PANAMJAS
Pan-American Journal of Aquatic Sciences

Environmental enrichment changes the ontogenic allometry of *Brycon orbignyanus* (Valenciennes, 1850): An experiment in a fish farm

SARAH O. SARAIVA[1, 2*] & PAULO S. POMPEU[1]

[1] *Laboratório de Ecologia de Peixes, Setor de Ecologia, Departamento de Biologia, Universidade Federal de Lavras, Caixa postal 3037, 37200-000, Lavras, MG, Brazil.*

[2] *Programa de Pós-graduação em Ecologia Aplicada, Setor de Ecologia, Departamento de Biologia, Universidade Federal de Lavras, Caixa postal 3037, 37200- 000, Lavras, MG, Brazil.*

[*] Corresponding author: sarahsaraiva@hotmail.com

Abstract. Farmed fish tend to be morphologically different and less diverse than their wild counterparts, as response to homogeneous conditions in hatcheries. In this sense, the enrichment of hatchery tanks can be used to minimize the effects of captivity on the morphology of fish. However, the ontogenetic allometry naturally change the body morphology as the fish grows. In this study, we aimed to verify whether the environmental enrichment change the ontogenetic allometry process of *Brycon orbignyanus*, popularly known as Piracanjuba. This species is threatened of extinction and its reproduction and release in nature is an attempt for mitigation within the Brazilian Plan for Conservation (PAN). Thus, we reared fish in two types of tanks: one untreated (i.e., normal rearing conditions) and the other one enriched with logs and artificial aquatic plants. Supporting partially our hypothesis, the environmental enrichment changed the ontogenetic allometry of *B. orbignyanus*. Fish reared in enriched tank were larger, with a differentiated morphology (especially fins), but surprisingly, with lower morphological variability. The morphologic differences detected was higher in younger fish. Our results indicates that the enrichment of hatchery tanks consists in an important management measure in fish farming, promoting a distinct ontogenetic allometry, which results in larger fishes, with traits modified to the exploration of a more complex environment. These morphological alterations may result in shorter time of hatchery and possibly in higher post-release survival rates.

Key words: Fish stocking, Hatchery tanks, Morphological plasticity, *Piracanjuba*, Structural complexity.

Resumo: O enriquecemento ambiental altera a alometria ontogenética de *Brycon orbignyanus (Valenciennes, 1850): un experimento em piscicultura*. Peixes cultivados tendem a ser morfologicamente diferentes e menos diversificados do que seus correspondentes selvagens, devido às condições homogêneas do ambiente de cultivo. Nesse sentido, o enriquecimento dos tanques de piscicultura pode minimizar os efeitos do cativeiro na morfologia dos peixes. No entanto, a alometria ontogenética altera naturalmente a morfologia do corpo à medida que o peixe cresce. Neste estudo, verificamos se o enriquecimento ambiental altera o processo de alometria ontogenética do *Brycon orbignyanus*, popularmente conhecida como Piracanjuba. Esta espécie encontra-se ameaçada de extinção e sua reprodução e soltura na natureza é uma tentativa de mitigação dentro do Plano Brasileiro de Conservação (PAN). Para tanto, criamos peixes em dois tipos de tanques: um controle (em condições normais de criação) e o outro enriquecido com troncos e plantas aquáticas artificiais. Apoiando parcialmente nossa hipótese, o enriquecimento ambiental mudou a alometria ontogenética de *B. orbignyanus*. Os peixes criados em tanques enriquecidos foram maiores, com morfologia diferente (especialmente as nadadeiras), mas surpreendentemente, com menor variabilidade morfológica.

As diferenças morfológicas detectadas foram maiores nos peixes mais jovens. Nossos resultados indicam que o enriquecimento dos tanques de cultivo consiste em uma importante medida de manejo na piscicultura, promovendo uma alometria ontogenética diferenciada, que resulta em peixes maiores e com características modificadas para a exploração de um ambiente mais complexo. Essas alterações morfológicas podem resultar num menor tempo de criação e, possivelmente, em maiores taxas de sobrevivência pós-soltura.

Palavras-chave: Complexidade estrutural, Estocagem de peixes, Piracanjuba, Plasticidade morfológica, Tanques de cultivo

Introduction

Morphological plasticity, i.e., the ability to change body shape, is often observed in fish (e. g. Gatz 1979, Casatti & Castro 2006, Leal *et al.* 2010, Souza *et al*. 2014). In hatchery environments, plasticity is particularly pronounced, and farmed fish tend to be morphologically different from their wild counterparts, because of the adaptations to the captive conditions (e. g. Swain *et al.* 1991, Hard *et al*. 2000, Saraiva & Pompeu 2016a).

Hatchery tanks are quite homogeneous and present high density, a less variable population, lacking of predators and prey, and constant food availability (Johnsson *et al.* 2014). On the other hand, in the wild, variables are spatially and temporally unpredictable, including turbidity level, water flow and structural complexity provided by gravel, rocks, plants and trees (Johnsson *et al.* 2014). As a result, farmed fish exhibit distinct colorations (Maynard *et al.* 1994), different body, head and fin proportions (Fleming *et al*. 1994, Solem *et al.* 2006, Belk *et al*. 2008) and less morphological variability (Taylor 1986, Saraiva & Pompeu 2016a) than natural stocks. In the case of fish reared for stocking (release into the natural environment), these morphological differences can result in low post-release survival rates (Maynard *et al.* 1994) making this practice inefficient as supplementation method of the natural populations (Agostinho *et al.* 2007).

Hence, the environmental enrichment of hatchery tanks may be proposed as means of minimizing the effects of captivity on the morphology of farmed fish (Näslund & Johnsson 2014). This technique consists of making the hatchery environment more similar to the wild by incorporating natural features with the aim to reduce maladaptive and aberrant traits in fish reared in these environments (Näslund & Johnsson 2014). There are various types of environmental enrichment, including the addition of sensory stimuli, greater complexity and increased ecological interaction (Batzina & Karakatsouli 2012). The main goals include increasing the animal well-being, the food prodution and, in the case of stocking, the chances of survival after release into the natural environment (Näslund & Johnsson 2014).

The structural enrichment consists in the addition, in the rearing environment, of physical structures such as shelter and substrates which increase the complexity (Näslund & Johnsson 2014). Some studies have evaluated the effects of this kind of enrichment on farmed fish (e. g. Berejikian *et al*., 2001, 2000, Brown *et al*., 2003, Brydges & Braithwaite, 2009, Roberts *et al*., 2011, Batzina & Karakatsouli, 2012). Regarding to morphology Garduño-Paz *et al.* (2010) obtained fish with a more fusiform body and smaller heads in enriched aquariums, and concluded that these traits are favorable for movement in complex environments. In a previous study, we demonstrated that structural enrichment can increase fish growth and the morphological variability of population, which are important features to survive in wild (Saraiva & Pompeu 2014, 2016b). However, the body proportions change as the fish grows through ontogenetic allometry (Wimberger 1992, Woods 2007, Rodríguez-Mendoza *et al.* 2011).

In this sense, the present study aimed to verify if the environmental enrichment changes the ontogenetic allometry in a neotropical fish species commonly farmed for stocking: *Brycon orbignyanus* (Valenciennes, 1850), popularly known in Portuguese as Piracanjuba. We test how the increment of structural complexity in the tank affects the morphological traits of this species during the first months of captivity. We hypothesized that the structural enrichment would change the ontogenetic allometry, resulting in morphological traits more adapted to the exploration of a complex environment, in a population with a more varied morphology. Native from Paraná River basin, *B. orbignyanus* has conservation status considered threatened due to river impoundments, riparian vegetation loss, pollution and invasive species (Rosa & Lima 2008; Lopera-Barrero 2009). Because of its importance in commercial and sport fishing and in attempt to supplement the wild populations, Piracanjuba is widely hatchery in Brazilian fish farms to post-release in reservoirs and rivers.

Material and Methods

To verify the effect of environmental enrichment in the morphology of *Brycon orbignyanus*, we conducted an experiment during the rainy season (in January 2012), at Volta Grande Fish Farming Station in Conceição das Alagoas, Minas Gerais state, Brazil. To obtain fish for the experiment we induced an artificial reproduction following the routine protocol of Volta Grande Fish Farming Station. First, we selected four females and eight males predisposed to reproduction (presenting production of gametes) among the breeders of wild origin available in the station. Then we kept Piracanjuba breeders in trios of two males and one female in aquaria (2000 L) and, to stimulate reproduction, we administered three doses of catfish crude pituitary extract (*Ictalurus punctatus* from North America), calculated according to the weight of each fish. About six hours later, since Piracanjuba do not spawn alone in captivity, we did the manual extrusion of gametes, depositing the oocytes from the female and the semen of the two males in the same beaker and immediately added water to allow fertilization. To avoid genetic differences among treatments, we mixed the fertilized eggs of all parents and transferred for incubators (at room temperature with constant water circulation), where eggs hatched and remained until the post-larva stage (when the yolk sac is consumed).

After three days of incubation, about 1600 post-larvae were transferred for each of the two rearing tanks used in this experiment. The number of post-larvae introduced per tank was calculated considering the average mortality rate for this species (= ~90%, according to the Volta Grande Fish Farming Station database) in order to obtain at least three collections of 50 individuals in each tank over a three-month experiment.

The two rearing tanks used were identical, made in concrete with a land bottom (3.00 meters long, 2.83 meters wide, and 0.75 meters deep) and located side by side. The tanks had a mesh screen cover to avoid predation by birds and to reduce the incidence of solar radiation. The water in tanks was constantly renewed and maintained at the same level. Throughout the experiment, the water quality parameters were monitored daily, as per routine, at the fish farming station. Fish in both tanks were fed once a day with identical amounts of commercial pellets for tropical fish (52% crude protein).

To test the enrichment effect on the fish morphology, we kept one tank as control and enriched the other. In the control we did not add any kind of structures. In the enriched tank, we added logs and artificial plants. To this, we used twenty-five plastic plants, which were hung from a kind of clothesline placed above the tank, so that the plastic filaments came in contact with the water. We also set six eucalyptus tree logs inside the tank, three arranged along the tank and the other three in a perpendicular way. To avoid the release of any resins and toxins in the water we kept the eucalyptus logs submersed for three months before the experiment. In addition, we monitored the water quality daily to confirm that there was no difference between the control and the enriched tank.

In each tank, we performed three fish collections: at day 30th, 60th and 90th after post larvae introduction, totalizing six samples (C1 = control tank, first collection; C2 = control tank, second collection; C3 = control tank, third collection; E1 = enriched tank, first collection; E2 = enriched tank, second collection; E3 = enriched tank, third collection). The short term of the experiment was due to the attempt to simulate what happens in the routine of the farm station, once the young fish are released in the nature with less than three months of life. At each sampling, 50 individuals were collected per tank using dip nets. Fish were euthanized with clove oil, fixed in 10% formalin and later preserved in 70% alcohol. The specimens voucher were deposited in the Ichthyological Collection of Universidade Federal de Lavras (CI-UFLA 786 -787).

In laboratory, we weighed and measured all fish collected. To analyze the morphometric of fish we took twenty-seven measurements based on Oliveira *et al.* 2009 on each specimen, including body, head and fins proportions (as shown in the table **S1**, available in the online version). We obtained the linear measurements directly using a digital caliper accurate to 0.01 mm manipulated always by the same person and always on the left side of body fish. We measured the areas of body and fins by drawing an outline each fish on paper. Then we digitalized the drawings and used the Image J software (U. S. National Institutes of Health, Bethesda, Maryland, USA) to calculate the areas. From the morphometric measurements, twenty-one ecomorphological traits were calculated (as shown in the table **S2**, available in the online version), considering its formulas and meanings according to Hora (1930), Gosline (1971), Gatz (1979), Watson & Balon (1984), Winemiller (1991), Pouilly *et al*. (2003) and Breda *et al.* (2005).

We considered each fish collected and measured as a replica of the treatment. In addition, concurrent studies accomplished at the same hatchery using the same tanks and the same type of environmental enrichment have indicated that there was no significant effect of the tank on fish morphology (Saraiva & Pompeu 2014, 2016b), which dismiss the lack of tank repetitions.

To assess whether environmental enrichment affected the *B. orbignyanus* growth in the first months of rearing, we compared the standard length of fish of the three collections from the control and the enriched tanks using a factorial ANOVA followed by Tukey's test (Harris 2001). To verify the existence of morphological differences between the samples (50 fishes in each collection), we performed a discriminant analysis (DCA) followed by the calculation of the Squared Mahalanobis Distances to assess the degree of differentiation (Xiang *et al.* 2008). The greater the Mahalanobis distance between the samples, the greater the difference between them. To monitor the ontogenetic allometry of Piracanjuba along the first months of life and verify the morphological differentiation caused by the enrichment we used Principal Component Analysis (PCA) to observe the distribution of individuals in the morphological space according to the ecomorphological traits analyzed (Harris 2001). We used a Broken-stick stop criterion for the selection of the axes (Jackson 1993). We performed PCA for the control and the enriched tanks, together and separately. To measure the morphological variability of each sample we calculated the distance from the centroid (CD), which is an estimate of the relative size of the morphological hypervolume occupied by the population (Winemiller 1991). Then we performed ANOVA between the distances from the centroid of the samples followed by Tukey's test to assess differences in the morphological variability among the samples. For this, we had to normalized the data to log(x+1).

Results

B. orbignyanus grew throughout the experiment. In the enriched tank, the growth was constant, but in the control tank, the fishes grew up more from the first to second month than from the second to third month. We observed significant differences in standard length between treatments ($F = 106.27$; $p < 0.001$), among periods ($F = 448.35$; $p < 0.001$), and when we considered the interaction between period and treatment ($F = 8.07$; $p < 0.001$). At the end of the experiment, Piracanjubas reared in the enriched tank were larger than those reared in the control tank. Since the first month, the fishes from the enriched tank had already grown more than fishes from control tank (Fig. 1, Table I).

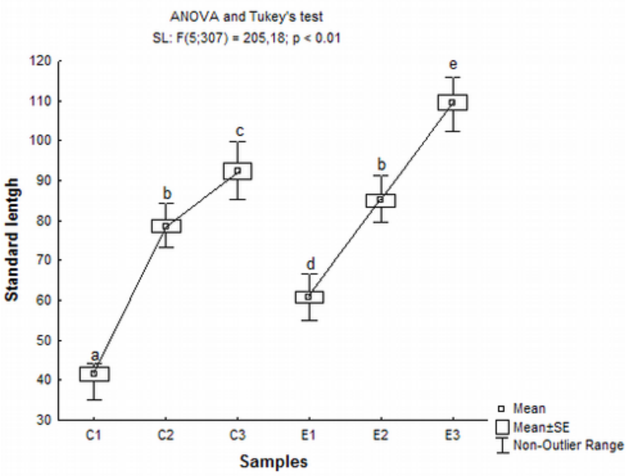

Figure 1. Piracanjuba standard length in control and enriched tank. After a significant ANOVA ($p < 0.05$). Tukey's test compared standard length averages among samples. Different letters indicate that samples did differ significantly and same letters indicate that samples did not differ. C1 = control tank, first collection; E1 = enriched tank, first collection; C2 = control tank, second collection; E2 = enriched tank, second collection; C3 = control tank, third collection; E3 = enriched tank, third collection.

Table I. P-values of Tukeys' test among samples. In the top right of the table is the result of the standard length comparison and in bottom left is the result of distance of the centroid. Highlighted in bold the significant values. C1 = control tank, first collection; E1 = enriched tank, first collection; C2 = control tank, second collection; E2 = enriched tank, second collection; C3 = control tank, third collection; E3 = enriched tank, third collection.

Samples	C1	C2	C3	E1	E2	E3
C1	-	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**
C2	0.11	-	**<0.01**	**<0.01**	0,085	**<0.01**
C3	0.99	0.38	-	**<0.01**	**0,031**	**<0.01**
E1	**<0.01**	**<0.01**	**<0.01**	-	**<0.01**	**<0.01**
E2	**<0.01**	0.45	**<0.01**	0.13	-	**<0.01**
E3	**<0.01**	0.83	**0.02**	**0.02**	0.99	-

Based on the analyzed traits, Piracanjubas from all six samples presented morphological differences among each other (DCA: Wilks' Lambda: 0.01378, F (105.1408) = 18.801, p <

0.001). Considering fish of the control and enriched tanks together, the morphological differentiation among them was sharper in the first month (dark and white circle), when fishes occupied a completely distinct morphological space (Fig. 2a). In fact, the morphological distance between fish of the control and the enriched tanks decreased with time (Table II). The first two PCA axes accounted for 37.34% of the variance: the first axis represented 24.57% and the second axis 12.77%. The analysis of the control and enriched tanks separately (Fig. 2b-c) showed that the samples from both tanks followed the similar shift pattern in morphological space, thus forming three distinct groups that corresponded to each collection. For control tank, the first two PCA axes accounted for 36.20% of the variance: the first axis represented 25.04% and the second axis 11.16%. For enriched tank, the first two PCA axes accounted for 40.30% of the variance: the first axis represented 31.00% and the second axis 9.30%.

Fish from the control and the enriched tank followed the similar shift pattern in morphological space, thus forming three distinct groups that correspond to each collection (Figs. 2b-c). Therefore, even under normal rearing conditions (control), the 30th, 60th and 90th day-old Piracanjubas differed morphologically one from another. In the enriched tank, fifteen ecomorphological traits were important for the differentiation among samples, while in the control tank twelve traits were important (Table III). Variables scores higher than 0.5 was positively associated to PCA axis, while the variable scores higher than -0.5 was negatively associated to PCA axis. We considered the variables (> |0.5|) the most important to our analysis. The enriched tank distinguished from the control mainly by the index of ventral flattening (IVF), relative area of the dorsal fin (RADsF), relative area of the pelvic fin (RAPlF), aspect ratio of the pelvic fin (ARPlF) and aspect ratio of the pectoral fin (ARPtF), which presented high contribution only in the enriched tank.

Regarding the morphological variability of the population, besides the significant difference among samples (ANOVA $F(5;308) = 13.64$; $p < 0.01$), only the environmental enrichment affected it (Fig. 3, Table III). There was no difference in the morphological variability over the three months of the experiment in the control tank. However, in the enriched tank, the 30th day-old fish showed lesser morphological variability than 60th and 90th day-old fish and lesser variability than all samples from the control tank.

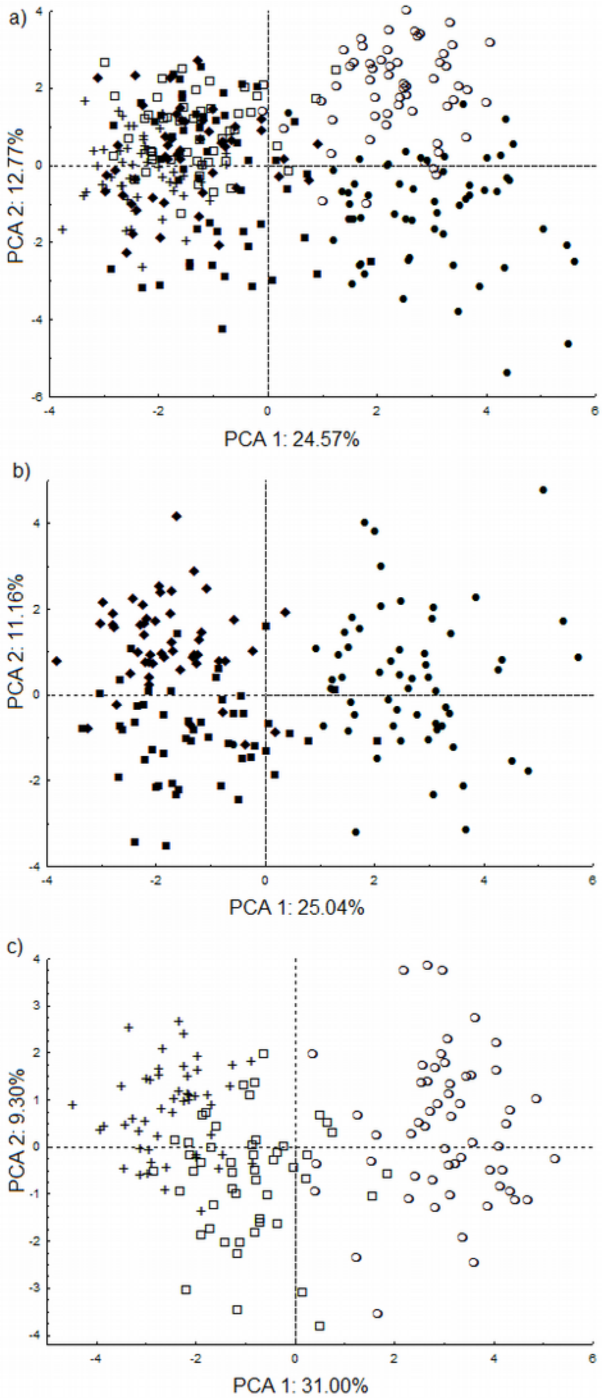

Figure 2. a) Simultaneous projection of the control and enriched tanks onto the first two axes of PCA. b) Individual projection of control tank onto the first two axes of the PCA. c) Individual projection of enriched tank onto the first two axes of the PCA. The percentage in axis corresponds to the explanation percentage to each PCA factor. Each symbol indicates the space occupied by individual fish from one of the collections: ● = C1. ■ = C2. ◆ = C3. ❍ = E1. ☐ = E2. + = E3. C1 = control tank, first collection; E1 = enriched tank, first collection; C2 = control tank, second collection; E2 = enriched tank, second collection; C3 = control tank, third collection; E3 = enriched tank, third collection. Sample size: C1=57. C2=50. C3=50. E1=56. E2=50. E3=50.

Table II. The Squared Mahalanobis Distances between samples in the bottom left of the table and its respective p-values in the top right of the table (all were significant). Highlighted in bold are the distances of each enriched tank sample relative to its respective control sample, that is, E1 compared to C1, E2 compared to C2 and E3 compared to C3.. C1 = control tank, first collection; E1 = enriched tank, first collection; C2 = control tank, second collection; E2 = enriched tank, second collection; C3 = control tank, third collection; E3 = enriched tank, third collection.

Samples	C1	C2	C3	E1	E2	E3
C1	-	<0.01	<0.01	<0.01	<0.01	<0.01
C2	34.32	-	<0.01	<0.01	<0.01	<0.01
C3	37.95	11.39	-	<0.01	<0.01	<0.01
E1	**14.64**	36.02	30.25	-	<0.01	<0.01
E2	37.14	**9.24**	5.65	32.21	-	<0.01
E3	52.51	11.53	**3.77**	44.15	8.10	-

Discussion

The environmental enrichment have changed the ontogenetic allometry of the hatchery fish supporting partially our hypothesis. *B. orbignyanus* reared in tanks with logs and artificial plants were larger, with distinct morphological traits, especially fins, but with lower morphological variability. The differences promoted by the environmental enrichment were more pronounced in the first month of the experiment, showing that younger fish are more susceptible to its effects. This may be explained because younger fish have greater phenotypic plasticity, so that the environment has a greater effect on ontogenetic allometry during the early stages of development (Woods 2007). Such plasticity have been linked to aspects of life history and is likely to be particularly important for survival (Hale 1999). Thus, to promote a major effect on the morphology of farmed fish, the enrichment of the rearing tanks should be applied since the initial stages. However, as the enrichment effect decreases over time, could be that the morphological changes detected are temporary and reversible.

In the enriched tank, *B. orbignyanus* presented longer lengths since the first month of the experiment and had a more constant growth than fish reared in the control tank, reaching longer lengths sooner. In a previous study we have already detected that Piracanjuba reach larger sizes when raised in enriched tanks (Saraiva & Pompeu 2014). This result has a practical application because obtaining larger fish in less time is the goal of many fish farmers, both from the production and conservation perspective. Larger fish are less vulnerable to predators, more resistant to starvation, more tolerant to physiological extremes (Sogard 1997), and presumably more capable of colonizing the natural environment. These characteristics are important because they can make the difference between survival and death, when captive fish are released into the natural environment.

Table III. Contributions of ecomorphological traits to the first two axes of the principal component analysis (PCA) for control vs. enriched tank. The values in bold indicate the traits that most contributed for differentiation among tanks in each axes. CI = compression index; IVF = index of ventral flattening; RBH = relative body height; REP = relative eye position; REA = relative eye area; RHeL = relative head length; RLCdP = relative length of the caudal peduncle; RHCdP = relative height of the caudal peduncle; RWCdP = relative width of the caudal peduncle; CICdP = compression index of the caudal peduncle; RADsF = relative area of the dorsal fin; RACdF = relative area of the caudal fin; ARCdF = Aspect ratio of the caudal fin; RAAnF = relative area of the anal fin; ARAnF = aspect ratio of the anal fin; RLPlF = relative length of the pelvic fin; RAPlF = relative area of the pelvic fin; ARPlF = aspect ratio of the pelvic fin; RLPtF = relative length of the pectoral fin; RAPtF = relative area of the pectoral fin; ARPtF = aspect ratio of the pectoral fin.

Traits	Control tank		Enriched tank	
	PCA 1	PCA 2	PCA 1	PCA 2
CI	**-0.50**	-0.46	-0.30	-0.46
IVF	0.46	0.03	**0.62**	-0.05
RBH	0.36	**-0.55**	**0.63**	-0.26
REP	0.43	0.11	0.43	0.11
REA	**0.67**	-0.26	0.39	**-0.52**
RHeL	**0.72**	-0.16	**0.69**	-0.44
RLCdP	**-0.74**	-0.03	**-0.74**	0.16
RHCdP	**-0.60**	0.49	**-0.69**	0.28
RWCdP	**-0.77**	-0.11	-0.52	0.06
CICdP	0.03	0.17	-0.04	-0.23
RADsF	-0.19	0.10	**0.59**	-0.15
RACdF	-0.38	-0.12	0.32	-0.05
ARCdF	**0.54**	0.31	0.13	-0.24
RAAnF	0.33	**-0.65**	**0.90**	-0.01
ARAnF	-0.23	**0.68**	**-0.84**	0.04
RLPlF	**-0.56**	-0.33	**-0.57**	-0.49
RAPlF	-0.37	-0.08	**0.59**	0.04
ARPlF	-0.17	-0.43	-0.44	**-0.50**
RLPtF	**-0.75**	-0.23	**-0.65**	**-0.51**
RAPtF	-0.47	-0.01	0.10	-0.20
ARPtF	-0.36	-0.28	**-0.51**	-0.39

Under normal rearing conditions (control tank), the morphological traits of *B. orbignyanus* changed naturally during the three months of the

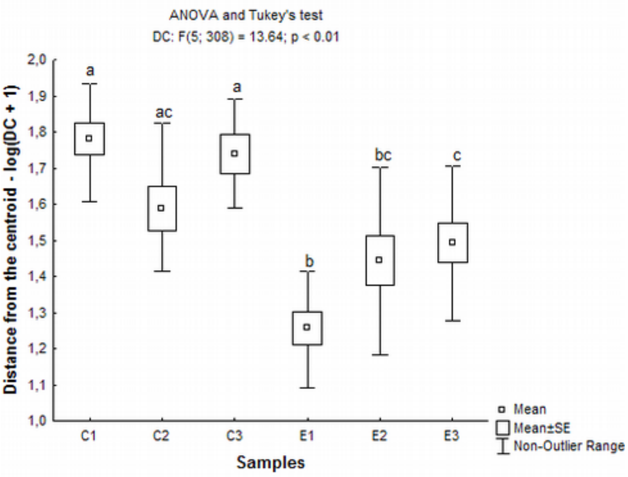

Figure. 3. Log of the distance from the centroid plus one [log (DC + 1)] for control and enriched tanks. After a significant ANOVA ($p < 0.01$), Tukey's test compared the log (DC + 1) values among samples. Different letters indicate that samples did differ significantly and same letters indicate that samples did not differ. C1 = control tank, first collection; E1 = enriched tank, first collection; C2 = control tank, second collection; E2 = enriched tank, second collection; C3 = control tank, third collection; E3 = enriched tank, third collection.

experiment, evidencing the ontogenetic allometry of this species in captivity. However, there was also morphological divergences caused by the environmental enrichment, since Piracanjuba reared in the enriched tank were different from those reared in the control tank. The ontogenetic allometry is already known for many fish species (e. g. Klingenberg & Froese 1991, Wimberger 1992, Woods 2007, Rodríguez-Mendoza *et al*. 2011) and the power of the environmental enrichment in changing the fish morphology (including *B. orbignyanus*) have been already detected in previous studies (Garduño-Paz *et al.* 2010, Saraiva & Pompeu 2014, 2016b). Here we show for the first time the effects of the environmental enrichment on the ontogenetic allometry in *B. orbignyanus.* In other words, the enrichment changes not only the resulting morphology of hatchery fish, but also the way they get there.

The morphological variability of the enriched tank was lower in the first month, and increased and equaled to the variability of the control in subsequent months. This result is surprising, since we expected that fish reared in enriched tank presented a most similar morphology to wild fish, which have a greater morphological variability (Taylor, 1986, Saraiva & Pompeu 2016a). Nevertheless, the environmental enrichment applied in this study, only mimic two aspects of the natural environment (logs and aquatic plants), which may have driven the morphology of Piracanjuba to the type most suitable to explore this environment, instead of having promoted an increase in morphological variability. Therefore, is important to test another types and combinations of enrichment.

By creating a different allometric pattern in Piracanjuba, the environmental enrichment affected specific morphological traits. Those most affected were the traits related to the dorsal, pelvic and pectoral fins, which are linked to the ability to perform maneuvers (Gosline 1971, Watson & Balon 1984), an important characteristic in a complex environment. The enrichment affected these traits probably because they favor fish swimming and foraging in the middle of logs and aquatic plants (Saraiva & Pompeu 2014). In nature during the young phase, the migratory species (including *B. orbignyanus*) inhabits marginal lagoons, where fish fry find high availability of shelter and food (Agostinho & Júlio Jr, 1999). As these environments are rich in macrophytes and wood debris, so fish reared in the enriched tanks and released in nature may present a morphological advantage to colonize this environments. However, such possible consequences should be object of further studies.

To our knowledge, this is the first study showing how the environmental enrichment affects the ontogenetic allometry of fish. In addition, this experiment was performed in a fish farm station using tanks instead of aquaria, showing that is possible and effective the application of the enrichment in practice. Piracanjuba reared in enriched tanks presents a distinct ontogenetic allometry, which results in larger sizes and morphological traits modified to the exploration of a structurally complex environment. Thus, the enrichment may be consist in an important management measure in fish stocking, allowing that the fish farmer release the fish earlier, reducing costs and the effects of domestication. However, in order to investigate if the morphological changes are temporary and reversible, adaptive or deleterious in the wild; it is necessary complementary and long-term studies. In the case of stocking for supplementation of native populations it is also important test another species and many types of enrichment, trying to mimic the natural environment as well as possible, in order to obtain farmed fish with a more varied morphology, similar to their wild counterparts and consequently increasing their survival chances.

Acknowledgements

We are most grateful to the *Companhia Energética de Minas Gerais* (CEMIG) for their support and the staff of the Volta Grande fish station for the essential help during the experiment, especially João de Magalhães Lopes, Alessandra Bedore and Sônia Maria Ramos. We thank the *Coordenação de Aperfeiçoamento de Pessoal de Nível Superior* (CAPES) for the Master's scholarship granted to SOS, the *Conselho Nacional de Desenvolvimento Científico e Tecnológico* (CNPq) and the *Fundação de Amparo à Pesquisa do Estado de Minas Gerais* (FAPEMIG) for the research fellowship granted to PSP (CNPq 30402/2014-3 and FAPEMIG PPM 00237/13 respectively). Finally, we are grateful to the Program of Post-Graduation in Applied Ecology of the *Universidade Federal de Lavras* (UFLA) by bidding the discipline PEC-533 (Scientific Publication in Ecology), during which this manuscript was partially written.

References

Agostinho, A. A., Gomes, L. C. & Pelicice, F. M. 2007. **Ecologia e manejo de recursos pesqueiros em reservatórios do Brasil.** Universidade Estadual de Maringá, Maringá, 501 p.

Agostinho, A. A. & Júlio-Jr, H. F. 1999. Peixes das Bacia do Alto Paraná. In. Lowe-McConnell, R. H. **Estudos Ecológicos de Comunidades de Peixes Tropicais**. 1 ed. USP, São Paulo, 374-400 p.

Batzina, A. & Karakatsouli, N. 2012. The presence of substrate as a means of environmental enrichment in intensively reared gilthead seabream Sparus aurata: Growth and behavioral effects. **Aquaculture**, 370-371: 54-60.

Belk, M. C., Benson, L. J., Rasmussen, J. & Peck, S. L. 2008. Hatchery-induced morphological variation in an endangered fish: a challenge for hatchery-based recovery efforts. **Canadian Journal of Fisheries and Aquatic Science**s, 408: 401-408.

Berejikian, B. A., Tezak, E. P., Riley, S. C. & Larae, A. L. 2001. Competitive ability and social behaviour of juvenile steelhead reared in enriched and conventional hatchery tanks and a stream environment. **Journal of Fish Biology**, 59: 1600–1613.

Breda, L., Oliveira, E. F. & Goulart, E. 2005. Ecomorfologia de locomoção de peixes com enfoque para espécies neotropicais. **Acta Scientarium Biological Sciences**, 27(4): 371-381.

Brydges, N. M. & Braithwaite, V. A. 2009. Does environmental enrichment affect the behaviour of fish commonly used in laboratory work? **Applied Animal Behaviour Science**, 118: 137–143

Casatti, L. & Castro, R. M. C. 2006. Testing the ecomorphological hypothesis in a headwater riffles fish assemblage of the rio São Francisco, southeastern Brazil. **Neotropical Ichthyology**, 4(2): 203–214.

Fleming, I. A., Jonsson, N. B., Gross, M. R. 1994. Phenotypic divergence of sea-ranched, farmed, and wild salmon. **Canadian Journal of Fisheries and Aquatic Sciences**, 51: 2808-2824.

Garduño-Paz, M. V., Couderc, S. & Adams, C. E. 2010. Habitat complexity modulates phenotype expression through developmental plasticity in the threespine stickleback. **Biological Journal of the Linnean Society**, 100(2): 407-413.

Gatz, A. J. 1979. Ecological morphologic of freshwater stream fishes. **Tulane Studies in Zoology and Botany**, 21: 91-124.

Gosline, W. A. 1971. **Functional morphology and classification of teleostean fishe**s. University of Hawaii, Honolulu, 208 p.

Hale, M. E. 1999. Locomotor mechanics during early life history: effects of size and ontogeny on fast-start performance of salmonid fishes. **Journal of Experimental Biology**, 202(11): 1465-1479.

Hard, J. J., Berejikian, B. A., Tezak, E. P., Schroder, S. L. & Knudsen, C. M. 2000. Evidence for morphometric differentiation of wild and captively reared adult coho salmon: a geometric analysis. **Environmental Biology of Fishes**, 58: 61–73.

Harris, R. J. 2001. **A primer of multivariate statistics**. Psychology Press. 634p.

Hora, S. L. 1930. Ecology, bionomics and evolution of the torrential fauna, with special reference to the organs of attachment. **Philosophical Transactions of the Royal Society of London**, 28: 171-282.

Jackson DA. 1993. Stopping rules in principal components analysis: a comparison of heuristical and statistical approaches. **Ecology,** 74(8): 2204–2214.

Johnsson, J. I, Brockmark & S., Näslund, J. 2014. Environmental effects on behavioural development consequences for fitness of captive-reared fishes in the wild. **Journal of Fish Biology**, 85: 1946–1971.

Klingenberg, C. P. & Froese R. 1991. A mulltivariate comparison of allometric growth patterns. **Systematic Zoology**, 40(4): 410-419.

Leal, C. G., Junqueira, N. T. & Pompeu, P. S. 2010. Morphology and habitat use by fishes of the rio das Velhas Basin in southeastern Brazil. **Environmental Biology of Fishes**, 90(2): 143–157.

Lopera-Barrero, N. M. 2009. Conservation of Brycon orbignyanus natural populations and stocks for their reproductive, genetic, environmental sustainability: a model for species threatened with extinction. **Ciencia e Investigación Agraria**, 36: 191-208.

Maynard, D. J., Flagg, T. A. & Mahnken, C. V. W. 1994. **A review of seminatural culture strategies for enhancing the postrelease survival of anadromous salmonids**. National Marine Fisheries Service, Seattle, 34 p.

Näslund, J. & Johnsson, J. L. 2014. Environmental enrichment for fish in captive environments: Effects of physical structures and substrates. **Fish and Fisheries**, 17: 1-30.

Oliveira, E. F., Goulart, E., Breda, L., Minte-Vera, C. V., Paiva, L. R. S. & Vismara, M. R. 2010. Ecomorphological patterns of the fish assemblage in a tropical floodplain: effects of trophic, spatial and phylogenetic structures. **Neotropical Ichthyology**, 8(3):569-586.

Pouilly, M., Lino, F., Bretenoux, J. G. & Rosales C. 2003. Dietary morphological relationships in a fish assemblage of the Bolivian Amazonian floodplain. **Journal of Fish Biology**, 62: 1137-1158.

Roberts, L. J, Taylor, J. & Garcia-de-Leaniz, C. 2011. Environmental enrichment reduces maladaptive risk-taking behavior in salmon reared for conservation. **Biological Conservation**, 144: 1972-1979.

Rodríguez-Mendoza, R., Muñoz, M. & Saborido-Rey, F. 2011. Ontogenetic allometry of the bluemouth, Helicolenus dactylopterus dactylopterus (Teleostei: Scorpaenidae), in the northeast atlantic and mediterranean based on geometric morphometrics. **Hydrobiologia**, 670(1): 5-22.

Rosa, R. S. & Lima, F. C. T. 2008. Os Peixes Brasileiros Ameaçados de Extinção. *In*: Machado, A. B. M., Drummond, G. M. & Paglia, A. P. (Eds.). **Livro Vermelho da Fauna Brasileira Ameaçada de Extinção**. Ministério do Meio Ambiente, Brasília, 1420 p.

Saraiva, S. O. & Pompeu, P. S. 2014. The effect of structural enrichment in hatchery tanks on the morphology of two neotropical fish species. **Neotropical Ichthyology**, 12(4): 891-901.

Saraiva, S. O. & Pompeu, P. S. 2016a. Fish hatchering and its effects on the morphology of *Prochilodus lineatus* (Actinopterygii: Prochilodontidae). **Brazilian Journal of Biology**, 76(1): 209-217.

Saraiva, S. O. & Pompeu, P. S. 2016b. Structural and social enrichment: effects on the morphology of a tropical hatchery fish. **Applied Ecology and Environmental Research**, 14(3): 381-395.

Sogard, S. M. 1997. Size-selective mortality in the juvenile stage of teleost fishes: a review. **Bulletin of Marine Science**, 60(3): 1129–1157.

Solem, Ø., Berg, K. & Kjøsnes, A. J. 2006. Inter- and intra-population morphological differences between wild and farmed Atlantic salmon juveniles. **Journal of Fish Biology**, 69(5): 1466–1481.

Souza, M. A., Fagundes, D. C., Leal, C. G. & Pompeu, P. S. 2014. Ecomorphology of Astyanax species in streams with different substrates. **Zoologia**, 31(1): 42–50.

Swain, L. B, Riddell, B. E. & Murray, C. B. 1991. Morphological differences between hatchery and wild populations of coho salmon (Oncorhynchus kisutch): environmental versus genetic origin. **Canadian Journal of Fisheries and Aquatir Sciences**, 48: 1783-1791.

Taylor, E. B. 1986. Differences in morphology between wild and hatchery populations of juvenile Coho Salmon. **The Progressive Fish-Culturist**, 48(3): 171-176

Xiang, S., Nie, F., & Zhang, C. 2008. Learning a Mahalanobis distance metric for data clustering and classification. **Pattern recognition**, 41(12): 3600-3612.

Watson, D. J. & Balon, E. 1984. Ecomorphological analysis of taxocenes in rainforest streams of northern Borneo. **Journal of Fish Biology**, 25: 371-384.

Wimberger, P. H. 1992. Plasticity of fish body shape: the effects of diet, development, family and age in two species of Geophugus (Pisces: Cichlidae). **Biological Journal of the Linnean Society**, 45: 197-218.

Winemiller, K. O. 1991. Ecomorphological diversification in lowland freshwater fish assemblages from five biotic regions. **Ecological Monographs**, 61: 343-365.

Woods, P. J. 2007. Habitat-dependent geographical variation in ontogenetic allometry of the shiner perch Cymatogaster aggregata gibbons (Teleostei: Embiotocidae). **Journal of Evolutionary Biology**, 20(5): 1783-1798.

Received: April 2018
Accepted: May 2019
Published: June 2019