Population Dynamics of Bowfin in a South Georgia Reservoir: Latitudinal Comparisons of Population Structure, Growth, and Mortality

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Abstract: The objectives of this study were to evaluate the population dynamics of bowfin (*Amia calva*) in Lake Lindsay Grace, Georgia, and to compare those dynamics to other bowfin populations. Relative abundance of bowfin sampled in 2010 in Lake Lindsay Grace was low and variable (mean ± SD; 2.7 ± 4.7 fish per hour of electrofishing). Total length (TL) of bowfin collected in Lake Lindsay Grace varied from 233–683 mm. Age of bowfin in Lake Lindsay Grace varied from 0–5 yr. Total annual mortality (*A*) was estimated at 68%. Both sexes appeared to be fully mature by age 2 with gonadosomatic index values above 8 for females and close to 1 for males. The majority of females were older, longer, and heavier than males. Bowfin in Lake Lindsay Grace had fast growth up to age 4 and higher total annual mortality than the other populations examined in this study. A chi-square test indicated that size structure of bowfin from Lake Lindsay Grace was different than those of a Louisiana population and two bowfin populations from the upper Mississippi River. To further assess bowfin size structure, we proposed standard length (i.e., TL) categories: stock (200 mm, 8 inches), quality (350 mm, 14 inches), preferred (460 mm, 18 inches), memorable (560 mm, 22, inches), and trophy (710 mm, 28 inches). Because our knowledge of bowfin ecology is limited, additional understanding of bowfin population dynamics provides important insight that can be used in management of bowfin across their distribution.

Key words: Amia calva, growth, mortality, size structure

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Bowfin (*Amia calva*) is the only extant species in the family Amiidae. Fossils of bowfin date to the Mesozoic era (Patterson 1973) and have been found on every continent except Australia (Nelson 1994). The current distribution of bowfin is limited to North America where it occurs in the Mississippi River basin from Minnesota south to Louisiana, in the St. Lawrence-Lake Champlain basin, and throughout the Great Lakes basin (except for Lake Superior; Scott and Crossman 1973, Boreske 1974, Lee et al. 1980). The species is also found in Atlantic drainages, including the Hudson River south to Florida and along the Gulf of Mexico Coastal Plain from Florida to Texas.

Bowfin are a top predator with a diet consisting of various fishes, crustaceans, and terrestrial vertebrates (Lagler and Hubbs 1940, Davis 2006). Adult bowfin commonly exceed 3.60 kg; the current world-record specimen was caught in 1980 from Florence Lake, South Carolina, and measured 915 mm (total length [TL]) and weighed 9.75 kg (International Game Fish Association 2011). Because bowfin often consume panfishes (e.g., small-bodied centrarchids and percids) and may compete with sport fishes such as largemouth bass (*Micropterus salmoides*), bowfin are generally considered harmful or a "nuisance" species by anglers and management agencies (Scarnecchia 1992, Davis 2006). Bowfin receive little attention from state fish and wildlife agencies in the form of harvest regulations. Louisiana is the only state with minimum commercial and recreational length limits (559 mm and 406 mm, respectively). Nonetheless, their piscivorous nature has led some fisheries managers to use bowfin as a management tool. Bowfin were introduced into Lake Winona, Minnesota, with the goal of decreasing bluegill (*Lepomis macrochirus*) densities (Mundahl et al. 1998). However, predation rates were insufficient to alter the bluegill population, possibly due to high fishing mortality caused by anglers who regularly caught and destroyed bowfin.

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In addition to their potential as a tool in fisheries management, bowfin are an important sport fish for specialty angling groups (e.g., Bowfin Angler's Group) and an emerging commercial species. While commercial harvest of bowfin in Louisiana was traditionally for flesh, wider markets have recently developed for bowfin caviar (Davis 2006, Koch et al. 2009b). Bowfin are highly fecund for their size with a 4.0 kg female capable of producing more than 55,000 eggs (Boschung and Mayden 2004). A majority of the egg harvest had been focused on populations in the Mississippi River basin (Koch et al. 2009b), but harvesters have begun to expand their range. For example, in 2011 the Georgia Department of Natural Resources (GDNR) received their first request for a permit to harvest bowfin for their eggs.

Regardless of how bowfin are managed, an understanding of population dynamics (e.g., growth, mortality) is important for monitoring responses to management actions and ensuring sustainable fisheries. Fish population dynamics often exhibit latitudinal patterns with fish from northern populations exhibiting slower growth, lower mortality, and greater longevity than southern populations (Quist et al. 2003, Denit and Sponaugle 2004, Heibo et al. 2005, Frisk and Miller 2006, Thorsen et al. 2010). Thus, understanding how population dynamics of bowfin vary across a large spatial scale provides additional insight on responses to management actions. The objectives of this study were to characterize abundance, age, growth, size structure, and mortality of a bowfin population in Lake Lindsay Grace, a small impoundment on the coastal plain of Georgia. The population dynamics of bowfin from Lake Lindsay Grace were then compared to three other populations in North America to provide insight on variations in the population biology of bowfin at multiple latitudes.

Methods

Lake Lindsay Grace (3134415N 8202625W) is located in Wayne County, Georgia, just southwest of the town of Jesup, Georgia. The lake is a 95-ha impoundment of Boggy Creek, which flows into Little Satilla Creek, a tributary of the Little Satilla River. The fish assemblage is composed of bowfin, bluegill, redear sunfish (*L. microlophus*), warmouth (*L. gulosus*), black crappie (*Pomoxis nigromaculatus*), brown bullhead (*Ameiurus nebulosus*), chain pickerel (*Esox niger*), golden shiner (*Notemigonus crysoleucas*), largemouth bass, and lake chubsucker (*Erimyzon sucetta)* (Bonvechio 2009). Lake Lindsay Grace is a blackwater lake characterized by high tannin concentrations and a pH of 5.9. Average depth of the lake is approximately 0.9 m, maximum depth is 3.6 m, and about 40% of the surface area is covered with aquatic vegetation, primarily gray fanwort (*Cambomba caroliniana*) and spike rush (*Eleocharis* spp.) (Bonvechio 2009).

Bowfin were collected from Lake Lindsay Grace using a boat-mounted electrofisher with a 5,000-W generator and a Smith-Root Model VII-V pulsator (Smith-Root, Inc., Vancouver, Washington); output varied from 4 to 6 amps of pulsed DC. Sampling occurred between 2 February and 25 March 2010. Although electrofishing transects were not standardized, sampling time was recorded for each transect and used to calculate relative abundance (fish h^{-1}). Captured bowfin were immediately placed on ice and returned to the GDNR regional office where total length (TL, mm), weight (g), and sex were recorded. Sex was determined based on the presence of a spot (i.e., ocellus) on the caudal peduncle, identifying the individual as male (Koch et al. 2009b), and confirmed by inspection of gonads. The leading pectoral fin ray was removed for age and growth analysis and stored in coin envelopes following methods described by Koch et al. (2009a).

Although no structure has been validated for aging bowfin, fin rays were selected as an aging structure due to their relatively high precision when compared to other hard structures (Koch et al. 2009a). Fin rays were mounted in epoxy as described by Koch and Quist (2007), sectioned using a Buhler IsoMet low-speed saw (Buhler, Inc., Lake Bluff, Illinois), and then examined under a stereoscope to estimate age. Two independent readers estimated age of each fish. If a discrepancy occurred between the two readings, then the age discrepancy was resolved between the two readers. Data were removed from further analysis if a consensus on the age was not reached. Images of fin ray sections were captured and the distance from the focus to each assumed annulus was measured using Image ProPlus software (Media Cybernetics, Image-Pro Plus, Silver Springs, Maryland).

Standard length categories were developed for bowfin following the methods described by Gabelhouse (1984), who suggested that minimum stock, quality, preferred, memorable, and trophy sizes of fish be determined from lengths within 20%–26%, 36%–41%, 45%–55%, 59%–64%, and 74%–80% of the world-record length (i.e., 915 mm for bowfin), respectively. Using these values, we calculated proportional size distribution (PSD) indices and compared index values with a chi-square test (Neumann and Allen 2007, Neumann et al. 2012). Pairwise comparisons were conducted and the experiment-wise error rate was controlled using a Bonferroni correction (i.e., α / number of pairwise comparisons). Sex ratios were determined and the gonadosomatic index (GSI) was calculated following Koch et al. (2009b).

Although all bowfin were sacrificed for aging, not all ages could be estimated. Thus, an age-length key was used to estimate age frequency for the sample (Ricker 1975, Quist et al. 2012). Total annual mortality was calculated using a weighted catch curve (Miranda and Bettoli 2007, Smith et al. 2012). Only ages that were considered fully recruited to the sampling gear (age 2 for males and age 3 for females) were used in the analysis. Sexes were combined for the mortality estimate.

Back-calculated length-at-age was estimated using the Dahl-Lea method:

$$L_i = L_c\left(\frac{S_i}{S_c}\right)$$

where L_i is the length when the *i*th increment was formed, L_c is the length at capture, S_i is the fin ray radius at annulus *i*, and S_c is the fin ray radius at capture (Quist et al. 2012). In addition, a von Bertalanffy growth model was fit to each bowfin population using the R statistical computing language (R Development Core Team 2009):

$$L_i = L_\infty \times (1 - e^{-K(t-t_0)})$$

where L_t = length at time *t*, L_∞ = the theoretical maximum length, *K* = the Brody growth coefficient (the rate at which fish approach L_∞), and t_0 = the time when length would theoretically equal 0 mm.

Population structure and dynamics of bowfin in Lake Lindsay Grace was compared to three other bowfin populations: the upper Barataria Estuary, Louisiana (Davis 2006), and Pool 11 and Pool 13 of the upper Mississippi River (UMR) in Iowa, Illinois, and Wisconsin (Koch et al. 2009b). Bowfin in the upper Barataria Estuary were collected bi-weekly from September 2005 to September 2006 using gill nets, trot and jug lines, and hook-and-line. All bowfin from Davis (2006) were aged using the gular plate. Fish in the UMR were collected during April 2007 (Koch et al. 2009b). Although modified fyke nets and boat-mounted electrofishing were used to collect bowfin, over 90% were collected using electrofishing. All fish from the UMR were aged using fin rays. A type-I error rate of 0.05 was used for all statistical analyses.

Results

Eighty-two bowfin were sampled from Lake Lindsay Grace using a total of 30.3 h of electrofishing from 32 transects. Transects averaged 3,411 sec but varied considerably between 900 and 10,056 sec, and catch rate of bowfin was generally low (mean = 2.7 fish h^{-1}, SD = 4.7). Bowfin varied in length from 233 to 683 mm TL (Figure 1) and exhibited a typical exponential length-weight relationship (weight = 37.898 $e^{0.068(TL)}$), where weight is in g and TL is in mm. Proposed standard length categories are provided in Table 1. Size structure of the bowfin populations in the UMR was generally larger than those from southern populations (Table 2).

Most (58 of 82) bowfin collected from Lake Lindsay Grace were male, with a sex ratio of 2.4 males per female. Males varied in length from 233–680 mm TL and females varied from 426–683 mm TL (Figure 1). The majority of females were longer and heavier than males, and only 3.4% and 21.0% of the males and females collected, respectively, exceeded 600 mm TL.

Age was estimated for 76 bowfin (52 males and 24 females) and between-reader agreement of age estimates was 93%. Age data for six male bowfin (348 to 515 mm TL) were not used because a consensus age could not be reached by the readers. Age of bowfin in Lake Lindsay Grace varied from 0 to 5 years, but 97.5% were age 1–4 (Figure 2). The majority of the males (69%) were age 0–2, but

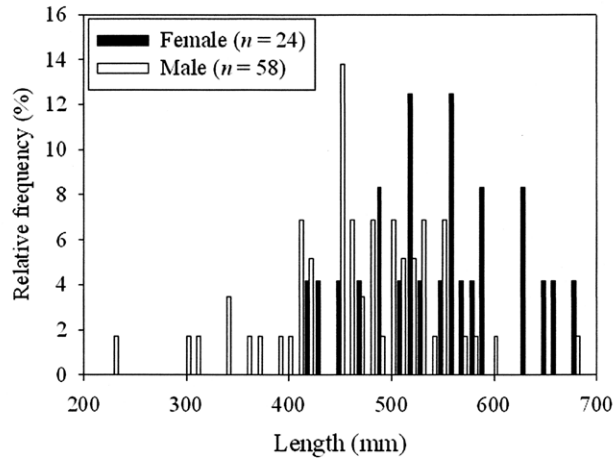

Figure 1. Length-frequency distributions of female and male bowfin sampled from Lake Lindsay Grace, Georgia, in 2010.

Table 1. Total length in millimeters (inches are provided in parenthesis) from which minimum stock, quality, preferred, memorable, and trophy lengths should be selected for bowfin based on the percentage of the world-record length (915 mm total length), and proposed minimum length values.

Stock	Quality	Preferred	Memorable	Trophy
		Minimum lengths		
183–329	329–375	412–503	540–586	677–732
(7.2–9.4)	(12.9–14.8)	(16.2–19.8)	(21.2–23.1)	(26.6–28.8)
		Proposed minimum lengths		
200 (8)	350 (14)	460 (18)	560 (22)	710 (28)

Table 2. Proportional size distribution (PSD) values for quality- (PSD), preferred- (PSD-P), memorable- (PSD-M), and trophy-length (PSD-T) bowfin by waterbody. Data for the upper Barataria Estuary, Louisiana, were obtained from Davis (2006) and data from the upper Mississippi River (UMR) were obtained from Koch et al. (2009b). Bowfin were sampled from Lake Lindsay Grace, Georgia, in 2010. Values (i.e., within an index) with the same letter were not statistically different using a chi-square test (i.e., $P > 0.0083$; 0.05/6 comparisons)

Waterbody	PSD	PSD-P	PSD-M	PSD-T
Lake Lindsay Grace	94^a	65^a	20^a	0^a
Upper Barataria Estuary	98^a	66^a	37^b	1^a
Pool 11, UMR	100^a	99^b	78^c	8^b
Pool 13, UMR	100^a	98^b	85^c	2^a

75% of the females were age 2–4. One age-0 (male) and one age-5 (female) fish were collected. Total annual mortality (*A*) of bowfin in Lake Lindsay Grace was estimated at 68%.

Most bowfin of both sexes appeared to be mature by age 1 (~75%) and all were mature by age 2. Female GSI values ($n = 24$) averaged 8.2 (SD = 3.4) and varied from 3.5–17.2; GSI values for males ($n = 58$) varied from 0.8 and 1.5 and averaged 0.9 (SD = 0.1). Mean length-at-age of bowfin on Lake Lindsay Grace for ages 1, 2, 3, and 4 were 243, 371, 451, and 501 mm, respectively (Figure 3). Growth of bowfin was further described with von Bertalanffy growth models (Table 3). Bowfin in Lake Lindsay Grace had the lowest theoretical maximum length and highest growth coefficient.

Discussion

Size structure of the bowfin population in Lake Lindsay Grace was different than the other populations to which it was compared, but appeared to be most similar to the population in upper Barataria Estuary. Most of the bowfin sampled in Lake Lindsay Grace were between 400–600 mm TL with a maximum length of 683 mm TL. In the UMR, bowfin were slightly larger than those in Lake Lindsay Grace with lengths varying between 392–807 mm TL; the majority of fish in the UMR were between 500–700 mm TL (Koch et al. 2009b). Lengths of bowfin from the upper Barataria Estuary primarily varied from 360–680 mm TL (Davis 2006).

There was a lack of small individuals in the Lake Lindsay Grace sample compared to other bowfin studies (Davis 2006, Koch et al. 2009b). Estimating the abundance of young age-classes of fishes is crucial for fisheries managers because it often provides information on recruitment variability and year-class strength. Furthermore, growth and mortality estimates can be biased due to selectivity of the sampling gear and subsequent lack of small fish (Vaughan and Burton 1994, Goodyear 1995, Taylor et al. 2005, Gwinn et al. 2010). Electrofishing appeared to be ineffective at capturing juvenile bowfin, suggesting that further studies are needed to describe early life history stages of this species.

Age structure and longevity of bowfin in Lake Lindsay Grace differed from the other bowfin populations. Most of the bowfin in Lake Lindsay Grace were ages 1–4; whereas, bowfin in the UMR varied from age 2 to 13, with the majority being ages 3–9 (Koch et al. 2009b). Ages of bowfin in the upper Barataria Estuary varied from 1–10, but most fish (95%) were age 2–7 (Davis 2006), more similar to longevity of bowfin in Lake Lindsay Grace. Reasons behind the lack of older bowfin in the system are unknown, but may be due to high angling mortality or biases associated with sampling. Koch et al. (2009a) found that gular plates tended to provide more variable and older age estimates than those from fin rays. Therefore, differences in age structure and maximum age of bow-

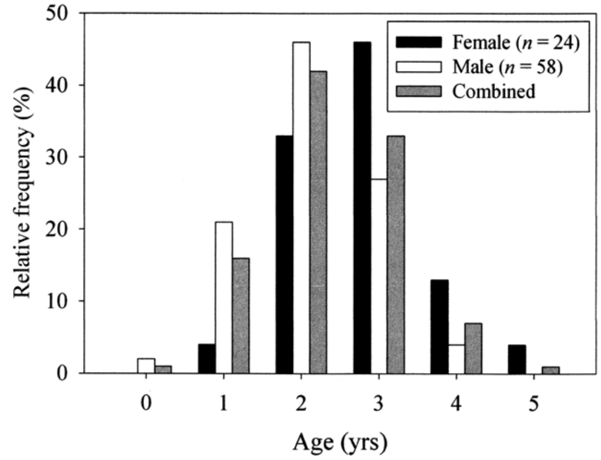

Figure 2. Age-frequency distributions of bowfin sampled from Lake Lindsay Grace, Georgia, in 2010.

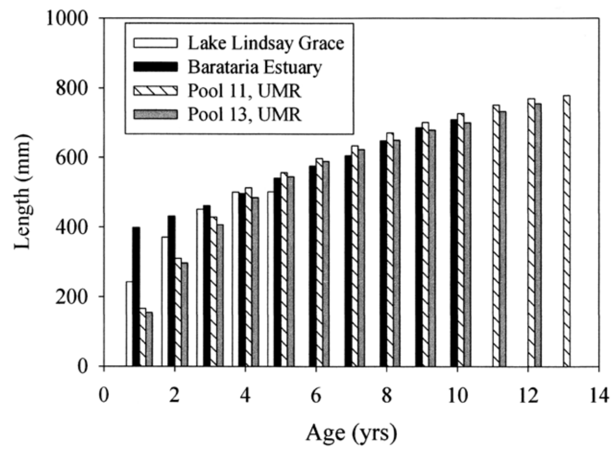

Figure 3. Mean back-calculated length at age of bowfin from Lake Lindsay Grace, Georgia, upper Barataria Estuary, Louisiana, and pools 11 and 13 from the upper Mississippi River in Iowa, Illinois, and Wisconsin. Samples from Lake Lindsay Grace were collected in 2010. Samples from Davis (2006) were collected in 2005 and 2006. Samples from pools 11 and 13 were collected in 2007 (Koch et al. 2009a).

Table 3. Parameter estimates from von Bertalanffy growth models for all bowfin data and by waterbody. Parameter estimates include the theoretical maximum length (L_∞; mm), growth coefficient (*K*), the theoretical age when length is zero (t_0; years), and their respective standard errors (SE). Raw data for the upper Barataria Estuary, Louisiana, were obtained from Davis (2006) and data from the upper Mississippi River (UMR) were obtained from Koch et al. (2009b). Bowfin were sampled from Lake Lindsay Grace, Georgia, in 2010.

	L_∞		*K*		t_0	
Waterbody	**Estimate**	**SE**	**Estimate**	**SE**	**Estimate**	**SE**
All	850.1	41.4	0.147	0.024	−2.737	0.489
Lake Lindsay Grace	603.8	31.4	0.625	0.164	−0.779	0.233
Upper Barataria Estuary	1,131.6	262.3	0.078	0.036	−3.523	1.027
Pool 11, UMR	809.2	14.0	0.229	0.015	−0.086	0.118
Pool 13, UMR	783.3	13.8	0.235	0.015	0.004	0.102

fin in the upper Barataria Estuary compared to the other populations may be a function of the hard structure used to age fish. In all populations, female bowfin were older and heavier than males (Davis 2006, Koch et al. 2009b). In addition, sex ratio differed across populations, but was likely a function of different sampling periods and gears.

Total annual mortality of bowfin in Lake Lindsay Grace was considerably higher than that reported in other studies. Davis (2006) estimated that bowfin total annual mortality rate was 58% in the upper Barataria Estuary, but Koch et al. (2009b) reported estimates of 34% for bowfin in Pool 11 and 37% in Pool 13 of the UMR. Similar to Davis (2006), both sexes began to mature shortly after their first year and were mature by age 2. In the UMR, males also matured at an early age, but females did not mature until age 3 (Koch et al. 2009b). Although fish were sampled during slightly different times of the year, GSI values for Lake Lindsay Grace and UMR (sampled in April) were nearly identical for males and females (Koch et al. 2009b).

Many species of freshwater fish exhibit sex-specific growth rates, with females exhibiting more rapid growth and attaining larger sizes than males (Schramm and Smith 1988, Neumann et al. 1994, Guy et al. 2002, Bonvechio et al. 2005). Similarly, Koch et al. (2009a) observed that female bowfin in the UMR were generally longer than males. Low number of females in our sample from Lake Lindsay Grace prevented evaluation of sex-specific differences in growth. Nonetheless, a larger proportion of bowfin that exceeded 600 mm TL were female, and the largest individual collected was a female. In general, bowfin in Lake Lindsay Grace had the fastest growth of any of the comparison populations (Davis 2006, Koch et al. 2009b). Perhaps the fast growth rate of bowfin observed in Lake Lindsay Grace was due to a low density of piscivores, as largemouth bass density is thought to be low (TFB, unpublished data).

Low sample size may have influenced growth and mortality estimates of bowfin in Lake Lindsay Grace. The accuracy and precision of growth and mortality parameter estimates is likely influenced by the life history and the exploitation history of that particular stock (Coggins et al. 2013). Fish that have little or no overlap of length groups typically have low bias in mortality and growth estimates, and estimated precision is generally improved (Westerheim and Ricker 1978, Coggins et al. 2013). Even though growth of bowfin in Lake Lindsay Grace was fast and the fish were not long-lived, lengths of bowfin overlapped considerably among ages. The lack of clear separation among age groups had unknown effects on our estimates, but likely reduced precision. Also, bowfin were sampled from the various populations at different times of the year and with slightly different sampling gears. Although we were primarily interested in evaluating general patterns of population demographics across systems, small differences in attributes like population structure (e.g., size structure) should be interpreted with caution. In contrast, comparing estimates of attributes such as growth rates is fairly robust to differences in sampling design.

Latitudinal patterns in fish population dynamics have been well documented (Quist et al. 2003, Heibo et al. 2005, Frisk and Miller 2006, Thorsen et al. 2010). Populations at northern latitudes often exhibit slower growth, greater longevity, and lower total annual mortality than southern populations. Several mechanisms are likely related to these latitudinal patterns. Braaten and Guy (2002) suggested that increased water temperature, longer growing season, and a higher number of degree days in southern latitudes was related to increased growth of various fishes in the Missouri River system. Beverton (1987) showed that growth rates of walleyes (*Sander vitreus*) were positively related with water temperature, which decreased with increasing latitude. Quist et al. (2003) argued that fast growth of walleyes in southern latitudes was attributed to longer growing season and high prey abundance.

Similar mechanisms are likely responsible for the patterns observed among bowfin populations. Bowfin in southern latitudes (Lake Lindsay Grace; upper Barataria Estuary, Davis 2006) grew faster, had lower age of maturation, and exhibited high total annual mortality rates when compared to bowfin populations from more northern latitudes (UMR, Koch et al. 2009b). Accounting for latitudinal differences in population dynamics may result in better management of bowfin and other species influenced by bowfin management. For instance, while Mundahl et al. (1998) found that bowfin were unsuccessful in decreasing bluegill densities in Minnesota, different results may be observed at southern latitudes where bowfin likely have more optimal feeding and growth conditions. Additionally, harvest of bowfin (e.g., for eggs) at southern latitudes may not have the same population-level effects as more northern populations because southern populations tend to grow faster, mature earlier, and have shorter life spans. Although results of our research were largely descriptive, they provide important information on the biology of bowfin that can be used to help guide management activities.

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