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Sexual Dimorphism in Growth of Freshwater Drum

Andrew L. Rypel*

Abstract - I examined sexual dimorphism in the long-lived *Aplodinotus grunniens* (freshwater drum) from five lakes and four rivers in Alabama. Using the Von Bertalanffy growth function combined with nonparametric statistics, I found males and females had similar annual growth rates from years 0–4 years of age, but then showed significantly different growth rates across subsequent ages. Female drum grew significantly faster through adulthood, and ultimately attained significantly larger sizes (L_∞ = 510.8 mm, TL) compared to males (L_∞ = 385.3 mm, TL). This study highlights the difference gender can have in evaluation and interpretation of population characteristics, especially for long-lived and highly fecund fishes such as freshwater drum.

Introduction

In order to evaluate the viability and balance of fish communities, managers often examine population characteristics (Aday et al. 2005, Pereira et al. 1992, Porath and Hurley 2005, Swingle 1950, Winemiller and Rose 1992), which have traditionally not incorporated the influence of gender. Yet, it has long been known that sexual dimorphism is a fairly common characteristic of many fishes worldwide (Komagata et al. 1993, Lombardo 1999, Love 2002, Ostrand et al. 2001, Purchase et al. 2005, Walsh et al. 2003). As such, further investigations into sexual dimorphisms could improve understanding of the autecology of fishes and dynamics of fish populations.

Aplodinotus grunniens Rafinesque (freshwater drum) is a pervasive species with the largest latitudinal range of any North American freshwater fish (Boschung and Mayden 2004). In Alabama's major rivers and impoundments, freshwater drum can account for ≈ 60% of total fish biomass by weight, far exceeding all other local species (Swingle 1953). Freshwater drum are also long-lived and in the Red Lakes, MN, have attained ages of 72 yrs (Pereira et al. 1995). Female drum are extremely fecund (> 1 million eggs per ovary), and one of the few freshwater fishes that maintain pelagic eggs for spawning (Bur 1984, Davis 1959). Given that freshwater drum have such high fecundity and longevity, good potential exists for sexual dimorphism, and several researchers have previously suggested that freshwater drum may exhibit sexual dimorphism in growth (Daiber 1950, Edsall 1967). Yet, most older studies (Butler and Smith 1950, 1965, Edsall 1967, Van Oosten 1938, Wrenn 1968) examining growth of freshwater drum (and other fishes) use fish scales to determine age, which are now known to be considerably less accurate than otoliths (Goeman et al. 1984). Additionally, growth comparisons during this era were, for the most part, done in a

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qualitative, non-statistical manner, which ultimately raises the question of whether the results were statistically significant or not. Just as importantly though is that despite a relatively strong body of literature concerning freshwater drum biology and growth in Lake Erie (Bur 1982, 1984, Edsall 1967, French and Bur 1996, Griswold and Tubb 1977), the upper midwest (Butler and Smith 1950, Moen 1955, Priegel 1969, Wahl et al. 1988) and the north (Pereira et al. 1992, 1995; Swedberg 1968), considerably less information is currently available on freshwater drum in the south and southeast (but see Rypel and Mitchell 2007, Rypel et al. 2006, Wrenn 1968).

The primary objective of this research was to evaluate sexual dimorphism in body size for freshwater drum. Historically, sexual dimorphism in growth of a fish species (e.g., using length-at-age data), was evaluated by simple visual examination of the data or by ad hoc comparisons of parameters from the non-linear, Von Bertalanffy growth function (VBGF). Yet, methods for setting confidence limits to VBGF parameters and subsequently comparing non-linear growth patterns statistically have only recently become available with the advent and combination of higher-end computing technologies with non-parametric statistics. In this paper, I apply non-parametric bootstrapping statistics to determine whether sexual dimorphism occurs for the freshwater drum in the southeast as it has been suggested (but without statistical validation) for freshwater drum in Lake Erie (Daiber 1950, Edsall 1967). This research will assist in a better understanding of freshwater drum autecology, ecology of fishes with similar life-history characteristics, and possibly even sexual dimorphism in general.

Materials and Methods

Fish were captured May through November 2001–2003 using boat electrofishing and gill nets (1.5" and 2" mesh size) from 9 separate water bodies in Alabama (Table 1). Each drum captured was wrapped in aluminum foil, identified with a unique number, and positioned on ice in coolers for transport back to an Auburn University laboratory. The weights (g) of all fish were measured, and the total lengths (TL, mm) recorded. Gender was determined by dissection and visual examination of the gonads. The gender of very small individuals could often not be discerned and thus were not used for this study.

Table 1. Size (TL, mm) and age (yrs) data for male and female freshwater drum captured from 9 separate waterbodies in Alabama, 2001–2003.

	Females			Males		
Site	N	Size range	Age range	N	Size range	Age range
Alabama River	13	156–337	0–5	10	61–476	1–5
Cahaba River	19	245–496	2–32	15	264–400	3–15
Choccolocco Creek	23	312–429	3–11	7	351–401	4–21
Claiborne Lake	10	181–385	1–9	13	155–344	1–8
Coffeeville Lake	14	230–555	2–17	3	161–299	1–3
Lake Logan Martin	28	297–465	2–20	15	307–467	2–19
Pickwick Lake	14	216–584	3–17	19	179–429	3–15
Tallapoosa River	17	238–443	3–15	17	268–404	4–17
Tensaw River	7	274–460	3–9	5	287–480	3–8

Otolith sagittae were dissected from each fish for age determination (Goeman et al. 1984). One (or possibly both) otolith sagittae from each fish were cross-sectioned with an inexpensive wet-stone grinder, placed in putty, and coated with mineral oil for determination of age. Ages of cross-sectioned otoliths were determined underneath a dissecting microscope by utilizing reflected and transmitted light sources. Age determinations were performed by two independent readers, which resulted in high (99%) agreement in age assignments between readers one and two. Residual age disputes were settled by a third independent reader whose age assignments matched either reader one or two in all disputed cases.

Length-at-age data for the 9 separate water-bodies was pooled into two primary samples—one for males and one for females—because (1) too few individuals were collected from each ecosystem to rigorously test for sexual dimorphism from each separate system, (2) a relatively equal number of males and females were collected from each ecosystem, and (3) interest was in the broader phenomenon of sexual dimorphism in drum across ecosystems of the southeast. Kolmogorov-Smirnov (K-S) tests were performed to detect whether there were significant differences in the size and age distributions between genders of freshwater drum. Growth for each gender was evaluated with the standard VBGF which is calculated as the equation:

$$L = L_{\infty}\left[1 - e^{-k\left(T - t_{o}\right)}\right], \qquad (1)$$

where L is the length (mm) at time T, L_{∞} (mm) is the maximum or asymptotic length, k is a growth rate constant, and t_o is the theoretical age-at-length zero.

Separate VBGF models were developed for males and females by minimizing a likelihood function described by Welsford and Lyle (2005):

$$-\lambda = -\Sigma_{i}\ln\left(\frac{1}{\sqrt{2\pi\sigma}}\exp^{\frac{-\left(L_{i} - \mu_{i}\right)^{2}}{2\sigma^{2}}}\right), \qquad (2)$$

where l is the likelihood minimum, L_i is the measured length of individual drum *(i)*, μ_i is the expected mean length-at-age, and σ is the standard deviation of μ_i. Residuals were subsequently plotted and examined at this stage to ensure that normal assumptions were not violated (i.e., lack of a trend in the plot of residuals against length-at-age).

A bootstrapping procedure was then performed using a macro in MS Excel® to generate confidence intervals around each gender's VBGF parameter estimates (L_{∞}, t_o, k). The bootstrapping procedure randomly re-sampled the length-at-age dataset for each gender with replacement 1000 times and fit equation (1) to each new dataset. This generated 1000 new estimates for each VBGF parameter of each gender. Using these estimates, I calculated 1000 expected lengths (*L*) for each age-class and each gender. Confidence intervals (95%) were assigned to each age class and VBGF parameter estimate based on percentile distributions. Significant differences in body size and parameter estimates between genders were evaluated with likelihood-ratio tests (Kimura 1980).

Results

I determined the ages of 145 female and 104 male freshwater drum. Male and female drum ages ranged from 1–21 years and 0–32 years, respectively. Sexual maturation across all sites occurred most often during years 3–4. Male and female sizes ranged from 61–480 mm and 156–584 mm TL, respectively. Length-frequency histograms for both sexes were normally distributed (K-S test: male $P = 0.80$, female $P = 0.10$), but Kolmogorov-Smirnov tests revealed a significant difference in length distributions ($P = 0.0003$) between freshwater drum genders with the female distribution favoring larger fish (mean TL = 340 mm, skewness = 0.27), and the male distribution favoring smaller fish (mean TL = 300 mm, skewness = 0.07). No significant difference between age distributions was revealed (K-S test: $P = 0.07$).

Visual examination of VBGF projections for male and female freshwater drum suggested separate growth rates between genders. Starting at age 2, female drum appeared to grow faster and, according to the VBGF, attained ultimately larger sizes ($L_\infty = 510.8$ mm), while male drum growth was slower and reached smaller maximum sizes ($L_\infty = 385.3$ mm). The bootstrap procedure produced 1000 separate estimates for $L_{\infty,}$ k, t_o, and L for each freshwater drum gender. Using this technique, 95% confidence intervals were created along each gender's VBGF (Fig. 1A) and their associated parameter estimates (Fig. 1B–D), allowing for statistical comparisons. Some age classes (e.g., age 0, age 32) were dropped during bootstrapping due to insufficient sample sizes to carry out the procedure.

By plotting bootstrapped parameters of k against L_∞, the difference in growth between each gender could be visualized. Females had higher initial growth rates, k (Fig. 1B) and t_o (Fig. 1D) at similar levels of L_∞ compared to males, and the confidence intervals did not overlap. By plotting bootstrapped values of t_o against k, differences in growth were again highly apparent (Fig. 1C). Females had higher t_o values at similar k values compared to males, and again, confidence intervals did not overlap. Likelihood-ratio tests revealed that differences in VBGF parameter estimates between genders were highly significant (Table 2).

Discussion

Utility of nonparametric statistics for detection of sexual dimorphisms

VBGF parameters are notoriously difficult to compare statistically for numerous reasons (Chen et al. 1992, Day and Taylor 1997, Trippel and Harvey

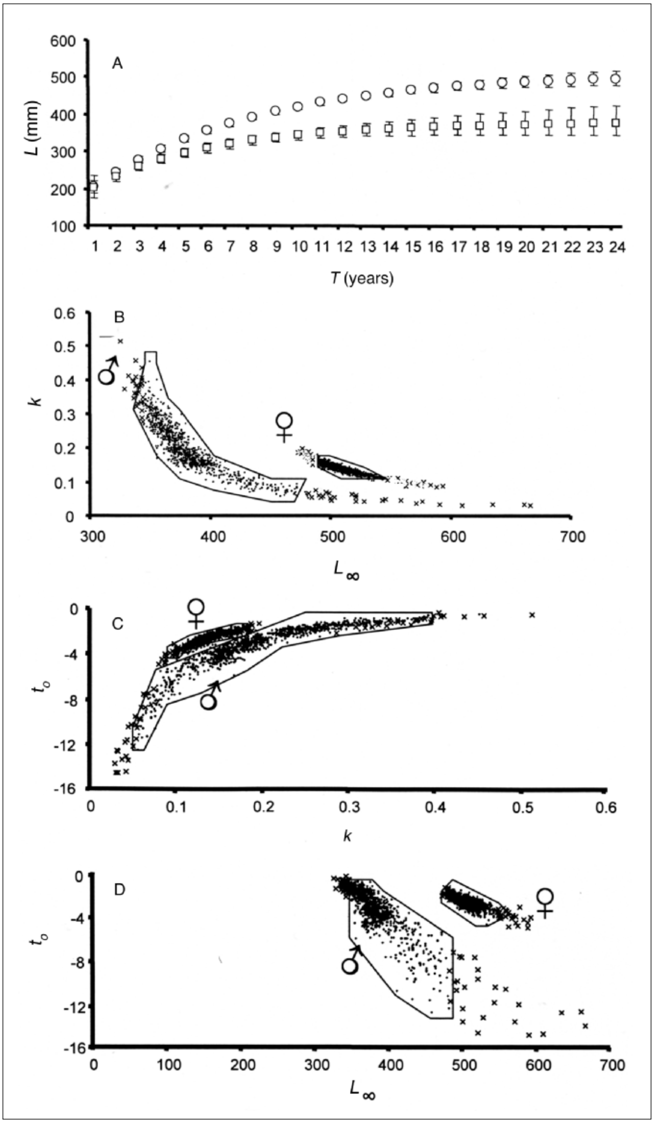

Figure 1. Comparisons of Von Bertalanffy growth functions (A) and growth parameters (B,C,D) for genders of freshwater drum captured from nine waterbodies throughout Alabama, 2001–2003. Confidence intervals (95%) are denoted by error bars in panel A and by elliptically shaped polygons in panels B, C, and D. For panel A, female gender is denoted by circles and male gender is denoted by squares For B, C, and D, observations which fell outside of the confidence regions are denoted by an x.

Table 2. Likelihood-ratio tests for gender differences in VBGF parameter estimates and various lengths-at-age for freshwater drum.

Parameter	Df	Log likelihood	Chi square	P
L_∞	1	-9916.0	3641.0	$P < 0.00001$
k	1	3056.1	546.2	$P < 0.00001$
t_o	1	-5576.3	438.7	$P < 0.00001$
L_1	1	-8318.2	2.8	$P = 0.25100$
L_6	1	-6648.3	5717.7	$P < 0.00001$
L_{12}	1	-6621.6	8362.9	$P < 0.00001$
L_{18}	1	-7999.1	6591.5	$P < 0.00001$

1991, Wang and Thomas 1995). This was especially challenging prior to the popularization and availability of personal computers, when it was considerably more difficult and time-consuming to fit non-linear functions such as the VBGF to length-at-age data. Yet, even with the relative ease of function-fitting associated with ever more powerful computers and software packages, assigning confidence limits to the VBGF and statistically comparing non-linear, asymptotic growth can still be challenging. In such cases, a general linear model (GLM) is ultimately not appropriate for detecting growth differences, and this inadequacy has left some searching for more suitable and sensitive statistics. Nonparametric statistics are a relatively new technique which allows for statistical comparison of non-linear growth models (Kimura 1980, Mooij et al. 1999, Welsford and Lyle 2005).

Female freshwater drum were significantly larger and had significantly higher growth rates compared to males. Female drum started at higher t_o values, grew faster (higher k), and reached larger sizes ($> L_\infty$) compared to males. Sexual dimorphism in growth was most noticeable in the bootstrapped plots of k against L_∞ and t_o against L_∞, and least noticeable in the plot of t_o against k. The t_o parameter is of little practical value because it specifies age at size-zero, which will undoubtedly be close to zero for any population. L_∞ seemed to be the most important VBGF parameter that drove sexual dimorphism in freshwater drum. This is intuitive because L_∞ integrates lifelong patterns in growth for any population. Thus, sexual dimorphism should be most apparent in this parameter, especially for long-lived fishes because of the relatively extensive time frames through which divergences occur. These results now provide statistical support for earlier research on freshwater drum in Lake Erie (Daiber 1950, Edsall 1967), which suggested (based on age estimates taken from scales) that freshwater drum may exhibit sexual size dimorphism.

Sexual dimorphism in freshwater drum compared to other fishes

Female freshwater drum were significantly larger than males. This trend was initially observed in differences between the size distributions for each gender, where the female distribution was skewed towards larger drum while the male distribution was skewed towards smaller drum. Meanwhile, age distributions for each gender were not significantly different from one another. Thus, the lengths of drum genders were different from one another even though the ages were not, which suggested separate growth rates. Suspected sexual dimorphisms were confirmed by analysis and comparisons of each VBGF model. Sexual differences in size were most noticeable (but with higher degrees of uncertainty) in the oldest fish and not apparent (with less uncertainty) in younger fish (ages 0–4). The observed sexual dimorphism in freshwater drum was consistent with previous research on saltwater sciaenids such as *Sciaenops ocellatus* Linnaeus (red drum), in which females attained larger sizes than males (Beckman et al. 1989, Nieland and Wilson 1993, Porch et al. 2002, Wilson and Nieland 1994).

Body-size dimorphisms are frequently related to gonadal size differences (Downhower et al. 1983, Parker 1992). For example, a divergence in body size between sexes could be related to different reproductive investments.

Female freshwater drum are one of the most fecund freshwater fishes (> 1 million eggs), which promotes a geometric relationship between female body size and fecundity wherein larger females produce exponentially more ova (Benton 1987, Swedburg and Walburg 1970, Wrenn 1968). Consequently, natural selection is most likely to favor females that maximize fitness by growing to the largest sizes. Yet, sperm count of males is less dependent on body size and growth; thus, males maximize reproductive fitness by alternative measures (e.g., fighting or sneaking).

Another possibility is related to the concept of "partial migration of niches," which states that female fish can often be larger than males because of a tendency to be more motile (Jonsson and Jonsson 1993). In these situations, migrant fish are often females, while resident individuals are typically males. This inclination for motility in females has inherent growth benefits associated with habitat shifting that are not available for less motile individuals (e.g., males). The "decision to move or migrate" is not fully understood yet, but is thought to be related to a combination of genetic and environmental factors like (1) food availability and current growth rates, (2) relaxed interspecific competition (density), and (3) temperature differences (Jonsson and Jonsson 2006, Olsson et al. 2006).

Is this the case for freshwater drum? There are actually some data to support this hypothesis for freshwater drum. Rypel (2004) used PCB contaminants in fish flesh at known distances from point-source pollution to measure the relative motility of freshwater drum genders in Lake Logan Martin, AL (see Bayne et al. 2002 for a good technique description). Female freshwater drum were considered to be highly motile compared to six other warmwater species and their respective sexes, while male freshwater drum were determined to be the most sedentary of any species or gender examined. This provides direct support for the partial migration hypothesis that natural selection favors a larger body size when migration costs are high. Female drum likely do move more than males, and this preference for niche shifting could account for a portion of the observed sexual dimorphism found in this study.

Finally, although freshwater drum are different from many freshwater fishes, there are fishes which share similar life-histories with this species. Winemiller and Rose (1992) referred to these species as periodic fishes (i.e., highly fecund, low juvenile survivorship and late age at maturity), some examples of which are *Lepisosteus oculatus* Winchell (spotted gar), *Polyodon spathula* Walbaum (paddlefish), and *Ictiobus bubalus* Rafinesque (smallmouth buffalo). All these species display analogous sexual dimorphism, with females attaining larger body sizes than males (Jennings and Zigler 2000, Love 2002, Wrenn 1968). This pattern among similar fishes (e.g., Winemiller and Rose 1992) could serve as a preliminary guide in predicting the pervasiveness and strength of sexual dimorphisms in nature.

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