

## **Influence of sex and habitat on the size and shape of anal and dorsal fins of the blackstripe topminnow *Fundulus notatus***

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The size and shape of the anal and dorsal fin in the blackstripe topminnow *Fundulus notatus* from lake and stream habitats across multiple ages and sexes were examined. Differences in the size and shape of anal and dorsal fins were sex-specific and not related to habitat differences. Males have longer and more pointed anal fins and longer, larger and more pointed dorsal fins than females. These sex differences occur predominantly in the older age class. The angle (*i.e.* pointedness) of the dorsal and anal fins is tightly correlated suggesting that fins follow a similar growth trajectory as individuals become sexually mature.

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Key words: habitat; lake; median fins; sexual dimorphism; stream.

### **INTRODUCTION**

Many species possess traits that serve several functions. The morphology (*e.g.* size and shape) of such traits often reflects the diverse tasks in which they are used. Studies exploring variation in multi-use traits can offer rich insights into their functional and adaptive significances. The anal and dorsal fins are two features in fishes that may be particularly enlightening, because they serve multiple functions that probably have strong fitness consequences. First, these fins are typically involved in fish movement and stability. Fishes actively manipulate the apparent size and shape of the dorsal and anal fins to aid in stabilization and manoeuvrability (Drucker & Lauder, 2001; Lauder & Drucker, 2004; Fish & Lauder, 2006; Webb, 2006; Standen & Lauder, 2007; Tytell *et al.*, 2008). Second, the dorsal and anal fins also frequently function in mate attraction and competitive displays. Males of many species often flare or flash their fins as part of their courtship activities or during male–male interactions (Foster, 1967; Robinson *et al.*, 2011). Finally, the fins play a direct role in reproduction by assisting in fertilization. Some species contain modified fin rays that essentially act like hooks, allowing a male to cling to a female (Kottelat & Lim, 1999). In other species, the two sexes will

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fold their anal fins in such a way as to create a funnel that is believed to help place the eggs on a substratum or ensure that sperm fertilize the eggs (Carranza & Winn, 1954; Foster, 1967).

Despite these multiple roles, surprisingly little is known about the variation that exists in these fins or how differences in environmental factors may affect them. Lake and stream habitats are ideal for pursuing such a question because fishes in these environments probably face very different selective pressures due to differences in several ecological characteristics (Jackson *et al.*, 2001). Streams have faster water velocities than lakes, which has strong implications for movements or manoeuvrability and stabilisation. Many lakes, including those in this study, contain higher predator abundances because of stocking programmes that introduce large piscivorous game fishes into lakes (Larimore & Bayley, 1996). This may impose strong selection on fin size or shape that could enable fishes to perform fast start responses (Tytell & Lauder, 2008; Blake *et al.*, 2009), which are often used to avoid predators (Webb, 1984).

Here, the size and shape of the anal and dorsal fin in the blackstripe topminnow *Fundulus notatus* (Rafinesque 1820) from lake and stream habitats were examined in both males and females. The original species description of *F. notatus* qualitatively describes a difference in anal and dorsal fin shape between males and females, with males having pointed anal and dorsal fins and females having rounded fins. This description did not consider differences in habitat, so the extent to which habitat may affect shape is unknown. In another morphometric study, the anal and dorsal fin base lengths (but not fin shape and size) were compared and it was found that these differed between the sexes and age-classes, but did not differ as a function of habitat (Welsh *et al.*, 2013).

This study examines the effects of habitat, sex and age on anal and dorsal fin size and shape. If aspects of the habitat (*e.g.* water velocity and predation) are an important source of selection on the size or shape of the anal and dorsal fins, then significant differences between lake and stream populations would be expected. Similarly, if courtship and fertilization are an important source of selection on fin size or shape, significant difference between the sexes would be found. An interaction between sex and habitat would be consistent with different environments altering the direction of sexual selection. The effect of age was incorporated so as to determine if these patterns differ as a function of development. Finally, correlations between anal and dorsal fin traits were examined in order to determine whether the two are tightly integrated or whether they vary independently of one another.

## MATERIALS AND METHODS

### STUDY SYSTEM AND FIELD COLLECTIONS

Individuals were collected from stream and man-made lake sites in east-central Illinois, U.S.A. Lake Decatur, Weldon Springs State Park and Homer Lake are reservoirs (*i.e.* they were constructed by impounding adjacent streams and rivers and contain a dam that periodically releases water). The other lakes were pits created for human activity (*e.g.* drainage and mining) and then later filled in with water. While it is not known the exact year most of these were created, there were no lakes in central Illinois until the construction of the first reservoirs in the early 1900s (Smith, 2002) and, thus, all of the sites were filled with water within the past 100 years (most likely within the past 50 years). To minimize the potential for gene flow between lake and stream populations to confound results, sampling was avoided in locations where the two habitat types met (*i.e.* below a dam or at the inlet or outlet of a lake). In total, 12 sites (six lakes and six

TABLE I. Number of specimens collected at each site that was of the appropriate size for use in the analyses. Note that for some specimens not every measurement of the fin was possible because of damage to the fins and, thus, sample sizes for a population for a particular analysis may be lower than the numbers shown here

Site (Latitude, Longitude)	Habitat type	Total specimens	Age class (years)		Sex	
			0	1	Male	Female
Homer Lake (40·0664° N; 87·9878° W)	Lake	15	7	8	8	7
Clear Lake, Kickapoo State Park (40·1417° N; 87·7402° W)	Lake	15	8	5	9	6
Long Lake, Kickapoo State Park (40·1349° N; 87·7427° W)	Lake	12	1	11	9	3
Philip's Tract (40·1319° N; 88·1518° W)	Stream	9	6	3	6	3
Salt Fork (40·1134° N; 88·0515° W)	Stream	13	9	4	6	7
Kaufman Park (40·1146° N; 88·2899° W)	Lake	13	0	13	5	8
Nursing Creek (39·7913° N; 88·4174° W)	Stream	9	1	8	5	4
Antique Creek (39·7919° N; 88·3682° W)	Stream	15	11	4	10	5
Weldon Springs State Park (40·1229° N; 88·9235° W)	Lake	27	15	12	18	9
Lake Decatur (39·8455° N; 88·8927° W)	Lake	11	0	8	5	3
Kickapoo Creek (40·2248° N; 88·7409° W)	Stream	19	8	11	8	11
Steven's Creek (39·9356° N; 88·9784° W)	Stream	20	7	13	9	11

streams) were sampled (Table I). *Fundulus notatus* was collected with seines and dip-nets from late August until mid October in 2010.

## MEASUREMENTS

Upon returning from the field, fish were euthanized with an overdose of MS-222, preserved in 10% formaldehyde and later transferred to 70% ethanol. After all sites were visited, individuals were measured for body size, age and sex. Size was determined using standard length ( $L_S$ ) measured to the nearest 0·1 mm with Vernier callipers, ageing was done to the nearest year using growth rings on the scales of the fish, observed under light microscopy (DeVries & Frie, 1996) and sex determination was done visually by examining lateral-line patterning and black markings on the fins: males have more pronounced vertical black barring along their sides and more small black-spot speckles on their fins than females (Carranza & Winn, 1954).

Because many specimens had fins that were pressed against their body, it was necessary to remove the anal and dorsal-fins from the specimens in order to obtain a good image of the fins. Each fin was removed by cutting along its base as close to the body as possible using dissection

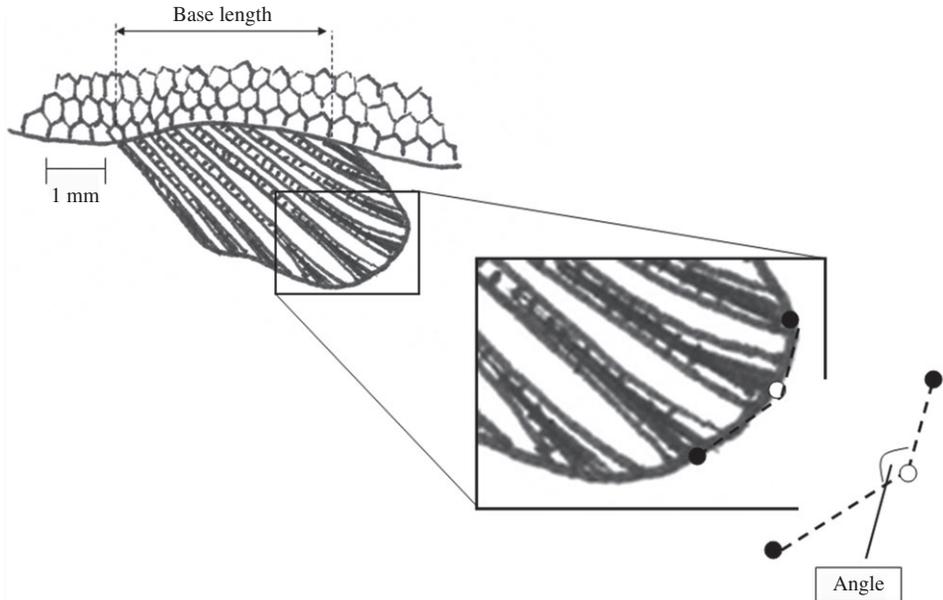


FIG. 1. Traits measured on each fin. Surface area is not shown. The enlarged area shows the angle trait (used to determine pointedness), which was measured by calculating the angle between the longest fin ray (O) and the fin rays on either side of the longest fin ray (● on either side of the O). The enlarged area shows both what the angle looks like on the fish fin and a diagrammatic sketch for clarity.

scissors. The fin was then spread out as much as possible by spreading the fin rays apart with forceps, and this fully extended fin was photographed using a Zeiss AxioCam ICc1 camera ([www.zeiss.com](http://www.zeiss.com)) connected to a dissecting microscope. Only those fins that could be spread out well (as judged visually) were used in the analysis. Each photograph contained a grid of 1 mm × 1 mm lines in the background for calibration. From each photograph, size and shape measurements of both the anal and dorsal fins were then determined using Zeiss AxioVision 4.8.2 or ImageJ 1.44 (<http://imagej.nih.gov/ij/>). Three separate traits were measured on each fin (Fig. 1): (1) the length of the fin base, which was measured as a straight line from the front of the first (most anterior) fin ray to the back edge of the last (most posterior) ray, (2) the surface area of the fin, as measured by tracing around the entire fin using the 'outline' feature and (3) the angle between the longest fin ray and the adjacent ray on either side (anterior and posterior to the longest ray). The angle is used as a quantitative description of the pointedness of the fin (which has up until now only been qualitatively described as 'pointed' or 'rounded'; Carranza & Winn, 1954): a smaller (more acute) angle is more pointed than a larger (more obtuse) angle.

## STATISTICAL ANALYSES

Individuals were classified into age-classes corresponding to the number of full years they completed (*e.g.* age-0 year are those individuals <1 year of age, age-1 year are individuals over 1 year of age but <2). Throughout all analyses, only individuals in age-classes 0 and 1 were considered because only about half of the populations contained individuals beyond the age 2 year-class. Also, all individuals < *c.* 32 mm were excluded from the analysis. Below this size, it is difficult to distinguish immature males from females (Foster, 1967) (see Table I for sample sizes).

Because these traits are influenced by the size of an individual, body size was first accounted for by regressing fin-base length, surface area and angle against  $L_S$  (raw measurements are available in Table S1, Supporting Information). The residuals were then analysed separately in a

generalized linear model that modelled the effects of sex, habitat and population nested within habitat and all their interactions. Because fish from the same population may not be independent samples, population or the interaction with population was used as the error term to test effects. In other words, habitat was tested over population and the effects of sex and its interactions with the other effects were tested over sex  $\times$  population (habitat).

Despite extensive collecting efforts, some populations were missing individuals from a particular age class and sex combination. Rather than deleting many populations from an analysis in order to include age as a factor, the data were analysed separately for each age class. To be conservative, only those populations that had at least two individuals of both sexes for a particular age were considered; however, the results are robust enough that they are qualitatively the same even if analyses were expanded to populations containing at least one individual of both sexes for a particular age. This procedure deleted four populations (Lake Decatur, Long Lake, Kaufman Park and Nursing Creek) from the age-class 0 analysis of anal-fin shape, five populations (Lake Decatur, Long Lake, Kaufman Park, Nursing Creek and Antique Creek) from the dorsal fin age analysis of dorsal fin shape, one population (Philip's Tract) from the age-class 1 analysis of anal-fin shape and three populations (Long Lake, Lake Decatur and Philip's Tract) from the age-class 1 analysis of dorsal-fin shape. Because these traits may all vary together and this could influence the results, a MANOVA was also performed to ensure that the results were not simply caused by multilinearity among traits. A MANOVA was performed on both the raw morphometric values and residuals in the same manner as described above (*e.g.* utilizing population and interaction with population as error terms). Unfortunately, because of damage to a substantial number of fins that made measuring one or more traits on the same fin impossible, there were significantly smaller sample sizes available for the MANOVAs than what was in the generalized linear model. Therefore, the results are not reported here. The MANOVA results, however, agree qualitatively with those from the generalized linear model analysis, so the results reported here are robust and do not simply reflect multilinearity among traits.

The extent to which traits were correlated with one another was also considered. Pearson correlation coefficients for both the raw trait values and the size-corrected traits were calculated for all individuals and then compared for each age and sex. All analyses were performed in SAS 2 ([www.sas.com](http://www.sas.com)).

## RESULTS

Habitat has no effect on any aspect of anal or dorsal fin size or shape. Instead, anal and dorsal fin traits differ as a function of sex, particularly among the older age class (*i.e.* age-class 1) (Tables SII–SVII, Supporting Information). Males have a longer anal fin base length and smaller (more acute) anal fin angle than females. Similarly, for the dorsal fin, males have a longer base length, larger surface area and smaller angle (Fig. 2). Differences in the angle are the only trait that appear in the earlier age class and the pattern is the same as for age-class 1 (*i.e.* males have a smaller angle than females).

There are strong correlations among raw trait values that are mediated by size. Anal fin base length, anal fin surface area, dorsal fin base length and dorsal fin area are positively correlated with size (Table II,  $P < 0.001$ ). In contrast, neither anal fin angle nor dorsal fin angle are tightly correlated with size, but they are tightly correlated with one another.

After controlling for  $L_S$ , functional within-trait relationships remain. For example, dorsal fin surface area is generally positively correlated with the dorsal fin base length. More interesting is the relationship that emerges between dorsal and anal fin angles. Even after controlling for  $L_S$ , dorsal fin and anal fin angle remain tightly correlated with one another across both age-classes (Table III and Fig. 3). The tight correlation occurs among age-1 year males and females, suggesting that the relationship arises owing to variation within each sex and not simply owing to variation between the

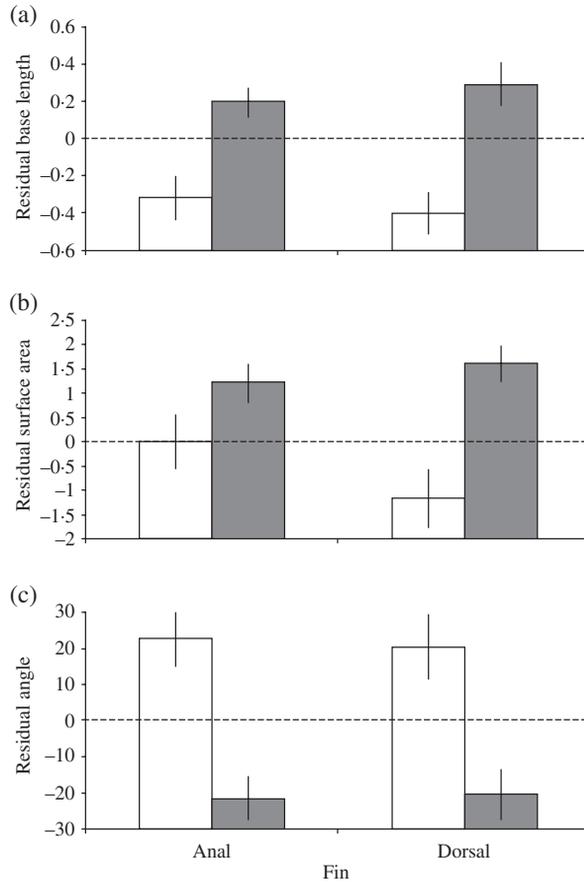


FIG. 2. Sexual dimorphism (□, females; ■, males.) of (a) residual fin base length, (b) residual fin surface area and (c) residual angle of the anal and dorsal-fins in age-class 1 year. Values are mean  $\pm$  s.e. Note the change in y axis scale. All comparisons are significant except for the residual surface area of the anal-fin.

sexes (age-class 1: males:  $r = 0.677$ ,  $P < 0.001$ ,  $n = 27$ ; females:  $r = 0.709$ ,  $P < 0.001$ ,  $n = 21$ ). For age-class 0, the relationship between dorsal and anal fin angle is positive for females but not statistically significant ( $r = 0.201$ ,  $P > 0.05$ ,  $n = 13$ ). For males, the relationship differs between habitats. In streams, anal fin angle and dorsal fin angle tend to be positively but not significantly correlated ( $r = 0.385$ ,  $P > 0.05$ ,  $n = 10$ ). There is a negative correlation, however, between dorsal angle and anal angle for age-0 year males from the lake habitat ( $r = -0.974$ ,  $P < 0.001$ ,  $n = 6$ ).

## DISCUSSION

The size and shape of dorsal and anal fins are similar between lake and stream habitats. This is surprising because dorsal and anal fins should influence manoeuvrability and the ability of fish to maintain their position in the water column (Fish & Lauder, 2006; Tytell *et al.*, 2008). The finding, however, is in accord with an earlier study that

TABLE II. Overall correlations between standard length ( $L_S$ ), anal-fin angle, anal-fin base length, anal-fin surface area, dorsal-fin angle, dorsal-fin base length, and dorsal-fin surface area. Pearson's correlation coefficients,  $P$  values and sample sizes ( $n$ ) are listed

	Anal fin			Dorsal fin			
	$L_S$	Angle	Base length	Surface area	Angle	Base length	Surface area
$L_S$	1	-0.11716	0.76248	0.88490	-0.21991	0.67616	0.74029
$P$		>0.05	<0.001	<0.001	<0.05	<0.001	<0.001
$n$		118	158	153	96	146	141
Anal-fin angle		1	-0.20890	-0.14470	0.58535	-0.12391	-0.14826
$P$			<0.05	>0.05	<0.001	>0.05	>0.05
$n$			117	117	77	110	107
Anal-fin base length			1	0.76708	-0.23431	0.64758	0.64283
$P$				<0.001	<0.05	<0.001	<0.001
$n$				153	95	144	139
Anal-fin surface area				1	-0.22833	0.64272	0.74697
$P$					<0.05	<0.001	<0.001
$n$					95	141	136
Dorsal-fin angle					1	-0.30247	-0.30984
$P$						<0.05	<0.001
$n$						94	95
Dorsal-fin base length						1	0.81093
$P$							<0.001
$n$							139
Dorsal-fin surface area							1

found sex differences but no effect of habitat on anal and dorsal fin base lengths (Welsh *et al.*, 2013). The same study found that habitat (lakes *v.* streams) affects body size, with fish being larger in streams, but found little effect on body shape.

Given that these fish live in drastically different environments, why do they not vary in shape? One possibility is that there has not been enough time for populations to have diverged in body or fin shape because the lake habitats are relatively young (<100 years). This argument is unsatisfying, however, because many studies have shown rapid evolution in fishes as a function of habitat differences (Hendry *et al.*, 2006). Another possibility is that even though these fish occur in different habitat types, they reduce the apparent differences through microhabitat selection. Many fishes are known to alter their activity in response to changes in flow, often by seeking out refugia (Liao, 2007). In the field, *F. notatus* is almost never seen in the main stem of streams and rivers but, rather, is primarily observed in shallow pools and side coves (pers. obs.).

Anal and dorsal fin size and shape may also be subject to very strong sexual selection that potentially overwhelms the effects of natural selection due to habitat type. Pronounced sexual dimorphism is often taken as a proxy for strong sexual selection (Andersson, 1994). In this study, males have longer and more pointed anal fins, and longer, larger and more pointed dorsal fins than females. Sexual dimorphism in anal and dorsal fin traits is common in fishes, and these differences are thought to emerge

TABLE III. Correlations among size corrected anal-fin angle, anal-fin base length, anal-fin surface area, dorsal-fin angle, dorsal-fin base length and dorsal-fin surface area across all individuals. Pearson's correlation coefficients ( $P$  values) and sample sizes ( $n$ ) are listed

	Anal fin			Dorsal fin		
	Angle residual	Base length residual	Surface area residual	Angle residual	Base length residual	Surface area residual
Anal-fin angle residual	1	-0.19119	-0.09579	0.58195	-0.11357	-0.13336
$P$		<0.05	>0.05	<0.001	>0.05	>0.05
$n$		117	117	77	110	107
Anal-fin base length residual		1	0.26710	-0.10674	0.27102	0.18161
$P$			<0.001	>0.05	0.001	<0.05
$n$			153	95	144	139
Anal-fin surface area residual			1	-0.08093	0.13211	0.31404
$P$				>0.05	>0.05	<0.001
$n$				95	141	136
Dorsal-fin angle residual				1	-0.22254	-0.22043
$P$					<0.05	<0.05
$n$					94	95
Dorsal-fin base length residual					1	0.62514
$P$						<0.001
$n$						139
Dorsal-fin surface area residual						1

due to male–male competition and female choice (Oliveira & Almada, 1995; Kottelat & Lim, 1999; Hankinson *et al.*, 2006; McGrath & Hilton, 2012). Likewise, in *F. notatus*, the sexual dimorphism in anal or dorsal fin size and shape is believed to be due to their sex-specific uses in courtship and spawning (Carranza & Winn, 1954; Foster, 1967).

Yet, exactly, why males have more pointed anal and dorsal fins than females is unclear. One possibility is that pointed anal fins are adaptive for sperm transfer. Under this hypothesis, pointed dorsal fins would evolve as a correlated response due to the strong correlation between anal and dorsal-fin traits. Another possibility is that these large, pointed and unpaired fins actually decrease male swimming ability because of drag and act as a handicap. The fact that (1) there is a larger amount of variability in fin shape among males compared with females and (2) this variability increases with age is consistent with the handicap hypothesis.

In conclusion, anal and dorsal fin shapes are surprisingly similar between individuals from lakes and streams despite the different demands presumably placed on swimming in these different habitats. Instead, anal and dorsal fin shape differs dramatically between the sexes, suggesting that they are possibly the targets of sexual selection. In addition, the pointedness of the two fins is highly correlated suggesting that they either share a common developmental pathway (perhaps as a module, as suggested by Mabee *et al.*, 2002 for fin positioning) or that they are under very similar selection pressures.

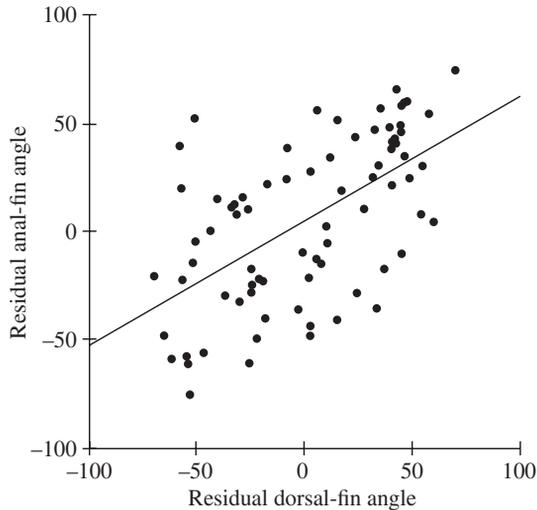


FIG. 3. The relationship between residual dorsal-fin angle and residual anal-fin angle. The curve was fitted by:  $y = 0.8287x + 2.2566$ .

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### Supporting Information

Supporting Information may be found in the online version of this paper:

**TABLE SI.** Raw morphometric measurements (mean and s. e. in parentheses) of both sexes from each site for (a) age-0 year and (b) age-1 year fish.

**TABLE SII.** Analyses of variance on residual anal-fin base length of (a) age-0 year and (b) age-1 year individuals. Significant ( $P < 0.05$ ) factors are shown in bold. MS is the mean square. Superscript numerals refer to the term used in conjunction with the mean-square error to generate the Satterthwaite approximation error degrees of freedom to calculate the  $F$ -value for that factor.

**TABLE SIII.** Analyses of variance on residual anal-fin surface area of (a) age-0 year and (b) age-1 year individuals. Significant ( $P < 0.05$ ) factors are shown in bold. MS is the mean square. Superscript numerals refer to the term used in conjunction with the mean-square error to generate the Satterthwaite approximation error degrees of freedom to calculate the  $F$ -value for that factor.

**TABLE SIV.** Analyses of variance on residual anal-fin angle of (a) age-0 year and (b) age-1 year individuals. Significant ( $P < 0.05$ ) factors are shown in bold. MS is the mean square. Superscript numerals refer to the term used in conjunction with the mean-square

error to generate the Satterthwaite approximation error degrees of freedom to calculate the  $F$ -value for that factor.

**TABLE SV.** Analyses of variance on residual dorsal-fin base length of (a) age-0 year and (b) age-1 year individuals. Significant ( $P < 0.05$ ) factors are shown in bold. MS is the mean square. Superscript numerals refer to the term used in conjunction with the mean-square error to generate the Satterthwaite approximation error degrees of freedom to calculate the  $F$ -value for that factor.

**TABLE SVI.** Analyses of variance on residual dorsal-fin surface area of (a) age-0 year and (b) age-1 year individuals. Significant ( $P < 0.05$ ) factors are shown in bold. MS is the mean square. Superscript numerals refer to the term used in conjunction with the mean-square error to generate the Satterthwaite approximation error degrees of freedom to calculate the  $F$ -value for that factor.

**TABLE SVII.** Analyses of variance on residual dorsal-fin angle of (a) age-0 year and (b) age-1 year individuals. Significant ( $P < 0.05$ ) factors are shown in bold. MS is the mean square. Superscript numerals refer to the term used in conjunction with the mean square error to generate the Satterthwaite approximation error degrees of freedom to calculate the  $F$ -value for that factor.

## References

- Andersson, M. (1994). *Sexual Selection*. Princeton, NJ: Princeton University Press.
- Blake, R. W., Li, J. & Chan, K. H. S. (2009). Swimming in four goldfish *Carassium auratus* morphotypes: understanding functional design and performance employing artificially selected forms. *Journal of Fish Biology* **75**, 591–617.
- Carranza, J. & Winn, H. E. (1954). Reproductive behavior of the blackstripe topminnow, *Fundulus notatus*. *Copeia* **1954**, 273–278.
- DeVries, D. R. & Frie, R. (1996). Growth and age estimation. In *Fisheries Technique* (Murphy, B. R. & Willis, D. W. eds). Bethesda, MD: American Fisheries Society.
- Drucker, E. G. & Lauder, G. V. (2001). Locomotor function of the dorsal fin in teleost fishes: experimental analysis of wake forces in sunfish. *Journal of Experimental Biology* **204**, 2943–2958.
- Fish, F. E. & Lauder, G. V. (2006). Passive and active flow control by swimming fishes and mammals. *Annual Review of Fluid Mechanics* **38**, 193–224.
- Foster, N. R. (1967). Comparative studies on the biology of killifishes (Pisces, Cyprinodontidae). PhD Thesis, Cornell University, Ithaca, NY, USA.
- Hankinson, S. J., Childress, M. J., Schmitter-Soto, J. J. & Ptacek, M. B. (2006). Morphological divergence within and between Mexican sailfin mollies, *Poecilia velifera* and *Poecilia petenensis*. *Journal of Fish Biology* **68**, 1610–1630.
- Hendry, A. P., Kelly, M. L., Kinnison, M. T. & Reznick, D. N. (2006). Parallel evolution of the sexes? Effects of predation and habitat features on the size and shape of wild guppies. *Journal of Evolutionary Biology* **19**, 741–754.
- Jackson, D. A., Peres-Neto, P. R. & Olden, J. D. (2001). What controls who is where in freshwater fish communities – the roles of biotic, abiotic, and spatial factors. *Canadian Journal of Fisheries and Aquatic Sciences* **58**, 157–170.
- Kottelat, M. & Lim, K. K. P. (1999). Mating behavior of *Zenarchopterus gilli* and *Zenarchopterus buffonis* and function of the modified dorsal and anal fin rays in some species of *Zenarchopterus* (Teleostei: Hemiramphidae). *Copeia* **1999**, 1097–1101.
- Larimore, R. W. & Bayley, P. B. (1996). The fishes of Champaign County, Illinois, during a century of alterations of a prairie ecosystem. *Illinois Natural History Survey Bulletin* **35**, 53–183.
- Lauder, G. V. & Drucker, E. G. (2004). Morphology and experimental hydrodynamics of fish fin control surfaces. *IEEE Journal of Oceanic Engineering* **29**, 556–571.
- Liao, J. C. (2007). A review of fish swimming mechanics and behaviour in altered flows. *Philosophical Transactions of the Royal Society B* **362**, 1973–1993.

- Mabee, P. M., Crotwell, P. L., Bird, N. C. & Burke, A. C. (2002). Evolution of median fin modules in the axial skeleton of fishes. *Journal of Experimental Zoology* **294**, 77–90.
- McGrath, P. E. & Hilton, E. J. (2012). Sexual dimorphism in longnose gar *Lepisosteus osseus*. *Journal of Fish Biology* **80**, 335–345.
- Oliveira, R. F. & Almada, V. C. (1995). Sexual dimorphism and allometry of external morphology in *Oreochromis mossambicus*. *Journal of Fish Biology* **46**, 1055–1064.
- Robinson, D. M., Tudor, M. S. & Morris, M. R. (2011). Female preference and the evolution of exaggerated male ornament: the shape of the preference function matters. *Animal Behaviour* **81**, 1015–1021.
- Smith, P. W. (2002). *The Fishes of Illinois*. Urbana, IL: University of Illinois Press.
- Standen, E. M. & Lauder, G. V. (2007). Hydrodynamic function of dorsal and anal fins in brook trout (*Salvelinus fontinalis*). *Journal of Experimental Biology* **210**, 325–339.
- Tytell, E. D. & Lauder, G. V. (2008). Hydrodynamics of the escape response in bluegill sunfish, *Lepomis macrochirus*. *Journal of Experimental Biology* **211**, 2259–3369.
- Tytell, E. D., Standen, E. M. & Lauder, G. V. (2008). Escaping flatland: three-dimensional kinematics and hydrodynamics of median fins in fishes. *Journal of Experimental Biology* **211**, 187–195.
- Webb, P. W. (1984). Body form, locomotion and foraging in aquatic vertebrates. *American Zoologist* **24**, 107–120.
- Webb, P. W. (2006). Stability and manoeuvrability. In *Fish Biomechanics* (Shadwick, R. E. & Lauder, G. V., eds), pp. 281–332. Amsterdam: Elsevier.
- Welsh, D. P., Zhou, M., Musmann, S. M., Fields, L. G., Thomas, C. L., Pearish, S. P., Kilburn, S. L., Parker, J. L., Stein, L. R., Bartlett, J. A., Bertram, C. R., Bland, T. J., Laskowski, K. L., Mommer, B. C., Zhuang, X. & Fuller, R. C. (2013). The effects of age, sex, and habitat on body size and shape of the blackstripe topminnow, *Fundulus notatus* (Cyprinodontiformes: Fundulidae) (Rafinesque 1820). *Biological Journal of the Linnean Society* **108**, 784–789.