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Letter to the Editor

Effect of environmental enrichment on the body shape of the pumpkinseed

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How the morphology of captive-reared fish is affected by structural enrichment in their rearing tanks is not well understood. Some studies have suggested that deficiencies in rearing environments could produce inappropriate body shape in salmonids (Vehanen and Huusko 2011). Garduño-Paz et al. (2010) have found significant differences in body and head shapes of 3-spine stickleback *Gasterosteus aculeatus*, depending on whether fish were reared in an environment with just gravel or in an environment enriched with large stones and artificial plants. Similarly, according to Saraiva and Pompeu (2014), structural enrichment has a strong effect on some morphological traits such as a smaller size of the head and enlarged fins in the Neotropical fish species *Brycon orbignyanus* (suggesting a differentiation that facilitates manoeuvrability). Although changes are much more likely to occur at early developmental stages than in later ones (Meuthen et al. 2018), several studies have shown that morphological plasticity remains high in juvenile and adult stages of the pumpkinseed *Lepomis gibbosus* (Yavno et al. 2014) as well as in adults of other fish species (Laporte et al. 2016). In order to determine if structural enrichment would have an effect on the body shape and on the size and position of fins in fish, pumpkinseed was selected as an adequate model species for its well-known phenotypic plasticity (Yavno et al. 2013). In this study, 11 morphometric variables (Figure 1A) were measured (±0.01 mm) in pumpkinseeds caught in the field and growing for 18 months under 3 different conditions: 1) nonenriched treatment (NON-EN), late juveniles growing in aquaria without structural enrichment (with just gravel at the bottom), 2) enriched treatment (EN), late juveniles growing in aquaria with structural enrichment (providing elements such as natural plants, small trunks, and stones), and 3) nonexperimental fish (NON-EXP), fish growing throughout the same period at the sampling site where the housed fish were caught (see details about methods in Supplementary material). Our prediction was that fish housed under structural enrichment would be similar in morphometric measurements to the fish growing in the field (since the habitat complexity was reproduced) whereas the fish maintained without structural enrichment would develop differently.

Results of the simplified Analysis of Covariance (ANCOVA) model for each morphometric measurement with fork length (FL ± 0.1 mm) as a covariate and experimental condition as a categorical factor showed significant effects of the experimental condition (NON-EN, EN, and NON-EXP) on 4 out of the 11 morphometric variables considered: anterior of dorsal fin to anterior of pelvic fin, anterior caudal peduncle depth, pectoral fin maximum length, and prepelvic length; and nearly significant ($P \sim 0.05$) on 2 other variables: pelvic fin maximum length and predorsal length (Supplementary Table S1). Tukey's HSD tests revealed that there were no significant differences in any of the previously mentioned morphometric variables between EN and NON-EN conditions (Supplementary Table S1). Nevertheless, Tukey's HSD tests also suggested a significant morphological difference related to body depth, anterior caudal peduncle depth, pectoral and pelvic fin maximum lengths, and the location of the dorsal and pelvic fins between pumpkinseeds from EN and NON-EXP conditions (Supplementary Table S1). In contrast, pumpkinseeds from NON-EN condition showed significant differences only in caudal peduncle depth and location of the pelvic fins with pumpkinseeds from NON-EXP condition (Supplementary Table S1).

A Principal Component Analysis (PCA) was performed in order to better understand these differences. The first 2 Principal Component (PC) axes from the pooled dataset explained 47.5% of the total variation. The first axis explained most of the variation (29.3%) and was mainly influenced by anterior caudal peduncle depth (factor loading: 0.761), pectoral fin maximum length (factor loading: −0.506), and pelvic fin maximum length (factor loading:
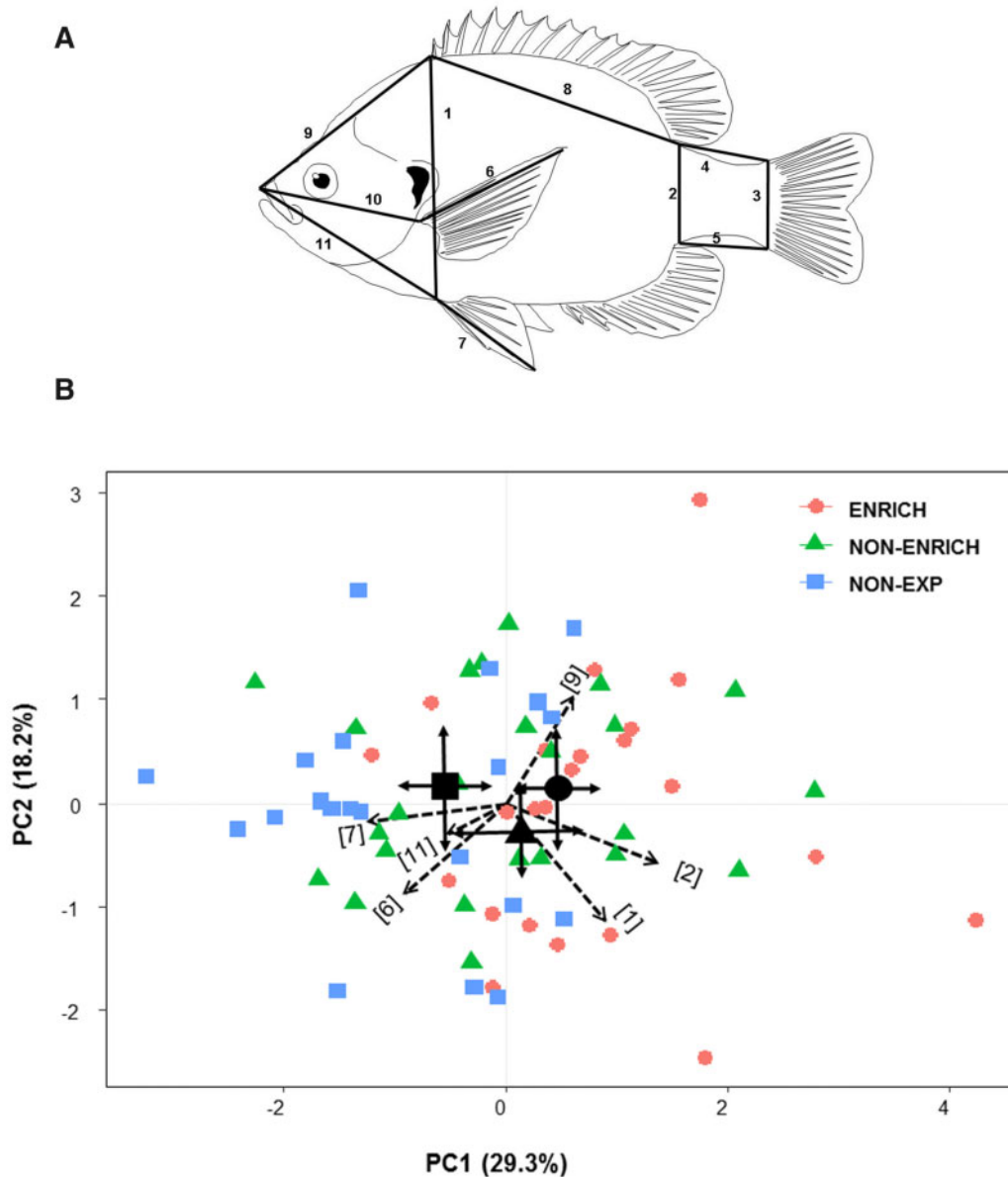
Figure 1. (**A**) Morphometric measurements used in this study: [1] anterior of dorsal fin to anterior of pelvic fin (body depth), [2] anterior caudal peduncle depth, [3] posterior caudal peduncle depth, [4] dorsal caudal peduncle length, [5] ventral caudal peduncle length, [6] pectoral fin maximum length, [7] pelvic fin maximum length, [8] dorsal fin base length, [9] predorsal length, [10] prepectoral length, [11] prepelvic length. (**B**) Scores for the dataset containing all individuals of the 3 experimental conditions (EN, NON-EN, and NON-EXP) on the first 2 principal component axes based on 6 morphometric measurements. Arrows represent the factor loadings of the morphometric measurements for the first 2 PCA axes. Black symbols represent the means and SD of the individual scores of the 3 experimental conditions for the first 2 PCA axes.

−0.690; Figure 1B). The second axis, which explained 18.2% of the variation, was associated with body depth (factor loading: 0.629) and predorsal length (Factor loading: −0.568) (Figure 1B). Thus, the first PC axis (Figure 1B) identified a gradient of morphometric measurements that contrasts individuals from EN condition with deeper caudal peduncles, and shorter pectoral and pelvic fins with individuals from NON-EXP condition which showed the opposite series of traits. The second PC axis contrasted EN condition individuals showing deeper body depths and more posteriorly located dorsal fins with NON-EXP individuals. Individuals from NON-EN condition showed intermediate morphometric measurements between EN and NON-EXP conditions (Figure 1B). In order to analyze morphological differences, a Generalized Linear Mixed Model

(GLMM) was performed with PC1 as the dependent variable, FL as the covariate and with the same factors as in the previous model. Tank effect was not found to be significant ($P > 0.05$) and it explained <1% of the variance, so that it was removed from the model. The final model explained 32.3% of the variance and showed significant differences for experimental conditions ($F_{2,63} = 14.2$, $P < 0.001$) and sex ($F_{1,63} = 8.5$, $P < 0.005$), but not for the interaction between experimental conditions and sex ($F_{2,63} = 1.4$, $P = 0.27$). Therefore, sex affected body shape in a similar way for the 3 experimental conditions.

These results are in concordance with other previous works that suggest that captivity conditions might produce body shapes different from the wild when important environmental characteristics are

not reproduced (Belk et al. 2008; Näslund and Johnsson 2014; Saraiva and Pompeu 2019). To some extent, pumpkinseeds housed in captivity developed morphological characteristics (such as deeper caudal peduncles and forward pelvic fins) allowing both burst swimming and higher maneuverability under low water velocities according to the results reported by Webb (1984). This suggests that factors other than enrichment based on structural elements would be responsible for the morphological differences observed between captive and wild pumpkinseeds. According to Yavno et al. (2013), under sustained flowing water conditions, pumpkinseeds develop more posteriorly located median fins and narrower body depths, whereas pumpkinseeds under static water conditions show the opposite traits. The restriction of swimming opportunities due to captivity conditions could be behind the development of specific shapes in fish such as a reduced streamlining, an increased angle of the median fins relative to the lateral line, and a more forward positioning and greater separation of paired fins (Hard et al. 2000). Other factors such as prey type and feeding mode, interspecific competition and predation pressure might be behind the differences found between experimental (enriched and nonenriched conditions) and nonexperimental pumpkinseeds (e.g., Yavno et al. 2014; Meuthen et al. 2018). The effects of captive environments may not be limited to morphology and may affect behavior and/or physiology (Näslund and Johnsson 2014). Under the perspective of experimental biology, the results of this study show that it should not be assumed that fish growing in captivity develop a similar body shape than fish in the field. Structural enrichment consisting in adding plants, trunks, and stones to the aquaria was ineffective for pumpkinseeds to reach a morphology similar to that of those living in the wild.

Acknowledgments

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