Ontogeny of Body Shape and Diet in Freshwater Drum (*Aplodinotus grunniens*)

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ABSTRACT

Ontogenetic changes in body shape were studied in Freshwater Drum, *Aplodinotus grunniens*, using geometric morphometrics. We examined a single cross-sectional sample of juveniles, sub-adults, and adults collected from the Ohio River near Racine, OH. Eleven landmarks on lateral profiles of fish were digitized and body shape was compared using relative warp analysis. Significant allometric growth was identified between four relative warp axes and centroid size. Several of the shape changes characterizing growth in *A. grunniens* appear to be functionally related to feeding. Gut content analysis was consistent with other research that found a dietary shift from soft-bodied prey (e.g., copepods, chironomids) in smaller individuals to hard-bodied prey (e.g., fishes) in larger individuals. Key shape changes that correspond to a shift in diet to larger and harder prey types include a more anteriorly positioned mouth, more expansive gape, and increased body depth.

Key words: allometry, geometric morphometrics, growth, relative warp, Sciaenidae, shape

INTRODUCTION

The Freshwater Drum, *Aplodinotus grunniens*, is the only North American member of the family Sciaenidae that lives in freshwater. Freshwater Drum can be recognized by the steep slope on the head from the snout to the dorsal fin, which produces a pronounced hump-backed appearance (Swedberg and Walburg, 1970). During the larval stage, *Aplodinotus grunniens* feed primarily on zooplankton such as copepods and cladocerans (Swedberg and Walburg, 1970). Juveniles are known to also feed on larval insects, such as mayflies and caddisflies, and adults are primarily bottom feeders whose diet consists mostly of fishes, mollusks, and crayfishes (Daiber, 1952; Edsall, 1967; Griswold and Tubb, 1977; Wahl et al., 1988).

The dietary shift from soft-bodied to hard-bodied prey (durophagy) necessitates the generation of increasingly higher bite forces. High bite forces are facilitated by the specialized pharyngeal jaw apparatus of *Aplodinotus grunniens* (Grubich, 2000, 2005; Wainwright 2005). Anatomical descriptions of pharyngeal morphology by Sasaki (1989) combined with laboratory dissections (Essner, pers. obs.) indicate that *A. grunniens* exhibit a robust pharyngeal jaw apparatus and hypertrophied epaxial musculature that contribute to the externally arched anterior profile observed in adults.

Crushing strength represents a potential limiting factor that is known to constrain prey resource utilization in other durophagous fish (e.g., wrasses; Wainwright, 1988). Another potential factor is gape size. *Aplodinotus grunniens* is known to exhibit size selectivity of prey based upon gape dimensions (Schael et al., 1991). Thus, gape dimensions might be expected to increase allometrically relative to the body, broadening the scope of potential prey. Other morphological features, such as mouth position, may also be expected to change ontogenetically in order to more effectively match the characteristics of a changing prey base. The extent to which allometric growth of the head is involved in this dietary shift is unclear. With these factors in mind, the primary objective of this study is to describe the growth trajectory of *A. grunniens* and to identify patterns of shape change associated with a changing diet.

MATERIALS AND METHODS

A total of 138 Freshwater Drum were collected on 16 September 2000 from the Racine Lock and Dam on the Ohio River near Racine, OH. Fish were fixed in 10% buffered formalin (Fisher Scientific) and preserved in 70% ethanol (Fisher Scientific). The sample consisted of juveniles, sub-adults, and adults ranging in size from 4-35 cm (standard length). All specimens were placed on a dissecting tray and pinned on the left lateral side. Photographs were taken with a Nikon D-80 digital SLR camera mounted on a copy stand, and images were scaled with a ruler.

A total of 11 homologous landmarks, were digitized with tpsDig (Fig. 1; Rohlf, 2009). A repeatability analysis was employed to assess landmark validity (Bailey and Byrnes,
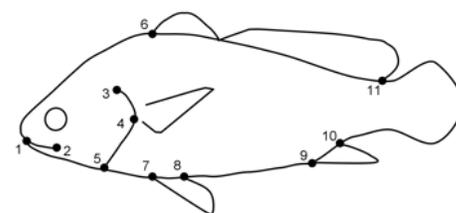

Fig. 1. Landmark locations in *Aplodinotus grunniens*: (1) tip of premaxilla; (2) end of premaxilla; (3) dorsal margin of operculum; (4) midpoint of operculum; (5) ventral margin of operculum; (6) origin of dorsal fin at junction of first dorsal fin ray; (7) origin of pelvic fin at junction of first pelvic fin ray; (8) origin of pelvic fin at junction of last pelvic fin ray; (9) origin of anal fin at junction of first anal fin ray; (10) origin of anal fin, at junction of last anal fin ray; (11) origin of dorsal fin at junction of last dorsal fin ray.

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1990). A sub-sample of 30 specimens was digitized twice and interlandmark distances were analyzed with PROC GLM (Systat v.11.0). Repeatability was estimated at 85% or greater for all 11 landmarks and each was subsequently retained for analysis. Age information was not available. Therefore we used size as a proxy for age (see Frederich and Sheets, 2010).

Relative warp analysis (RWA) was conducted using tpsRelw (Rohlf, 2008) in order to examine patterns of shape change across ontogeny. Relative warp analysis is equivalent to a principal components analysis of partial warp scores produced by thin-plate splines when not weighted by bending energy (Zeldtich et al., 2004). The technique provides a visual representation of ontogenetic shape change via deformation grids. A consensus configuration was superimposed on all landmark configurations and size was computed as centroid size (square root of the sum of squared distances of a series of landmarks to their common centroid). Centroid sizes were transformed using log10 in order to meet the assumptions of regression. Relative warp scores were then regressed against log10 centroid size, (NCSS 2007) in order to compute growth trajectories (Loy et al., 2001). Significant relationships between RWs and size were interpreted as being indicative of allometric rather than isometric growth (Birch, 1999; Hood and Heins, 2000).

Because *Aplodinotus grunniens* is known to exhibit sexual size dimorphism (Rypel, 2007), we tested a subset of sexually mature specimens for evidence of sexual shape dimorphism, prior to pooling male and female specimens. A total of 16 individuals (8 males, 8 females) were dissected, and their gonads examined in order to determine sex. A separate RWA was conducted on these individuals in order to generate RW scores that could be tested for sex effects with MANOVA (NCSS 2007).

Gut contents were analyzed from a subset of 23 specimens across a range of body sizes (juveniles, sub-adults, and adults). Specimens were dissected and stomach and intestines were removed. Gut contents were washed onto a petri dish with 95% ethanol (Fisher Scientific). Contents were examined under a dissecting scope, and observations were recorded.

RESULTS

A MANOVA of the first three RW axes indicated no significant differences between males and females (Wilks' lambda = 0.80, $F_{3,12} = 1.03$, P = 0.41). This provided justification for pooling specimens in subsequent analyses.

A RWA of the pooled specimens resulted in four RW axes that were retained based upon examination of a scree plot. Combined, these axes explained 74% of the variance in the data. Relative warp axes 1-4 explained 29, 25, 13, and 7 % of the variance, respectively. Linear regressions of RWs against log10 centroid size indicate significant allometry for all four axes (Fig. 2). Relative warp 1 (P < 0.0001, r^2=0.55) describes shape change associated with mouth position and body depth, with large-bodied fish exhibiting a more anteriorly directed mouth and deeper body than small-bodied fish. Relative warp 2 (P < 0.001, r^2=0.08) describes shearing in the head and oper-
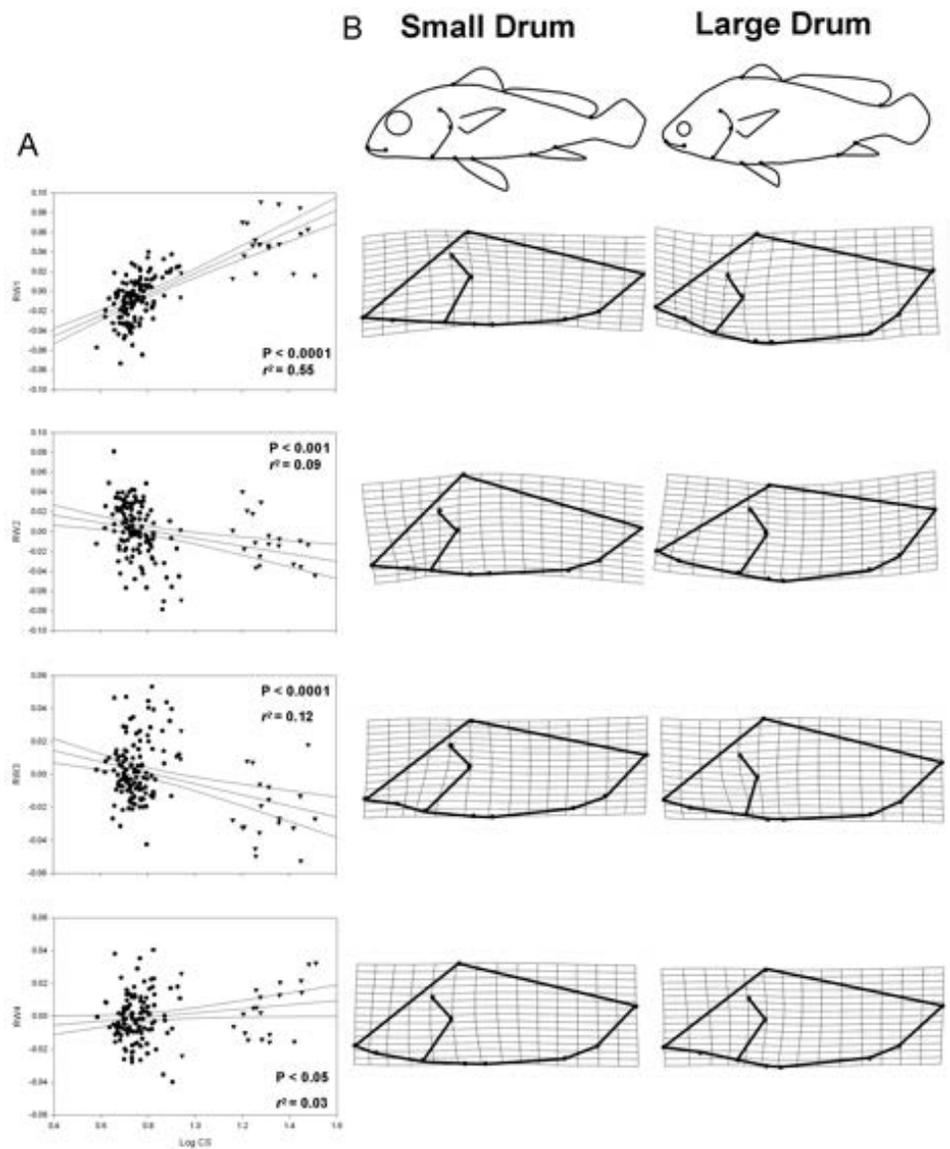

Fig. 2A,B. A) Linear regressions of RW axes 1-4 versus log10 centroid size (square root of the sum of squared distances of landmarks to their common centroid) with 95% confidence intervals. (●) indicates specimens from size range lacking evidence of fish in diet (pre-dietary shift); (▼) indicates specimens from size range with evidence of fish in diet (post-dietary) shift. B) Deformation grids showing shape changes at axis extremes, illustrating general differences between small-bodied and large-bodied drum.

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cular region and dorsoventral movement in the posterior dorsal fin. Relative warp 3 (P < 0.0001, r^2=0.12) describes anteroposterior movement of the ventral end of the operculum. Lastly, RW4 (P < 0.05; r^2=0.03) describes gape expansion and anterior movement of the pelvic fin in large-bodied versus small-bodied fish.

Gut content analysis (Table 1) verified previous observations of a dietary shift from soft to hard prey with increasing size (Daiber, 1952; Edsall,1967; Griswold and Tubb, 1977; Wahl, et al., 1988). Fish were the most frequently encountered prey item in the guts of larger drum in our sample (i.e., standard length > 7.0 cm; centroid size > 14.0).

Table 1. Gut contents from a sub-sample of 23 individuals over a range of body (centroid) sizes. Note the shift from soft-bodied prey to hard-bodied prey as centroid size increases.

Standard Length (cm)	Centroid Size (cm)	Gut Contents
4.77	4.34	copepod
5.32	4.77	copepods
5.25	4.96	copepods, chironomids
6.86	6.30	copepods
9.35	8.42	chironomids
9.26	8.61	copepods, plants
9.52	8.73	chironomids, plants
9.39	8.78	fish
15.40	14.53	dragonfly nymph
16.78	15.99	fish
16.87	16.75	fish
18.10	17.66	unidentified remains
18.92	18.11	fish
18.70	18.95	fish
21.48	20.65	fish, plants
21.78	20.67	fish
23.12	22.80	fish
23.32	22.90	fish
27.83	26.31	fish
27.75	28.12	unidentified arthropod
28.31	28.25	fish
29.89	30.34	fish
34.90	32.46	fish

DISCUSSION

Results of the dietary analysis are consistent with the findings of Sheridan and Tarter (1987) who examined gut contents of *Aplodinotus grunniens* collected from the same region of the Ohio River and determined that fish were the most important food item in adults (90.2% frequency). *Aplodinotus grunniens* have a reputation for being primarily molluscivores, to the extent that their common name "gaspergou" is a corruption of the French word "casburgot" meaning shellfish breaker (Read, 1945). Despite this, we found no evidence of mollusks in our dietary samples. In contrast, other authors have encountered large numbers of mollusks in gut contents (e.g., French and Bur, 1996; French, 1997). One explanation for this discrepancy is seasonal variation. A number of authors have found evidence of changing feeding patterns throughout the year, often with adults switching to greater piscivory from August-November (Dendy, 1946; Griswold and Tubb, 1977; this sample was collected in September). In addition, there appears to be substantial geographic variation in diet. Wahl et al. (1988) found dietary differences between *A. grunniens* collected from lakes versus rivers. Moreover, there are likely important latitudinal effects on diet, given that *A. grunniens* span a larger latitudinal range than any other North American freshwater fish (Rypel, 2007).

The substantial variation in diet in *Aplodinotus grunniens* provides important context for functional interpretations of feeding morphology. Specifically, it points to a paradox described by Liem (1980) in benthic feeding cichlids; whereby, specialized feeding morphology may produce substantial dietary breadth due to behavioral modulation. Clearly, drum are effective at capturing and processing a range of prey types (especially fish), despite exhibiting pharyngeal morphology that appears to be specialized for molluscivory. Detailed information regarding the feeding behavior of drum is lacking. Nevertheless, we do know that they engage in suction feeding based upon anecdotal observations in the laboratory (Daiber, 1950). High-speed video of prey capture and processing behavior will be key to testing the functional significance of feeding and pharyngeal crushing in relation to morphology in drum.

The majority of ontogenetic shape change in *Aplodinotus grunniens* (RW1) involves deepening of the body and repositioning of the mouth, such that it is more anteriorly directed (less sub-terminal) in large-bodied fish (Fig. 2). Increased body depth in this region indicates significant allometric growth. The extent to which muscular hypertrophy in this region relates to dietary changes is currently unclear. The repositioning of the mouth to a more anterior position may enhance feeding opportunities by being better situated for encountering prey in the water column. Moreover, it may offer reduced interference with the substrate as the lower jaw depresses during suction feeding (e.g., Van Wassenbergh et al., 2009). In addition, the allometry in gape dimensions (RW4) indicates that larger fish exhibit gape expansion during growth, relative to smaller fish. This may allow large *A. grunniens* to consume relatively larger prey than small *A. grunniens* (Fig. 2). However, the low r^2 values associated with RW 2-4 suggest that caution is warranted when interpreting these axes (Fig. 2).

Two relative warp axes (RW2 and RW4) describe shape changes associated with the dorsal and pelvic fins, respectively, indicating a potential shift in locomotor behavior. The kinematics of swimming in drum has yet to be studied and thus an examination of movement over a large size range is needed to elucidate the effects of shape change on locomotion.

Future research should attempt to quantify feeding and locomotor behavior in Freshwater Drum with high-speed video and/or cineradiography in order to test the functional significance of ontogenetic changes in morphology, as well as to establish their ecological relevance.

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