

Ontogeny and Allometry of Body Shape in the Blacktail Shiner, *Cyprinella venusta*

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Ontogenetic changes in body shape and its associated allometry were studied in the Blacktail Shiner, *Cyprinella venusta*, using geometric morphometric methods. We used a single, large sample ($n = 397$; 182 males, 215 females), collected in Catahoula Creek, Jourdan River drainage, Hancock County, Mississippi. Ten body landmarks were digitized from each specimen, which yielded partial warp scores that were used as shape variables to describe body shape change during ontogeny, assess sexual dimorphism, and investigate the relationship between reproductive status and ontogenetic body shape change. We also assessed the effect of sexual dimorphism on size and body shape. The null hypothesis of isometry during ontogeny was strongly rejected by multivariate regression of shape on size for both sexes (males, $P < 0.0001$, $F = 21.970$; females, $P < 0.0001$, $F = 16.238$). We found large, highly significant sexually dimorphic differences in the body shapes of males and females (MANOVA for overall shape, $P < 0.0001$, $F = 7.535$, Wilks' lambda, 0.758), which remained significant using MANCOVA with size as a covariate (log SL, $P < 0.0001$, $F = 34.872$, Wilks' lambda, 0.438; log CS, $P < 0.0001$, $F = 34.829$, Wilks' lambda, 0.439). Moreover, the ontogeny of body shape differs between males and females. There were highly significant shape differences among reproductive classes within males and females. These findings suggest that change in reproductive status may occur in concert with body shape change.

THE study of body shape in fishes has been a subject of research investigations for over a century. Only recently have geometric morphometric methods been used to understand body shape change and its associated allometry during ontogeny (Bookstein, 1991; Rohlf, 1998; Zelditch et al., 1998). As a result, the ontogeny of body shape change has been studied for only a small number of fishes, including the Piranha, *Pygocentrus* (Fink and Zelditch, 1995a, 1995b; Zelditch and Fink, 1995), Threespine Stickleback, *Gasterosteus* (Walker, 1993, 1997); Sea Bass, *Dicentrarchus* (Loy et al., 1996); Sea Bream, *Diplodus* (Loy et al., 1998); and Callichthyid Catfish, *Callichthyes* (Reis et al., 1998). These studies have shown that body shape changes during ontogeny are not simply the result of uniform large-scale events (e.g., dorsoventral elongation) but that localized small-scale shape changes unique to each species contribute to its ontogeny. Interestingly, none of these studies detected sexual dimorphism in body shape within the study species, although small sample sizes in several studies did not allow a rigorous evaluation.

Even less is known about body shape ontogeny in cyprinid fishes. Studies of development in cyprinids include an overview of larval development within ostariophysian fishes by Fuiman (1984) and qualitative descriptions of larvae and posttransformational fishes in *Notropis*

(Loos and Fuiman, 1978; Loos et al., 1979). The present paper analyzes ontogeny of body shape in the Blacktail Shiner, *Cyprinella venusta*, a common freshwater cyprinid inhabiting medium to large river tributaries of the southeastern and central United States. The objectives of the study were to describe ontogenetic body shape change and its concomitant allometries in a common North American minnow, to assess sexual dimorphism in the ontogeny of shape change, and to investigate the relationship between reproductive status and ontogenetic changes in body shape.

MATERIALS AND METHODS

We chose a single, large sample ($n = 397$ specimens, Table 1) for our analyses to avoid any potential confounding effects associated with multiple collections from different times or localities. The sample (Mississippi State University, MSU 933) was taken by minnow seine on 26 May 1970 from Catahoula Creek below the mouth of Dead Tiger Creek, Jourdan River drainage, Hancock County, Mississippi. Specimens were fixed in 10% formalin and preserved in 50% isopropyl alcohol. The study site has been described by Heins and Clemmer (1975), and various aspects of the reproductive biology of *C. venusta* at Catahoula Creek have been de-

TABLE 1. SIZE DISTRIBUTION (SL, mm) OF SPECIMENS. Size classes were not used in statistical analyses but illustrate the size distribution of the sample [(n = 182 males (range 22–87 mm, mean 43 mm), 215 females (range 22–72 mm mean 43 mm)].

SL size class mm	20	25	30	35	40	45	50	55	60	65	70	75	≥80
Males	5	12	25	37	32	16	17	24	5	2	3	1	2
Females	4	9	46	29	35	33	18	18	9	12	2	0	0

scribed by Heins and Dorsett (1986) and Heins and Baker (1987).

We tested the effect of alcohol preservation on shape using another sample of fresh-caught specimens. Our results showed that isopropyl alcohol does not significantly change shape data after three months of storage when compared to initial observations of formalin-fixed fish (pers. obs.).

We collected data for 10 landmarks on each individual (Fig. 1) using a two-dimensional video-based data capture system that included a BW CCD video camera and PCVISION+ frame-grabber. Landmarks were obtained using the digitizing software program MORPHOSYS (vers. 1.29, C. Meacham and T. Duncan, 1990,

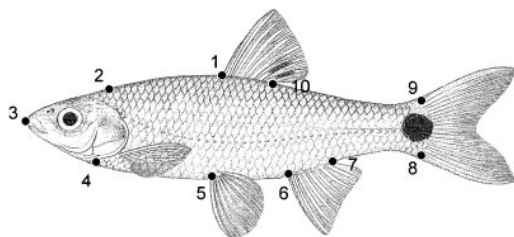


Fig. 1. Landmarks used to capture body shape variation in *Cyprinella venusta*; all landmarks were located on midline of the body in each specimen: (1) origin of dorsal fin, basal junction of first dorsal fin ray; (2) nape of neck, posterior boundary of supraoccipital bone; (3) tip of snout, upper margin of mouth; (4) posterior margin of opercular series; (5) origin of pelvic fin, basal junction of first pelvic fin ray; (6) origin of anal fin, basal junction of first anal fin ray; (7) origin of anal fin, basal junction of the last anal fin ray; (8) origin of caudal fin, basal junction of ventral-most caudal fin ray; (9) origin of caudal fin, basal junction of dorsal-most caudal fin ray; (10) origin of dorsal fin, basal junction of the last dorsal fin ray. A series of 103 specimens were digitized twice (three months between capture sessions) to evaluate measurement error associated with these landmarks. Paired *t*-tests of centroid size (CS) on these repeated digitizing sessions were nonsignificant ($P = 0.954$, $t = 0.058$), root mean square error (RMS) was 0.034 mm and percent incongruence (PI) 0.055% (Hildebolt and Vannier, 1988).

unpubl.). The landmarks were analyzed using morphometric (tpsREGR vers. 1.18, F. J. Rohlf, 1998, unpubl.; tpsRELW vers. 1.14, F. J. Rohlf, 1997, unpubl.; MORPHEUS vers. 1-30-98, D. Slice, 1998, unpubl.) and statistical (SAS vers. 6.12, SAS Institute Inc., 1996; NTSYS vers. 2.02c, Applied Biostatistics Inc., 1998, unpubl.) programs.

Following image capture, we determined the sex and reproductive condition of fish by gonadal examination. Males were classed into five stages of reproductive condition using a scheme modified from Heins and Machado (1993). Sexually immature (latent, LA) males had very small, threadlike testes that were transparent to cloudy white or translucent. The enlarged, opaque white testes of sexually mature males were categorized into four classes of enlargement, including small (MA1, threadlike), moderate (MA2, cordlike), large (MA3, rope-like), and very large (MA4, bulging-convoluted).

We determined the reproductive condition of females, using with some modification, the ovarian classification of Heins and Rabito (1986), which should be consulted for further details. Sexually immature (latent, LA) females had ovaries without developing eggs (translucent to white oocytes). Sexually mature females in all other stages of ovarian condition had, in their follicles, one or two groups of gametic cells undergoing ovum formation. Early maturing (EM) females had ovaries containing one group of translucent to white oocytes. Ovaries of late maturing (LM) females contained a single, bimodal group of oocytes that were white to cream colored. Mature (MA) females had ovaries containing two distinct groups of oocytes in the follicles, the larger ones being cream to yellow. Ovaries of ripening (MR) females also had two separate groups of follicular oocytes, the larger oocytes being translucent with elevated vitelline membranes. Ovaries of ripe (RE) females had one group of white to cream oocytes in the follicles with ovulated, ripe eggs (transparent with elevated vitelline membranes) in the ovarian lumina.

A preliminary study of adult *C. venusta* demonstrated highly significant sexual dimorphism in both size and shape variables; therefore, sexes were treated separately throughout the statistical analyses. We used standard length (SL in mm) and centroid size (CS) as measures of size. Centroid size is a geometrically based measure that is the square root of the sum of the squared distances of landmarks to their centroid (Bookstein, 1989, 1991). Both SL and CS were log transformed prior to statistical analysis.

We described shape changes during ontogeny using geometric morphometric methods (Bookstein, 1991, 1996; Rohlf and Marcus, 1993). Shape variables were extracted from the landmark data using tpsREGR. Landmark configurations for each specimen were aligned, translated, rotated, and scaled to a unit centroid size by the generalized least squares fit criterion (GLS) described by Rohlf and Slice (1990). Using the consensus configuration of all specimens as the starting form (i.e., tangent configuration of Rohlf et al., 1996), partial warps representing the nonuniform shape variables and uniform components (Bookstein 1996) were obtained from tpsREGR and used in subsequent analyses. The thin plate spline interpolating function (TPS) was used to visualize overall, uniform, and nonuniform shape changes.

Sexual size dimorphism (SSD) was tested using sexually mature adults (males scored MA1 to MA4, females scored EM to RE) because SSD is often manifested only in sexually mature individuals (Pryon, 1996; Stamps, 1993). Tests for sexual dimorphism in size and shape were conducted using ANOVA and MANOVA, respectively. MANCOVA was used to evaluate sexual dimorphism in shape with size held as a covariate (log SL and log CS) as described by Adams and Funk (1997). Differences in the ontogenetic trajectory of shape changes of males compared with females were evaluated by comparing the slopes of multivariate regressions using partial warp scores as variables. The overall hypothesis of ontogenetic allometry was tested by multivariate regression of shape variables (partial warp scores and uniform components) regressed on size (log SL and log CS) as described by Rohlf et al. (1996) and discussed by Rohlf (1998), Zelditch et al. (1998), and Monteiro (1999). Monteiro (1999) discusses the use of Goodall's F as a test statistic for multivariate regression of shape variables.

Evaluation of size and shape change among reproductive classes within sexes was examined using the same set of analyses described above. Reproductive classes were determined by separating fish of each sex into groups representing

different stages of reproductive condition: males, LA, MA1-MA3, MA4; females, LA, EM-LM, and MA-RE. The number of MA4 males was too small to include in statistical analyses.

RESULTS

ANOVAs testing sexual size dimorphism showed there were significant differences in size between the sexes (log SL, $P = 0.004$, $F = 8.389$; log CS, $P = 0.006$, $F = 7.760$), with adult males being larger (mean, 53.5 mm in SL) than adult females (mean, 49.1 mm in SL). Analysis of sexual dimorphism in shape (partial warp scores and uniform components appended for overall shape variability) showed highly significant and large differences in shapes of males and females (Fig. 2; overall shape, $P < 0.0001$, $F = 7.535$, Wilks' lambda, 0.758; uniform shape, $P = 0.038$, $F = 3.298$, Wilks' lambda, 0.984; nonuniform shape, $P < 0.0001$, $F = 8.315$, Wilks' lambda, 0.766). MANCOVAs of shape by sex with size held constant (log SL and log CS treated as covariates) also showed highly significant shape differences between sexes (log SL, $P < 0.0001$, $F = 34.872$, Wilks' lambda, 0.438; log CS, $P < 0.0001$, $F = 34.829$, Wilks' lambda, 0.439).

Shape sexual dimorphism is evident in overall, uniform, and nonuniform components of shape space (Fig. 2). Males have relatively longer heads (landmarks 2-3-4), especially dorsally (from the nape of neck to snout, landmarks 2, 3), whereas females have smaller and more symmetrical head shapes. The shape of the abdomen from the attachment sites of the pelvic fin (landmark 5) to those of the anal fin (landmarks 6 and 7) is distinctly different, with females exhibiting an abrupt shape change involving the insertion site of the anal fin. Finally, tail shape (including the caudal peduncle) differs between sexes. Males have relatively wider and longer tails than females (landmarks 7, 8, 9 and 10) and the tails of females are ventrally deflected slightly at the attachment of the caudal fin (landmarks 9 and 10).

The null hypothesis of isometry during ontogeny in each sex is strongly rejected by the results of multivariate regression of shape on size (males, $P < 0.0001$, $F = 21.970$; females, $P < 0.0001$, $F = 16.238$). Thus, there is allometric body shape change during ontogeny within both males and females of *C. venusta* (Fig. 3). The heads of the smallest (youngest) females are relatively longer and more asymmetrical (the dorsal aspect, landmarks 2 and 3, being longer), than in large adults (Fig. 3). Thus, the postcranial body grows faster than the head and head shape changes to a more symmetrical

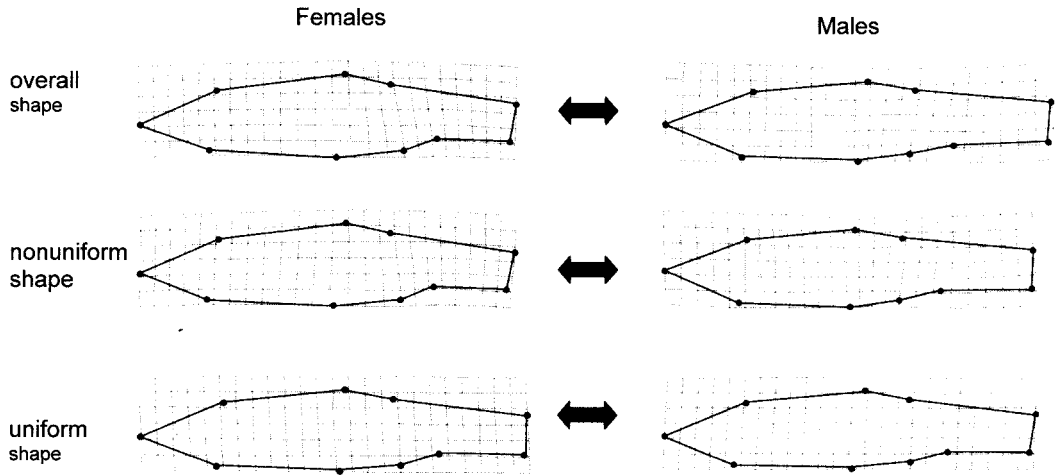
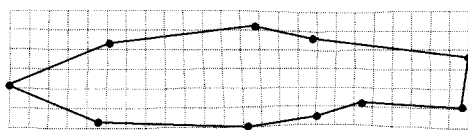


Fig. 2. Ontogenetic shape changes in males and females decomposed into overall, uniform, and nonuniform components. These visualizations reflect shape change between the consensus of males and consensus of females with all specimens included in the shape space ($n = 397$ specimens).

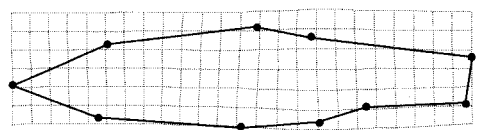
form in adult females. Juvenile males begin with similar, relatively long and asymmetrical heads but retain asymmetrical head shape as large adults. Ontogenetic shape change in the abdomen (landmarks 5, 6 and 7) is dramatic in females; adults exhibit an abrupt shape change at the anal fin. Tail shape and overall body depth changes in both males and females involve enlargement of the tail and midbody. Both juvenile males and females have relatively narrow, ventrally deflected tails. In females, the ventral deflection is retained in adults, whereas in

males a more symmetrical tail develops (landmarks 7, 8, and 9).

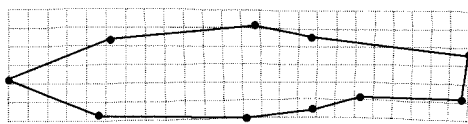
A comparison of the smallest (youngest) males with the smallest females shows them to share many aspects of body shape. A notable difference occurs in the abdomen (landmarks 5, 6, and 7) where some local shape differences that emerge in the adults already are evident. Tests of the differences in ontogenetic trajectory between males and females, as represented in the allometric relationship described in the multivariate regression of shape on size, showed



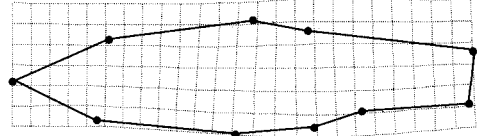
Small (juvenile) Females



Large Adult Females



Small (juvenile) Males



Large Adult Males

Fig. 3. Ontogenetic shape changes within males and females. Visualizations reflect shape changes within females (with only females included in the shape space, $n = 215$) along a multivariate regression of small to large specimens, and a similar set of visualizations within males (with only males included in the shape space, $n = 182$).

that differences in slopes were not significant ($P = 0.09$, $F = 1.568$, Wilks' lambda, 0.945).

MANOVAs testing for shape differences among reproductive classes within males and females were highly significant (overall shape in males, $P < 0.0001$, $F = 5.810$, Wilks' lambda, 0.632; females, $P < 0.0001$, $F = 6.098$, Wilks' lambda, 0.447). Similarly, MANCOVAs of shape among reproductive classes with size as a covariate (log SL and log CS) were highly significant within males and females. Tests of the differences in ontogenetic trajectory between reproductive classes within males were marginally nonsignificant ($P = 0.062$, $F = 1.648$, Wilks' lambda, 0.857). Similar tests for ontogenetic trajectory by reproductive classes within females yielded slopes that were significantly different ($P < 0.0001$, $F = 2.440$, Wilks' lambda, 0.693). These results show that the trajectory of shape change among male reproductive classes (fish scored LA vs MA1-3) are not different, even though there are significant shape differences among the classes. Within females, there are significant differences in the trajectory of shape change among female reproductive classes (fish scored LA vs EM-LM vs MARE) that accompanies significant differences in shape among the groups.

DISCUSSION

Our study of ontogenetic shape change in *C. venusta* demonstrates both uniform and non-uniform (localized) shape transformations during growth and development. The postcranial body elongates antero-posteriorly, and the tail and midbody regions deepen dorso-ventrally in both males and females. These shape changes are reflected in the uniform components of shape change as well as in the highest spatial scales of nonuniform shape change.

Previous geometric morphometric studies of ontogeny investigating species as different in body shape as piranhas (Fink and Zelditch, 1995a, 1995b; Zelditch and Fink, 1995), three-spine stickleback (Walker, 1993), sea bass (Loy et al., 1996) and catfish (Reis et al., 1998) have also demonstrated that shape change at the highest spatial scales (spanning the entire body) involves postcranial elongation and midbody deepening. These studies also have shown localized shape change in several body areas, usually including the head.

We found significant SSD between sexually mature adults. A number of previous studies (Heins and Baker, 1987; Heins and Dorsett, 1986; Pryon, 1996) also have found significant SSD in *C. venusta*, which may be the result of sexual selection (Heins, 1990). Three body ar-

eas in *C. venusta* that show localized shape change differ significantly in males versus females. Head shape, abdomen shape, and tail shape take different forms in each sex. Thus, our study demonstrates that significant sexual dimorphism in both size and body shape emerge during ontogeny.

The ontogeny of shape change in *C. venusta* differs in males as compared with females. The smallest males and females in our sample (SL < 30 mm) generally have similar body shapes; however, small differences in the three areas (head, abdomen, tail) where differing localized shape change occurs during ontogeny are already evident between them. Changes in head shape are accentuated as male ontogeny progresses, whereas changes in abdomen shape are pronounced in the ontogeny of females.

For each sex, the reproductive groupings generally were expected to show progressive changes in shape concomitant with reproductive maturation and subsequent involvement in sexual activities. We found a significant relationship between reproductive status and ontogenetic shape change. Within both males and females, reproductive classes had significantly different body shapes and in females the trajectories of shape change among reproductive classes were significantly different. The finding that body shape varies with major differences in reproductive status within a sex may simply reflect that reproductive status varies broadly with age. Nonetheless, the demonstration of body shape change associated with reproductive status suggests that changes in reproductive status throughout ontogeny may occur in concert with body shape change.

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