fish in the Paraíba do Sul River basin, this species may serve as a model organism for assessing morphological responses of fishes to river damming. This study investigated how *A. bimaculatus* body shape responds to river damming comparing fishes collected immediately above and below dams in a tropical river. We hypothesized that environmental contrast between reservoir and river habitats results in morphological divergence in fish body shape. Our predictions are that individuals from lotic habitats have a more hydrodynamic body shape and are poorly adapted for maneuverability (i.e., more fusiform, shorter dorsal and anal-fin bases) compared with those from lentic habitats. We also expected that connectivity between reservoir and river habitats constrains morphological differentiation in fish body shape.

## Material and methods

### Study area

The Paraíba do Sul River in southeastern Brazil is 1,080 km long, and has a watershed area of 57,000 km<sup>2</sup>, draining into the Atlantic Ocean. The climate is mesothermic, with hot and wet summers and dry winters. Typical winter and summer flows are 109 m<sup>3</sup> s<sup>-1</sup> and 950 m<sup>3</sup> s<sup>-1</sup>, respectively; annual rainfall ranges from 100 to 300 cm, with the average generally over 200 cm (Carvalho and Torres 2002). The investigated impoundments are separated at least 120 km from each other and vary in reservoir area, retention time, landscape composition and hydrological connectivity (Fig. 1; Table 1).



**Fig. 1** Location of the paired study sites in Paraiba do Sul River (PSR) Basin and schematic map showing each impoundment: Funil (1); Santa Cecilia (2); Ilha dos Pombos (3)

Funil Dam forms the largest reservoir in the Paraíba do Sul River. The vegetation around the reservoir is very poor, a result of previous agricultural use for coffee plantations and pasture (Branco et al. 2002). The downriver section consists of lotic and shallow waters, with diverse riparian vegetation and higher habitat complexity due to rocky substrates (Terra and Araújo 2011). Unlike Funil, the other two impoundments are run-of-the-river and low-head dams with some degree of hydrological connectivity (Table 2). Santa Cecilia Dam consists of eight floodgates with a permanent side connection between reservoir and downriver habitats. As a

consequence, all water flows through a narrowed side channel, increasing water velocity to approximately  $4.3\text{--}5\text{ m s}^{-1}$ . The most similar environmental and hydrological conditions between the reservoir and downriver habitats are found in Santa Cecilia location. Both reaches are densely populated urban settlements surrounded by pasture and lack riparian vegetation. Ilha dos Pombos is located approximately 190 km from the river estuary. The vegetation, composed of trees, bushes and macrophytes, is scattered along the reservoir bank and surrounded by pasture and sand mining. The downriver is characterized by shallow runs embedded in

**Table 1** Collection sites, number of examined specimens (*n*) and impoundment features

Site name	<i>n</i>	Dam coordinates	Hydrological connectivity	Depth (m) max/mean	Time of construction	Area (km <sup>2</sup> )	Volume (10 <sup>6</sup> m <sup>3</sup> )	Retention time (days)
Funil/reservoir	30	22°31'43.5"S	without	70/20	1969	40	890	10–55
Funil/downriver	30	43°34'05.7"W		9.2/3.0				
St. Cecilia/reservoir	30	22°28'52.6"S	permanent	9.4/5.3	1952	2.7	4.35	<1
St. Cecilia/downriver	31	43°50'20.2"W		6.1/3.1				
I. Pombos/reservoir	30	21°51'11.6"S	intermittent	32/12	1924	4.26	7.87	<1
I. Pombos/downriver	31	42°36'24.6"W		7.4/3.5				

Habitat codes: *res* = reservoir; *down* = downriver

**Table 2** Main physical features of each impoundment

Features/reservoirs	Funil	Santa Cecília	Ilha dos Pombos
Location	Itatiaia, RJ	Barra do Pirai, RJ	Carmo, RJ
Capacity (MW)	216	<sup>a</sup>	164
Maximum height (m)	85	10	12
Usable volume (hm <sup>3</sup> )	6,200	2.17	6.77
Dam length (m)	385	176	514
Altitude (a.s.l.)	440	353	108

<sup>a</sup> Pumping station designed to divert 160 m<sup>3</sup> s<sup>-1</sup> to a hydroelectric complex

bedrock with rocky outcrops. In this location there is a vertical-slot fish ladder which works only during high-flow events.

#### Data collection

In July and August 2011, we collected 182 individuals of *A. bimaculatus* (9.3±0.9 cm standard length; mean ± standard deviation) using gill nets. At least, 30 individuals were collected from each habitat (reservoir and downriver sections) of the three dams. A standardized fishing effort was applied in each habitat, along a stretch of approximately 2 km from the dam. Ten sets of three gillnets (20×2.5 m; 25, 50 and 75 mm mesh size) were randomly distributed within each habitat. Only adults individuals, i.e. those larger than the size at the first maturation (Vazzoler 1996) were selected to avoid eventual allometric effects of body size in the morphological analyses. All specimens were fixed in 10 % formalin for 48 h, stored in 70 % ethanol and deposited in the reference collection of the Laboratório de Ecologia de Peixes, Universidade Federal Rural do Rio de Janeiro.

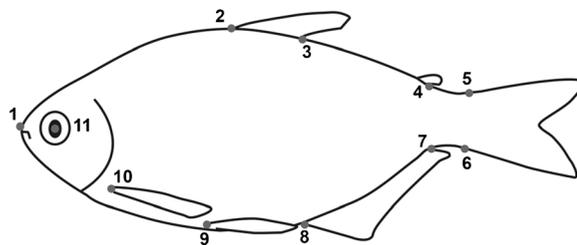
Geometric morphometrics methods were used to quantify body shape. It is a tool for analysing shape variation that retains information on spatial covariation among landmarks (Rohlf and Marcus 1993). Each fish was placed on a polystyrene board with a small oval pit covered with black EVA foam. The pit helps to place the fish absolutely straight on the polystyrene board. Photographs of the left side of each individual with a reference scale were taken with a digital camera (Canon PowerShot-G9, Japan) mounted on a tripod, and then analysed using the tps software package (available at: <http://life.bio.sunysb.edu/morph/>).

We placed a set of 11 homologous landmarks (Fig. 2) in each image using tpsDig software (Rohlf 2005). To account for bending of specimens, we unbent landmarks using the landmarks at the tip of snout, center of eye and two temporary landmarks set along the midline (in the middle of body and in the middle of caudal peduncle) of each individuals to implement ‘unbend specimens’ function in tpsUtil (Rohlf 2004a). We resized landmark coordinates using the reference scale and aligned landmark coordinates using least-squares superimposition to remove effects of scale, translation, and rotation with tpsRelw (Rohlf 2004b). Partial warps, uniform components and centroid size were computed for each specimen with tpsRelw. Partial warps describe localized shape variation and uniform components depict shape variation owing to compression, dilation and shear across the entire form (Zelditch et al. 2004). The centroid size (the square root of the summed squared distance between each landmark and the configuration centroid) is typically used as an estimate of overall body size (Bookstein 1991). As centroid size was highly correlated with standard length ( $r=0.99$ ;  $P<0.0001$ ), it was used as our measure of body size.

#### Data analysis

We conducted univariate analysis (ANOVA) to examine size differences in fish body size between habitats for pooled data, but size differences were not found ( $F_{1,180}=2.64$ ;  $P=0.10$ ). However, as we were interested in body shape differences, we focused our analyses on size-independent body morphology.

To test the hypothesis that significant shifts in body shape are associated with river damming, we performed



**Fig. 2** Landmarks used for morphometric analysis of *Astyanax bimaculatus*: 1 tip of snout; 2 anterior insertion of dorsal fin; 3 posterior insertion of dorsal fin; 4 posterior insertion of adipose fin; 5 insertion of the last dorsal ray on the caudal fin; 6 insertion of the last ventral ray on the caudal fin; 7 posterior insertion of anal fin; 8 anterior insertion of anal fin; 9 pelvic fin insertion; 10 pectoral fin insertion; 11 center of eye

a multivariate analysis of covariance (MANCOVA) using SPSS version 17. For all multivariate analyses, partial warps and uniform components served as dependent variables describing body shape. Habitat type (reservoir or river), location (comparison among reservoir-river pairs), and the interaction between habitat and location served as fixed effects, while the centroid size was a covariate to control for shape variation due to body size. We tested for heterogeneity of slopes (interaction between centroid size and the main terms of interest) and found no significant difference for all terms (habitat and location), thus these interaction terms were excluded from the final model.

To test the degree of shape divergence between habitats, we conducted a discriminant function analysis (DFA). Pairwise comparisons of specific groups were performed based on Procrustes distance. This distance is an absolute measure of the degree of shape difference between two configurations, and therefore does not depend on factors like the variation within samples (Klingenberg et al. 2003). We used permutation methods to test against the null hypothesis of no mean difference between samples. Canonical variate analysis (CVA) was used to assess morphological variation in fish body shape among locations, between habitats, and also to visualize the origin of shape differences between reservoir and downriver individuals. All these analyses were performed in MorphoJ software package (Klingenberg 2011).

## Results

MANCOVA revealed significant morphological divergence between habitats and locations, while the interaction between habitat and location was not significant (Table 3). Discriminant function analysis indicated significant shape differences between individuals from reservoir and downriver habitats (Mahalanobis distance=1.06;  $T$ -square=51.27;  $P$ =0.0009), and correctly classified 70.3 % of all individuals. Permutation test using Procrustes distance between *A. bimaculatus* from Santa Cecília Reservoir and from Santa Cecília Downriver was not significant, whereas permutation between the lentic and lotic habitats for the other two dams were significant (Table 4). The largest amount of morphological divergence in fish body shape between paired habitats was observed for the location without hydrological connectivity between habitats.

**Table 3** Results of MANCOVA for effects of habitat, location and their interaction on body morphology for *Astyanax bimaculatus*

Effect	<i>F</i>	d.f.	<i>P</i>	Partial variance (%) <sup>a</sup>
Centroid size (allometry)	4.86	18, 158	<0.001	35.7
Habitat (H)	2.65	18, 158	<0.001	23.2
Location (L)	4.87	36, 316	<0.001	35.7
H × L	1.32	36, 316	0.130	13.0

<sup>a</sup>Partial variance explained by each term was estimated using Wilks's partial  $\eta^2$  (according to Langerhans and DeWitt 2004)

The CVA of fishes from different locations indicated that all groups included in the analysis were clearly distinct from each other (Fig. 3). CVA scores were used to visualize the origin of fish body shape variation between reservoir and river samples, but not for shape differences among habitats pairs because our model was not developed to explore shape variation between locations. To gain confidence in local effects as the causal explanation for body shape changes, our model needs to replicate “environmental specificities”—e.g., multiple dams with distinct degree of hydrological connectivity. Fish from river habitats were streamlined, had a shorter dorsal and anal-fin bases, a more anteroventrally pectoral fin and an upward-pointing mouth than fish inhabiting reservoirs (Fig. 3).

## Discussion

In this study we extended the geographical and taxonomical knowledge of how dams alter fish morphology,

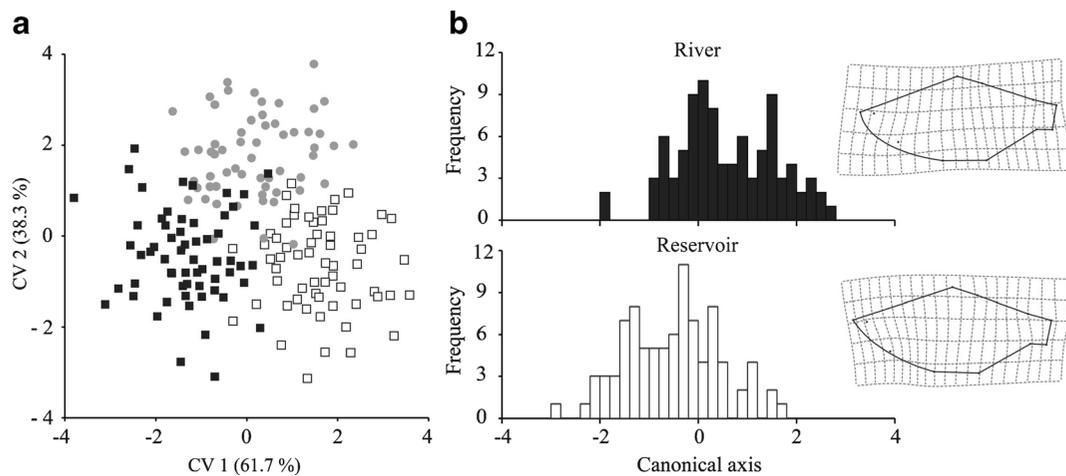
**Table 4** Pairwise comparisons of Procrustes distance between groups

Groups	F/res	F/down	S/res	S/down	I/res
F/down	<b>0.165</b>				
S/res	<b>0.146</b>	0.107			
S/down	<b>0.157</b>	0.112	0.104		
I/res	<b>0.180</b>	0.072	<b>0.184</b>	<b>0.208</b>	
I/down	<b>0.111</b>	0.099	<b>0.141</b>	<b>0.150</b>	<b>0.123</b>

Location codes: *F* = Funil; *S* = Santa Cecília; *Ilha dos Pombos* = I

Habitat codes: *res* = reservoir; *down* = downriver

In bold: significant values ( $P$ <0.01)



**Fig. 3** Canonical variate analyses for location (**a**), habitats (**b**) and Thompson transformation grids depicting shape differences in *Astyanax bimaculatus* between river and reservoir individuals. *Black squares* = Ilha dos Pombos; *white squares* = Santa Cecilia; *gray circles* = Funil

revealing a common pattern of morphological differentiation caused by impoundments. Moreover, we also observed that hydrological connectivity (e.g., fishways) and environmental homogeneity may have a major role in constraining body shape differentiation in freshwater fishes.

The observed morphological patterns between reservoir and river individuals were consistent with functional morphological principles indicating adaptive divergence due to three main reasons: (i) functional traits of fish swimming suggests adaptive roles for morphological differences; (ii) similar morphological differentiation has been found in distantly related species affected by river fragmentation; (iii) similar patterns of divergence has been identified worldwide. Generally, selection on fishes in lotic environments result in fusiform body shapes that minimize drag, reduce the energy expenditure and enable prolonged swimming, whereas increased body depth in lentic waters facilitates faster burst speeds and increases maneuverability (Alexander 1967; Webb and Weihs 1986). Recent studies have highlighted that similar patterns between lentic and lotic environments may be expected as a rule in regulated rivers (Esguícero and Arcifa 2010; Haas et al. 2010; AvanriFar et al. 2011; Franssen 2011). In our study, individuals from reservoir habitats were deeper-bodied and had longer dorsal and anal-fin bases, features associated with unsteady swimming in lentic environments. On the other hand, individuals from lotic habitats had a more streamlined body and were poorly adapted for maneuverability. According to Langerhans (2008), the absence of strong selection pressures for steady

locomotion allows selection favoring alternative locomotor activities (e.g., fast-starts, complex maneuvering) to drive phenotypic responses.

Environments with high predator pressure may imply morphological changes, such as deeper posterior bodies and larger caudal peduncle to increase burst swimming (Walker and Bell 2000; Langerhans and DeWitt 2004; Langerhans 2008). As the studied species is a small-bodied characin fish strongly preyed upon by several piscivorous fishes, we presume that the predation regime could be an important source of shape variability. However, all locations investigated are characterized by the presence of potential *Astyanax* spp. predators, namely *Hoplias malabaricus* (Bloch, 1794), *Oligosarcus hepsetus* (Curvier, 1829), *Rhamdia quelen* (Quoy and Gaimard, 1824), *Plagioscion squamosissimus* (Heckel, 1840) and *Cichla kelberi* Kullander and Ferreira 2006 (see Santos et al. 2013). Although the piscivorous guild may vary from one impoundment to other, the predator pressure may be considered parallel among locations and, consequently, should play a minor role on the investigated fish body shape differentiation.

As expected, the least amount of morphological divergence was observed at Santa Cecilia location. This was probably caused by either the highest hydrological connectivity or by environmental homogeneity between the two habitats. Our findings are in agreement with the assumption of similar selection pressure, which posits that if organisms face similar selective pressures they will generate similar solutions (Schluter 1996; Losos et al. 1998). It is known that modifications in physical attributes of natural environments due to river damming

affect fish morphology and may drive phenotypic changes (Cunico and Agostinho 2006; Haas et al. 2010). On the other hand, hydrological connectivity may also be related to morphological similarity. Although the side channel facilitates fish movements between habitats, it is questionable whether the increased water velocity may be restricting upriver fish migrations. Within this context, we raise two hypotheses to explain the morphological similarity found at Santa Cecília location: (i) unidirectional gene flow—fish migrations are restricted to downriver direction due to increased water velocity; (ii) population mixing—two-way movements are possible. This second process might effectively reduce the magnitude of phenotypic differentiation regardless of the source of divergence (genetic or plasticity) (Langerhans 2008). On the other hand, gene flow may constrain adaptive divergence of population by reducing the independence of their gene pools, or promotes it when high gene flow occurs in a set of populations that inhabit different environments (reviewed in Crispo 2008).

We detected the largest amount of morphological divergence in Funil and Ilha dos Pombos impoundments. It was probably due to the loss of connectivity and strong environmental differences between the reservoir and downriver habitats. Although there is a fish ladder in Ilha dos Pombos Dam, it works only during high-flow events, making fish movements between habitats infrequent. Fish passage systems have been criticized for their low efficiency in facilitating two-way routes, high selectivity and inefficiency in allowing downstream return by adults, eggs, and larvae (Godinho and Kynard 2009). Thus, the presence of a fishway alone certainly does not guarantee that fish are able to surmount physical barriers. According to Roscoe and Hinch (2010), an effective fish passage system should allow up- or downriver passage of the fish without delay, energetic costs, stress, disease, injury or other fitness associated costs.

It is unknown whether morphological patterns in fishes inhabiting impounded rivers are caused mainly by phenotypic plasticity or genotypic differences, or by a combination of both (Day et al. 1994; Robinson and Wilson 1996; Nosil and Crespi 2004; Crispo 2008). Documenting patterns of differentiation is an important step in the investigation of fish adaptations to fragmented environments. As we see, there are many factors responsible for morphological differentiation, precluding the development of a general rule that explains the influence of river fragmentation on fish

morphology. However, any of these sources of divergence can drive microevolutionary change within a species, leading to speciation (Rice and Hostert 1993; Losos et al. 2000; Agrawal 2001; Kaneko 2002).

To date, we have focused on the role of fish movements between reservoir and downriver stretches constraining shape divergence, but population mixing between reservoir and upriver reaches is another issue that needs to be considered. However, recent studies performed in temperate and tropical basins have shown that river stretches above dams are poor migration corridors, thus reducing gene flow and leading to phenotypic differences (Franssen 2012; Hudman and Gido 2013). Moreover, mark-recapture and tagging researches indicate that when tropical fish species inhabits or disperses throughout lotic stretches, they hardly ever return to lentic waters (Agostinho et al. 2007; Antonio et al. 2007; Pompeu et al. 2012). Therefore, these previous studies lead us to suspect that population mixing between *A. bimaculatus* individuals from reservoir and upriver stretches has a minor influence on the restriction of shape differentiation.

Results of this study demonstrate that particular environmental characteristics of impoundments play a critical role in *A. bimaculatus* shape differentiation. Thus, it is highly recommended that future studies take into account regional specificities caused by different models and operational routine of dams. Furthermore, the divergence pattern between fishes inhabiting reservoir and downriver habitats was consistent with previous studies (Haas et al. 2010; AvanriFar et al. 2011; Franssen 2011), suggesting that distantly related fish groups (geographically and taxonomically) exhibit similar responses to novel environments created by dam closure. Finally, to elucidate the role of river damming in shaping morphological divergence, we encourage common garden experiments, translocations, genetic analysis, and to evaluate the efficiency of fish passage systems (e.g., mark-recapture and tagging methods). These approaches will be needed to identify whether the observed patterns are attributable to selection on heritable traits or phenotypic plasticity.

**Acknowledgments** This study was supported by the Brazilian National Council for Scientific and Technological Development, CT-Hidro Programme (Process 474875/2009-1 and 4556247/2009-4). The Rio de Janeiro Carlos Chagas Filho Research Support Agency also supplied financial support for this project (Process E-26/112.118/2008 and E-26/102.704/08). We thank Rafael J. Albieri, Paulo César and Luciano Silva for field assistance.

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