Evolutionary Ecology Research, 2017, **18**: 383–391

Body streamlining is related to higher growth in Bahamian mosquitofish

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ABSTRACT

Background: Theory and empirical work indicate that streamlined body shapes (deep/wide anterior body tapering to a shallow/narrow caudal peduncle) enhance steady-swimming performance (cruising). Because steady-swimming performance reduces the cost of movement, better cruisers should have a competitive advantage.

Hypothesis: More streamlined individuals have higher foraging success and competitive ability in the wild.

Organism: Bahamian mosquitofish (*Gambusia* sp.).

Times and places: Eleven populations on Abaco Island, Bahamas (291 females; 150 males) sampled in 2009 and 2010.

Methods: We measured growth rate (RNA : DNA ratios) as a surrogate for foraging success and competitive ability. We obtained 16 relative warps from 10 anatomical landmarks that describe body shape. We tested for an association between growth rate and morphology using multivariate analysis of covariance.

Results: Individuals with more streamlined bodies had higher growth rates across all populations. Specifically, higher growth rates were associated with shorter caudal peduncles and shallower bodies in females, and deeper heads and shorter/shallower caudal peduncles in males. These results indicate that streamlining favours greater foraging success and competitive ability.

Keywords: ecomorphology, geometric morphometrics, livebearing fishes, Poeciliidae, RNA : DNA ratios

INTRODUCTION

Functionally relevant traits affect an organism's performance, which in turn should influence its fitness (Arnold, 1983). Therefore, studies that test hypotheses of phenotype–performance associations in the wild can provide insights into how natural selection shapes

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functional traits (Irschick and Garland, 2001). In fishes, body shape is related to swimming performance (Oufiero *et al.*, 2011; Ingley *et al.*, 2014, 2016). Among swimming modes, steady swimming (cruising) involves constant-speed locomotion in a straight line and is commonly employed by fishes in activities such as searching for food (which may be limiting or patchily distributed) or mates (Langerhans, 2010). Functional morphology theory predicts that cruising ought typically to be enhanced by more streamlined body shapes, which can be achieved via a deep/wide anterior body tapering to a shallow/narrow caudal peduncle (Langerhans and Reznick, 2009; Tokić and Yue, 2012). Experimental work, such as that in the livebearing fish *Gambusia affinis*, has demonstrated that more streamlined individuals in fact have better steady-swimming performance, showing increased endurance (Langerhans, 2009b).

Since steady-swimming performance reduces the cost of movement, better cruisers are predicted to find and consume food more quickly and possess greater energy supplies for growth and/or reproduction (Plaut, 2001; Domenici, 2003; Blake, 2004). Because of the inherent difficulty in measuring swimming performance in the wild, this relationship has never been tested. However, owing to the correlation between body shape and locomotor performance, we would expect individuals with more streamlined bodies to be better competitors if the relationship between locomotor performance and competitive ability is present in the wild (Langerhans, 2009b, 2010). In the present study, we used wild populations of Bahamian mosquitofish (*Gambusia* sp.) to test the hypothesis that more streamlined individuals, because of being stronger steady swimmers, are better competitors. We used growth rate as a surrogate for competitive ability and tested the relationship between growth rate and body shape.

MATERIALS AND METHODS

Bahamian mosquitofish are small, livebearing fish that inhabit a wide variety of aquatic habitats in the Bahama Archipelago (Langerhans *et al.*, 2007; Heinen-Kay *et al.*, 2014; Giery *et al.*, 2015). We examined Bahamian mosquitofish from 11 tidal creeks on Abaco Island, Bahamas (Table 1;

Table 1. Number of specimens of Bahamian mosquitofish analysed in the present study from 11 populations on Abaco Island, The Bahamas

	Sample size	
Population	Females	Males
Sand Bar	21	18
Twisted Bridge	22	8
Cherokee Sound	25	8
Blue Holes	15	12
Treasure Cay	47	16
Crossing Rocks	26	8
Sandy Point	38	26
Indian River	47	25
Stinky Pond	22	17
Double Blocked – Down	8	5
Double Blocked – Up	20	7

$n = 291$ females; $n = 150$ males). These tidal creeks vary in their degree of hydrological connectivity to adjacent marine areas, spanning the whole gradient of hydrological connectivity found in the area [for detailed information on the study sites, see Araújo *et al.* (2014)]. Prior work has shown that growth rates in Bahamian mosquitofish are enhanced in populations inhabiting high-connectivity tidal creeks, owing to their strongly reduced population densities and presumably higher per-capita resource availability (Araújo *et al.*, 2014). But whether body shape influences growth rates within populations has yet to be tested.

Specimens were collected with dip nets in the summers of 2009 and 2010. Upon collection, individuals were euthanized in eugenol and immediately a small piece of muscle tissue was removed from the right side of the caudal peduncle and placed in RNAlater (Ambion®; Life Technologies, Austin, TX), refrigerated for 24 hours and then frozen at −20°C. Specimens were immeditely frozen after tissue removal. Growth rate was measured as the ratio between the amount of RNA and DNA in tissue samples (Ali and Wootton, 2003). Faster growing fish synthesize more proteins and hence have a higher RNA concentration per cell, whereas the concentration of DNA in cells is constant through time. Consequently, the RNA : DNA ratio is tightly correlated with growth rate in several fishes (Caldarone *et al.*, 2001; Dahlhoff, 2004) and has been used as a measure of body condition, foraging success, and fitness (Bulow *et al.*, 1981; Buckley *et al.*, 1999; Svanbäck and Bolnick, 2007; Bolnick and Lau, 2008; Bolnick and Araújo, 2011). RNA : DNA quantification followed Caldarone *et al.* (2001).

In the laboratory, specimens were thawed, weighed (0.01 g), and photographed for morphometric analysis. Secondary sexual characters or gonad inspection were used to determine age class (juvenile vs. adult) and sex. Only adult individuals were analysed. Morphology was captured from digital images as two-dimensional Cartesian coordinates for landmarks in lateral view. Images were obtained with a DSLR Canon Rebel T3 camera with a macro 60 mm lens. The images were obtained at a distance of 100 mm from the lateral line with the camera lens placed parallel to the sagittal plane of each fish. The coordinates of 10 landmarks (Fig. 1) were registered for each specimen, using the software *tpsDIG2.10* (Rohlf, 2008).

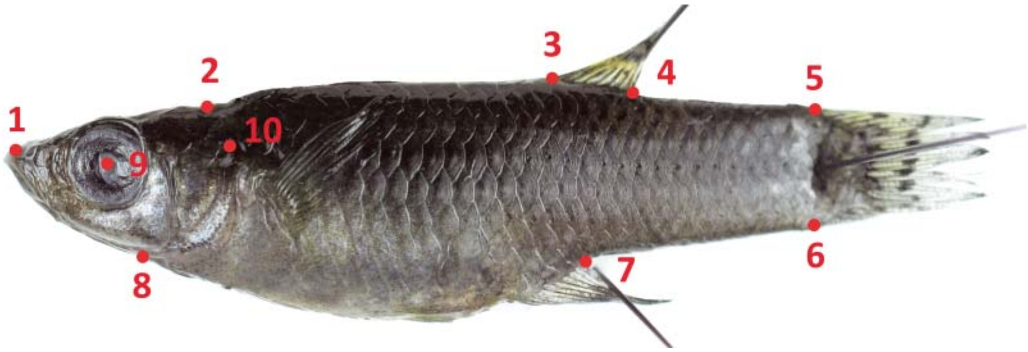

Fig. 1. Female Bahamian mosquitofish showing the body landmarks used in this study: (1) most anterodorsal point of premaxilla, (2) most posterodorsal point of skull, (3) anterior insertion of dorsal fin, (4) posterior insertion of dorsal fin, (5) dorsal insertion of caudal fin, (6) ventral insertion of caudal fin, (7) posterior insertion of anal fin, (8) most posteroventral point of skull, (9) centre of the eye, and (10) most posterodorsal point of opercle (Langerhans *et al.*, 2007).

Body shape was analysed using landmark-based morphometric techniques (Mitteroecker and Gunz, 2009). We aligned landmark coordinates using Generalized Procrustes Analysis [i.e. rotating, translating, and scaling coordinates to remove positioning effects and isometric size effects (Rohlf and Slice, 1990)], and used the resulting Procrustes shape coordinates to calculate geometric shape variables – relative warps (RWs). Shape variables were calculated in MorphoJ 1.06a (Klingenberg, 2011). We calculated body size as centroid size (the square root of the summed, squared distances of all landmarks from their centroid).

Because of low sample sizes (Table 1), populations were analysed together. For each sex, we conducted a multivariate analysis of covariance (MANCOVA) with body shape as the dependent variable (16 RWs), and ln-transformed centroid size, growth rate (ln-transformed RNA : DNA), and population as independent variables. Body size was included in the models to statistically control for multivariate allometry, as well as associations between body size and growth rate, since growth rates are body size dependent in this species (Araújo *et al.*, 2014). We included the 'population' term to control for between-population variation (which could obscure individual-level associations between shape and growth rate), but did not include interactions between population and growth rate because they were not significant. We therefore focus on how individual body shape co-varies with growth rate in similar manners across populations. All significance tests used Type III sums of squares.

To determine the nature of morphological variation associated with growth rate, we performed a canonical analysis of the growth rate term from the MANCOVA following Langerhans and Makowicz (2009), and used canonical scores to visualize how body shape varies with growth rate. Briefly, we conducted a principal components analysis of the sums of squares and cross-products matrix of the growth rate term of the MANCOVA to derive an eigenvector of divergence. This divergence vector describes the linear combination of shape variables showing the greatest correlation with ln-transformed growth rate, while controlling for other terms in the model, in Euclidean space. MANCOVAs were conducted in JMP Pro® 11 (SAS Institute Inc., Cary, NC). Shape changes associated with growth rate were visualized using multivariate regressions of the Procrustes shape coordinates on canonical scores in MorphoJ 1.06a (Klingenberg, 2011).

RESULTS

MANCOVAs examining variation in body shape revealed significant effects of centroid size (indicating multivariate allometry), population, and growth rate for both sexes (Table 2). Higher growth rate was associated with shorter caudal peduncles and shallower bodies in

Table 2. Results of MANCOVAs examining the relationship between body shape and growth rate in Bahamian mosquitofish

	Females				Males			
Factor	*F*	d.f.	*P*	*r*	*F*	d.f.	*P*	*r*
Centroid size	25.0	16, 263	<0.001		7.8	16, 122	<0.001	
Population	5.4	160, 2265.1	<0.001		2.7	160, 1061	<0.001	
Growth rate	2.1	16, 263	0.009	0.34	4.4	16, 122	<0.001	0.61

Note: Growth rate as measured by ln-transformed RNA : DNA. *F*-ratios were approximated using Wilks' λ values for the population term. *r* = canonical correlation between the growth rate term and body shape.

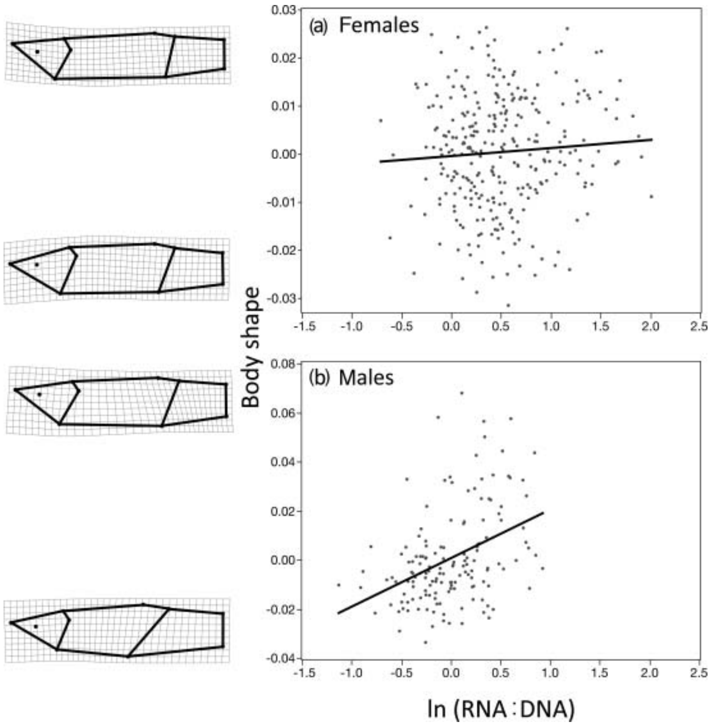

Fig. 2. Relationship between body shape and growth rate in Bahamian mosquitofish. The y-axis displays the scores of individuals on the divergence vector derived from MANCOVA. The x-axis displays growth rate. The deformation grids show deviations from the mean body shape. The deformations presented correspond to (a) $y = -0.03$ and $+0.03$ and (b) $y = -0.04$ and $+0.08$.

females, and deeper heads and shorter/shallower caudal peduncles in males (Fig. 2). In both sexes, individuals with higher growth rates had more upturned snouts.

DISCUSSION

We found a positive relationship between body streamlining and growth rate in natural populations of Bahamian mosquitofish. These results are consistent with the hypothesis that fish that can search for food in a more energetically efficient manner enjoy greater foraging success and competitive ability in the wild. Such a scenario should generate a pattern where streamlining imparts a fitness advantage under natural conditions of resource competition.

In order to understand the evolutionary implications of the relationship between steady-swimming performance and competitive ability, we should note that this expected relationship should hold across many ecological contexts (e.g. low and high predation environments), as long as steady-swimming performance (cruising) is important for maintaining energetic efficiency during resource acquisition. Whenever resource competition is important for overall fitness, this relationship should translate into a fitness advantage. However, as predation pressure increases, selection should favour fast-start ability, because it increases survival during predator attacks (Langerhans, 2009a). As a result, in high-predation environments, swimmers with better fast-start ability should have a fitness advantage despite potentially having lower competitive ability. Because these two primary swimming modes cannot be optimized simultaneously in most fishes (Langerhans, 2010), fish inhabiting high- and low-predation environments differ predictably in overall performance (Oufiero *et al.*, 2011; Ingley *et al.*, 2016). Because of the correlation between swimming performance and body shape (Langerhans, 2009b), this evolutionary scenario should lead precisely to the pattern observed among several fishes, where populations living in low-predation environments generally show more streamlined body shapes, while populations in high-predation environments have body shapes with more posterior allocation – a smaller cranial region and larger caudal region (Langerhans *et al.*, 2004, 2007; Gomes and Monteiro, 2008; Langerhans and Makowicz, 2009; Ingley *et al.*, 2014).

This evolutionary scenario assumes that (i) streamlining increases cruising ability, (ii) better cruising ability imparts a competitive advantage, (iii) posterior allocation increases fast starts, and (iv) fast starts increase survival. Assumptions (i), (iii), and (iv) have been demonstrated experimentally (Langerhans *et al.*, 2004; Langerhans, 2009a, 2009b) and our results indicate that assumption (ii) is true. The link between locomotor performance and total fitness (survivorship and lifetime fecundity) in the wild has never been empirically demonstrated. To the extent that higher growth rates increase an individual's fitness, our results suggest that streamlining may indeed impart a fitness advantage in the low-predation environments dominated by competition. In support of this conclusion, empirical evidence demonstrates that higher growth rates increase fecundity in the threespine stickleback, *Gasterosteus aculeatus* (Ali and Wootton, 1999; Huntingford *et al.*, 2001) and that larger body sizes – which might be attained via faster growth – are positively related with fecundity in several livebearing fishes (Gomes and Monteiro, 2007; Martin *et al.*, 2009; Zandonà *et al.*, 2011). It is important to note that growth rates are not equivalent to fitness, as this would ignore the fitness components arising from predation, parasitism, and sexual selection, in addition to the fact that selection may not always favour the fastest growth rate (Arendt and Reznick, 2005).

The correlation between body shape and the growth rate term was stronger in males than in females (Table 2), which might result from real differences between the sexes or might reflect an artifact of using RNA:DNA ratios as a measure of growth rate. Our tissue samples consisted of muscle tissue from the caudal peduncle. In fishes, females are expected to invest energy in reproduction at the expense of somatic tissue growth, in particular at older ages (Vondracek *et al.*, 1988; Ali and Wootton, 1999; Belk and Tuckfield, 2010). This can create a more complicated relationship between somatic growth rate and competitive ability in females. In this study, growth rate of muscle tissue from pregnant females might thus not provide as accurate an estimate of competitive ability as for males. Because we included pregnant females in our samples (about one-third of the females examined), as well as adults of varying age, this also could potentially explain the weaker association between body shape and growth rate in females than males. That said, if we statistically adjust for pregnancy status in our analysis, our results are unchanged, as the magnitude, statistical significance, and nature (divergence vector) of the association between body shape and growth rate is unaltered (and is consistent within pregnant and non-pregnant females). Thus, the weaker relationship in females does not simply reflect the combination of pregnant and non-pregnant females. Yet, whether age or more detailed reproductive information (e.g. stage of embryo development, size and number of offspring) might provide more insight into a source of the weaker shape–growth rate relationship in females requires further study.

In both sexes, individuals with higher growth rate had more upturned snouts. Our *a priori* hypothesis centred on locomotor morphology (streamlining), not feeding morphology. But trophic traits could additionally influence feeding performance, and hence growth rates and overall body condition. Upturned snouts combined with slender bodies in fishes is associated with feeding at mid-water (Svanbäck and Eklöv, 2004; Ruehl and DeWitt, 2005), so that higher growth rate in Bahamian mosquitofish could potentially reflect greater efficiency of feeding on resources (e.g. zooplankton) found in this microhabitat. This is consistent with a previous study showing that copepods and cladocerans (two taxa common in the mid-water zone) are the preferred food types of Bahamian mosquitofish in this system, as opposed to lower-quality benthic resources [i.e. snails and bivalves (Araújo *et al.*, 2014)].

In conclusion, our results advance our understanding of the potential fitness consequences of streamlining and its implications for the evolution of fish morphology in the wild. Future work should try to directly measure natural selection on swimming performance in both low- and high-predation environments.

ACKNOWLEDGEMENTS

We thank the Bahamas Department of Fisheries for collection permits. Friends of the Environment provided logistical support. G. Becca, S. Giery, C. Hammerschlag-Peyer, Z. Jud, and L. Yeager provided help during laboratory processing. M.S.A. thanks CAPES (BEX 4496/08-6) for a scholarship. This research was funded by FAPESP (2010/15567-8) and NSF (OCE 0746164 and DEB 0842196).

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