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Ontogenetic allometry of body shape in *Serrasalmus brandti* (Lütken, 1875) (Characiformes: Serrasalmidae)

Alometria ontogenética da forma corporal em *Serrasalmus brandti* (Lütken, 1875) (Characiformes: Serrasalmidae)

Mauro J. Cavalcanti[1*]; Jailza Tavares de Oliveira-Silva[2], Paulo Roberto Duarte Lopes[2]

[1]Ecoinformatics Studio

[2]Departamento de Ciências Biológicas, Universidade Estadual de Feira de Santana - UEFS

*Email: maurobio@gmail.com

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Resumo As alterações ontogenéticas na forma do corpo da piranha-branca, *Serrasalmus brandti*, foram analisadas com técnicas de morfometria geométrica. Foram obtidas coordenadas Cartesianas de 16 marcos anatômicos definidos com base na morfologia externa de 133 exemplares provenientes de 11 localidades na Bacia do Rio São Francisco. As coordenadas alinhadas pela análise de Procrustes foram usadas para construir variáveis de forma. Uma regressão multivariada do tamanho do centroide sobre as variáveis da forma foi determinada para testar a hipótese de modificações significativas da forma ao longo da ontogenia. A análise mostrou diferenças estatisticamente significativas de forma com o tamanho (teste generalizado de Goodall $F_{[28,\ 3668]}$ = 2.0175, p = 0.001), indicando que a forma do corpo nesta espécie não é ontogeneticamente estável. A maior parte das modificações ontogenéticas da forma ocorrem na região anterior do corpo, podendo ser descritas por um aumento no comprimento da cabeça e uma diminuição na altura do corpo nos exemplares maiores

Palavras-Chave: *Serrasalmus*, América do Sul, morfometria geométrica, ontogenia

Abstract The ontogenetic body shape changes in the white piranha, *Serrasalmus brandti*, were analyzed with geometric morphometrics techniques. The Cartesian coordinates of 16 anatomical landmarks were obtained from the external morphology of 133 specimens of *S. brandti* collected in 11 localities along the São Francisco River basin. The Procrustes-aligned landmark coordinates were used to construct shape variables. A multivariate regression of the shape variables on centroid size was determined to test the hypothesis of significant shape changes along ontogeny. The analysis showed statistically significant differences in shape with size (Goodall's generalized test $F_{[28,\ 3668]}$ = 2.0175, p = 0.001), indicating that body shape in this species is not ontogenetically stable. Most of the ontogenetic shape changed observed in *S. brandti* occur in the anterior region of the body and can be described by an increase in head length and a decrease in body depth in the larger specimens.

Keywords: *Serrasalmus*, South America, geometric morphometrics, ontogeny.

Introduction

The genus *Serrasalmus* Lacepède 1803 comprises about 30 species of South American freshwater fishes, commonly known as piranhas, that are characterized by a rhomboid body, sharp teeth, and powerful jaws (Jégu 2003, Nelson 2006).

The species of *Serrasalmus* are morphologically very similar and present several problems of identification, nomenclatural inconsistencies, and uncertainties in phylogenetic relationships. Phylogenetic analyses based on molecular data have shown the existence of one well-supported monophyletic clade including *Serrasalmus*, *Pygocentrus* Müller & Troschel, 1844, and part of *Pristobrycon* Eigenmann,1915, that was also demonstrated to be identifiable on the basis of morphological characters (Freeman *et al.* 2007).

The white piranha or pirambeba, *Serrasalmus brandti* Lütken, 1875, the species here studied, is a benthopelagic species which occurs in the São Francisco River basin in Brazil (Britski *et al.* 1988, Pompeu 1999) and attains about 22 cm in total length. This species has been included in the molecular phylogenetic analyses performed by Orti *et al.* (2008), which positioned it in a clade along with all other extant species of *Serrasalmus* and *Pygocentrus*.

In the present study, the hypothesis that significant ontogenetic changes in body shape do occur in *Serrasalmus brandti* are examined with techniques of geometric morphometrics, that allow the precise and detailed analysis of shape variation in organisms on the basis of coordinate data from homologous anatomical landmarks (Adams *et al.* 2004), These methods represent an interesting alternative to traditional morphometrics, based on measured distances, and have demonstrated to be particularly relevant to allometric studies in fishes (Walker 1993, Zelditch & Fink 1995, Loy *et al.* 1996, Reis *et al.* 1998, Hood & Heins 2000, Frederich & Sheets 2010, Rodrıguez-Mendoza *et al.* 2011, Vergara-Solana *et al.* 2013).

Materials and Methods

The analysis was performed on the Cartesian coordinates of 16 two-dimensional landmarks defined on the basis of the external morphology (following Fink 1993), from 133 specimens of *Serrasalmus brandti*, ranging from 40 to 160 mm in standard length (Figura 1). Landmark coordinates were obtained from digitized images taken from the left side of each specimen with a Sony DSLR-A 200K (Alpha) digital camera with a resolution of 10.2 megapixels, using the program TPSDig v2.26 (Rohlf 2015).

Figura 1. Locations of the 16 anatomical landmarks (numbered points) recorded on each specimen of *Serrasalmus brandti*.

Specimens examined were captured in 11 localities along the basin of São Francisco River (Northeastern Brazil) (Figura 2) and are deposited in the fish collection of Museu de Zoologia, Divisão de Peixes, Universidade Estadual de Feira de Santana, preserved in alcohol 70%.

Figure 2. Map of South America displaying the locality records of the specimens of *Serrasalmus brandti* included in this study.

The geometric size of each specimen was estimated by the centroid size, defined as the square root of the summed squared distances of all landmarks to the centroid of the configuration (Bookstein 1991), transformed to decimal logarithms.

For each specimen, the landmark coordinates were aligned and superimposed by Generalized Procrustes Analysis (Adams *et al.* 2004), scaling the configurations to unit centroid size and then centered and rotated them, in order to minimize the sum of squared distances between the landmarks of each configuration to the corresponding landmarks of a reference or "consensus" configuration (computed as the mean landmark configuration of all specimens). The scores of a principal components analysis of the Procrustes superimposed specimens described deviations of each specimen from the reference configuration and were used as shape variables in subsequent multivariate statistical analyses (Adams *et al.* 2004).

Patterns of ontogenetic shape changes were analyzed by multivariate regression of the shape variables onto $\log_{10}$ centroid size (Rohlf 1998, Monteiro 1999). The fit of the multivariate regression model was tested using a generalization of Goodall's (1991) F-test. A permutation test, with 1000 random permutations of the data, was used to assess the significance of the F statistic. Computations were performed using the program TPSRegrw v1.44 (Rohlf 2015). Thin-plate splines deformation grids were used to graphically depict the patterns of shape variation among the landmarks.

Results

The multivariate regression of the shape variables on centroid size with 1000 random permutations was highly significant (Goodall’s $F_{[28, 3668]} = 2.0175$, $P = 0.0012$).

As depicted by the thin-plat splines deformation grids (Figura 3), most of the ontogenetic shape changes observed in *S. brandti* occur in the anterior region of the body (landmarks 3, 11, 12, and 16), and can be described by a compression of the head and an overall elongation of the body along the anteroposterior axis, with a shallowing of the mid-body and the tail region more homogeneous in shape. Larger specimens thus are blunt-headed head and show a relatively slender body, whereas smaller specimens are sharp-snouted an d present a relatively higher body.

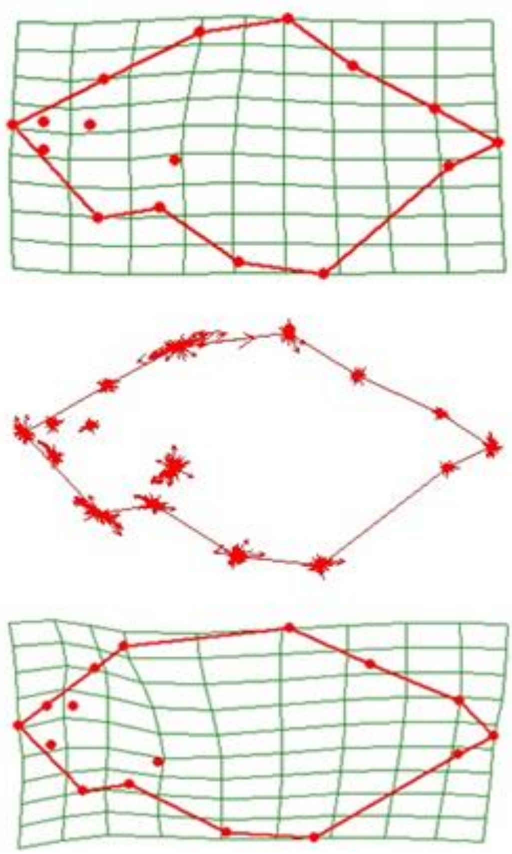

Figure 3. Shape changes, expressed as deformation grids using thin-plate splines, as a function of size in *Serrasalmus brandti* estimated by a multivariate regression of shape variables on centroid size: (top) estimated shape for a very small specimen; (middle) mean configuration with vectors indicating landmark displacements for increasing size; (bottom) estimated shape for a very large specimen. Shape changes for maximum and minimum centroid sizes were multiplied by three for clarity.

Discussion

The results of this study support the hypothesis that the patterns of shape variation during ontogeny in *S. brandti*, as depicted by geometric morphometric techniques, are not ontogenetically stable and change significantly along development, corroborating those reported for other species of *Serrasalmus* and the related genus *Pygocentrus*. In Venezuela, Machado-Allison & Garcia (1986) documented ontogenetic modifications in the head morphology of *S. rhombeus* and *P. notatus*. These changes can be interpreted functionally, taking into account the differences in diet and feeding behavior between juvenile and adult individuals observed in several piranha species (Machado-Allison & Garcia 1986, Nico & Taphorn 1988). Larvae and juvenile individuals of *S. spilopleura* are known to use mats of floating aquatic vegetation as shelter as well as a foraging ground for the smaller food items they consume (Nico & Taphorn 1988, Sazima & Zamprogno 1985). Adults individuals, in turn, are aggressive predators with a specialized carnivorous diet, usually living in shoals and using active predatory tactics (Sazima & Machado 1990); such ontogenetic diet shift might thus selectively favor a slender body and larger jaws. In the specific case of *S. brandti*, in his study of the feeding habits of this species in four floodplains lakes in São Francisco River, Pompeu (1999) concluded that trophic ontogeny as reported for other species of *Serrasalmus* also occurs in this species.

These results also corroborate a study of a species in the related genus *Pygocentrus* using geometric morphometrics (Zelditch & Fink 1995). That study also found evidence of allometric shape changes in *P. nattereri*, with an elongation of the mid-body and a compression of the head and anterior relative to the anteroposterior region of the body similar to the patterns of ontogenetic shape change reported here.

We suggest that these changes may be interpreted as the morphological response to the evolutionary development of a specialized carnivorous diet in the adult stage in this species.

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