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Evaluation of ageing accuracy with complementary non-lethal methods for slow-growing, northern populations of shoal bass

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Abstract

In the upper Chattahoochee River basin, where some populations of shoal bass, *Micropterus cataractae* Williams & Burgess, are imperilled, age and growth data are lacking. Age and growth of shoal bass in this basin were assessed with non-lethal means using scales and mark–recapture. Mark–recapture data allowed for estimation of accuracy and determination of effects of any scale-based inaccuracies on growth models. Scale-based age estimates were accurate for 57% of the samples, and errors of 1 to 3 years included equal numbers of over- and underestimates of age. von Bertalanffy growth models based on scale ages were similar to those based on mark–recapture ages for ages 3–8 but noticeably divergent for younger and older fish. Scales provided estimates of longevity up to 12 years of age, and growth models produced from mark–recapture suggest scale ages underestimated age, especially for older fish. These populations of shoal bass live longer and grow slower than other populations, suggesting regional management strategies may be needed.

KEYWORDS

age accuracy, age validation, mark and recapture, *Micropterus cataractae*, scales, von Bertalanffy

1 | INTRODUCTION

Age data provide insights into growth, mortality, harvest and recruitment of fish populations. Because age data are generally estimated from interpretations of annuli from hard-parts, assessment of the precision, bias and accuracy associated with a given ageing technique is needed to determine the reliability of the estimates (Beamish & McFarlane, 1983; Campana, 2001). Many hard structures of fish (e.g. otoliths, scales and spines) have been validated to form discernible annual increments, but it is uncommon for validation to be conducted for the population of interest in the wild. Instead, many biologists rely on validation from previously published studies to be applicable to other populations of interest (Campana, 2001).

Otoliths are widely accepted as the most precise and accurate structure for estimating age of many fish species including black bass, *Micropterus* spp. (Maceina & Sammons, 2006; Maceina et al., 2007; Robillard & Marsden, 1996); but the lethality of their use can be a drawback for species and populations that are rare, threatened, endangered or of conservation concern. Scales are a common non-lethal alternative to otoliths, but many studies have shown their limitations compared to otoliths (e.g. Maceina & Sammons, 2006; Maceina et al., 2007; Robillard & Marsden, 1996). Issues that affect the reliability of scale-based age estimates include regeneration and resorption during times of stress (Simkiss, 1974) and decreased discernibility of annuli (Quist, Pegg & DeVries, 2012). Although perhaps not as reliable as otolith-based estimates, scale-based age estimates may still be acceptable for informing management in certain situations. For example, biologists in northern states routinely use scale-based estimates for black bass management, primarily because of their non-lethal nature, even though the accuracy of results is likely less than otoliths (Maceina et al., 2007).

Shoal bass, *M. cataractae* Williams & Burgess, is a fluvial-specialist species occurring only in Georgia, Alabama and Florida, USA (Taylor & Peterson, 2014) and is considered vulnerable to extinction (Jelks et al., 2008). Although some robust populations exist where sacrificing individuals for age estimation with otoliths is a viable option [e.g. Flint River, Georgia (Ingram & Kilpatrick, 2015); Chipola River, Florida (Woodside, Paxton & Kierl, 2015)], many other populations are too small and fragmented to risk sacrificing fish for age estimation [e.g. Big Creek, Georgia (Dakin, Porter, Freeman & Long, 2015)]. In north Georgia, extant populations of shoal bass occur in the Chattahoochee River below Morgan Falls Dam, Big Creek, Chattahoochee River above Lake Lanier and Chestatee River, but their long-term viability is uncertain. The population below Morgan Falls Dam is stocked and intermixed with several non-native species of black basses resulting in a high proportion of hybrid individuals (Dakin et al., 2015; Porta & Long, 2015) and is not a subject of this study. The population in Big Creek suffers from low genetic diversity, likely as a result of low population size and limited habitat availability (~2 km of stream; Dakin et al., 2015). Population status of the remaining two populations (Chattahoochee River above Lake Lanier and Chestatee River) has not been assessed, but Lake Lanier may isolate these populations from other shoal bass populations (Dakin et al., 2015). Age-based demographic variables are needed to assess the status of these populations, but sacrificing individuals from these three populations to obtain otoliths for age estimation was deemed undesirable, making scales the choice of hard structure for ageing. Other non-lethal alternatives for estimating age of black bass have been investigated (e.g. fin spines, fin rays; Klein, Bonvechio, Bowen & Quist, 2017; Morehouse, Donabauer & Grier, 2013; Rude et al., 2013), but none have been found to provide data quality equal to that obtained from otoliths. Furthermore, scales occur in sufficient quantity over the entire body of the fish to allow for repeated collection over time. Resampling scales from marked individuals through time can provide a means for assessing accuracy of age estimates, wherein young-of-year fish are sampled to determine the size at which the first annulus forms and individuals across a range of ages are resampled and re-examined through time to validate increment formation across a range of ages (Campana, 2001).

Although collecting scales from multiple individuals over time would provide a measure of accuracy, another method independent of age estimation would provide a further check. Because ages estimated from scales generally are less precise and often underestimate actual age (Heidinger & Clodfelter, 1987; Maceina et al., 2007), population parameter estimates (e.g. growth functions) resulting from scale ages may be biased, but to what degree is often unknown. Passive integrated transponder (PIT) tags provide long-term identification of individuals over time (Cooke, Hinch, Lucas & Lutcavage, 2012; Harvey & Campbell, 1989), and measures of change in length over time with subsequent recaptures can be used to model growth (Brenden, Hallerman & Murphy, 2006; Isley & Grabowski, 2007). This age-independent growth model can be compared to an age-dependent growth model, where scales are used to provide the age estimates, and differences in growth model parameters (e.g. von Bertalanffy K and L_∞) would provide further insight into age inaccuracies from scales.

This project evaluated age and growth of northern populations of shoal bass using scales and mark–recapture over 3 years. The objectives of this project were to: (1) determine precision of scale-based annuli counts between readers; (2) assess accuracy of scale-based ages by determining the presence of the first and subsequent annuli across a range of fish sizes; (3) estimate and compare growth models derived from scale-based estimates of age (age dependent) and changes in length over time from recaptured individuals (age independent); and (4) compare growth models with those from other populations.

2 | MATERIALS AND METHODS

2.1 | Study area

This study focused on three shoal bass populations in the upper Chattahoochee River basin in the Piedmont ecoregion of northern Georgia, USA (Figure 1). These populations are isolated from each other by Lake Sidney Lanier, a large impoundment of the Chattahoochee River. Impoundments have been shown to isolate and fragment shoal bass populations throughout their range (Taylor, Papes & Long, 2017; Taylor & Peterson, 2014; Williams & Burgess, 1999), including in the upper Chattahoochee River basin (Dakin et al., 2015). Shoal bass populations occur in the Chattahoochee and Chestatee rivers upstream of Lake Lanier and downstream in a 2-km reach of Big Creek, a tributary of the Chattahoochee River (Dakin et al., 2015).

2.2 | Data collection

This project used mark–recapture to obtain scale samples from individual shoal bass over a 3-year period following animal care use protocol #AG138 approved by the Institutional Animal Care and Use Committee at Oklahoma State University. Fish were sampled in shoal habitats using back pack and boat electric fishers. Fish were sampled in autumn (October–November) 2013–2014 and in spring (May) 2014–2015 in Big Creek and in spring (May) 2013–2015 in Chattahoochee and Chestatee rivers. Total length (TL, mm) was measured, and a sample of approximately five scales from the dorso-lateral region of each fish was obtained (Quist et al., 2012). Fish were tagged intraperitoneally with PIT tags to allow identification of individuals through time and released. Scales were taken from areas adjacent to previously sampled regions when fish were recaptured in subsequent surveys to avoid regenerated scales.

The number of annuli and the age of each fish were estimated by two readers trained on a common data set of approximately 100 black bass scales from a reference, consensus-aged collection (Campana, 2001; data from Long & Fisher, 2001). Because fish were from spring and autumn samples, each reader initially counted the number of annuli observed rather than estimating age (e.g. a spring-caught fish may not have an annulus at the edge; Beckman & Wilson, 1995; Crawford, Coleman & Porak, 1989; Olmsted & Kilambi, 1978). The separate

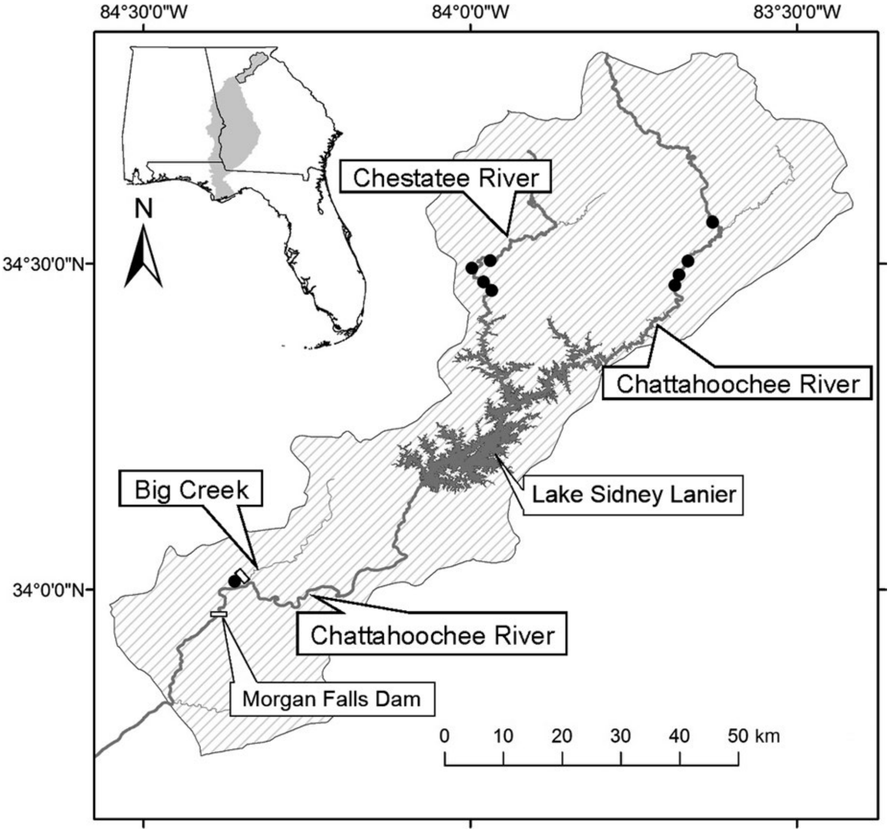

FIGURE 1 Map of the Upper Chattahoochee River basin (UCRB, hatched area), Georgia, USA, where shoal bass were sampled from Big Creek, the Chattahoochee River and the Chestatee River (black dots) to estimate age and growth. The inset map (top left) shows the location of the UCRB (outlined area) within the range of shoal bass (light grey)

treatment of annuli counts from age estimates reduced interpretation error between spring- and autumn-caught fish (Campana, 2001). Fish scales were placed between two microscope slides and viewed with a microfiche reader. Readers independently examined one non-regenerated scale from each fish twice without knowledge of fish size, location or capture history and counted the number of annuli. If the two counts for a reader agreed, it was considered the reader's final count; if not, a third count was made as the final. Final annuli counts that were agreed between readers agreed were adopted as the consensus count for each fish. Differences between readers were resolved by a consensus count by both readers in concert. To assign age, all fish were re-examined in concert with consideration given to consensus annuli counts and season of capture but not size, to avoid potential bias in age assignment. For fish captured in autumn, annuli counts were considered the age. For fish captured in spring, the edge was considered the last annulus, which was sometimes discernible and counted during annuli counts. In these cases, the annuli count was the age estimate; otherwise, one was added to the annuli count to estimate age. All data were pooled among systems because the interest was in the effects of ageing methods on these populations as a group, not in determining whether differences existed among populations.

2.3 | Data analyses

Precision of annuli counts was assessed between readers with coefficient of variation (CV) (Chang, 1982) calculated as

$$CV_j = 100 \times \frac{\sqrt{\frac{\sum_{i=1}^{R}(X_{ij}-X_j)^2}{R-1}}}{X_j}$$

where X_{ij} is the ith count of the jth fish, X_j is the mean count of the jth fish and R is the number of times each fish was counted. Because the CV estimate requires the mean count of a particular fish in the denominator, 1 was added to all counts to avoid dividing by zero. Between-reader CV estimates were then plotted against the final, consensus annuli count to determine how precision changed with number of annuli counted.

Annulus formation was assessed using estimated ages of individuals that had been captured and subsequently recaptured 1 year later. In the absence of known age, which was the case for the three natural populations studied, a determination of the location of the first annulus and the periodicity of annulus formation for the entire range of estimated ages would be equivalent to age validation (Campana, 2001). To locate the first annulus, total length of fish assigned age 0 in autumn and age 1 in spring in reference to sizes of known-age young-of-year (YOY) was assessed. Hatchery-reared, known-age YOY shoal bass stocked in the Chattahoochee River below Morgan Falls Dam ranged in mean size from 24 mm TL in April to 88 mm TL in August (Long, Klein & Mauldin, 2004; Porta, 2011; Porta & Long, 2015). Length–frequency plots were used to further interpret size distributions of these early age classes. To verify annulus periodicity, age assignments at recapture were plotted against initial age assignments (in years) plus the known elapsed time interval between capture events (years). The data were fit with linear regression and 95% CIs were constructed to determine significant departures from 0 for the intercept and unity for the slope. Age error was calculated as the estimated age at recapture minus initial age estimate plus the elapsed time interval between capture events. Age error was then plotted against total length at recapture to determine whether a systematic bias in age error was evident.

Using spring-caught fish, parameters of the von Bertalanffy growth equation were estimated with scale-based age estimates with the equation:

$$L_t = L_\infty \lfloor 1 - e^{(-k*(t-t_0))} \rfloor$$

where L_t = length at time t (age in years), L_∞ is the asymptotic length, e is the base of the natural logarithm, k is the growth coefficient and t_0 is the time at which fish has 0 length (Isley & Grabowski, 2007). The von Bertalanffy growth model parameters t_0, k and L_∞ were estimated using non-linear tools in packages FSA and nlstools for R (VBGF; Ogle, 2016) and 95% confidence intervals were calculated. von Bertalanffy parameters were estimated for the age-independent data set using measured TL for marked (L_m) and recaptured (L_r) fish in spring 1 year apart (Δt) and Wang's (1998) modification of Fabens' (1965) method for mark–recapture data (Isley & Grabowski, 2007; Ricker, 1975):

$$L_r = L_m + \left(L_\infty - L_m\right)\left(1 - e^{-K\Delta t}\right)$$

This method allows for individual variation in growth and was estimated using non-linear tools in packages FSA and nlstools for R (FABENS2; Ogle, 2016). Only recaptures that were measured in successive years (1 year apart) were used, so that growth was modelled on an annual basis (Ricker, 1975). In the absence of age (t) estimates, the parameter t_0 could not be estimated and was set equal to 0 (Isley & Grabowski, 2007). With the resulting von Bertalanffy equation parameters estimated (t_0, K and L_∞) without reference to age, the equation can be solved for each age class to estimate the expected TL. Comparison of the two growth curves allowed assessment of the effect of age estimation errors arising from the use of scales. These growth curves were also compared to von Bertalanffy curves from otolith-based age estimates of other shoal bass populations (Ingram & Kilpatrick, 2015; Porta & Long, 2015; Sammons, 2016; Woodside et al., 2015).

3 | RESULTS

Seven hundred scale samples (i.e. one scale per fish per capture event) were examined; 634 of these were useable for age analysis (i.e. not damaged or regenerated). Of these 634 samples, 542 came from 475 individual fish that were tagged for mark–recapture. Most of the shoal bass samples came from Big Creek (48.6%); 25.0% came from Chattahoochee River and 26.4% from Chestatee River.

3.1 | Precision

Between-reader mean CV from all fish was 11.2% (N = 634, SE = 0.6), and mean CV was higher for younger fish (0 and 1 annuli; Figure 2). Mean CV ranged between approximately 5%–10% after fish exhibited 1 annulus.

3.2 | Validation

3.2.1 | First annulus

Fish assigned as age 0 in autumn ranged in size from 64 mm TL to 116 mm TL (Figure 3), conforming to sizes of known-age YOY shoal bass (Long et al., 2004; Porta, 2011; Porta & Long, 2015). In spring

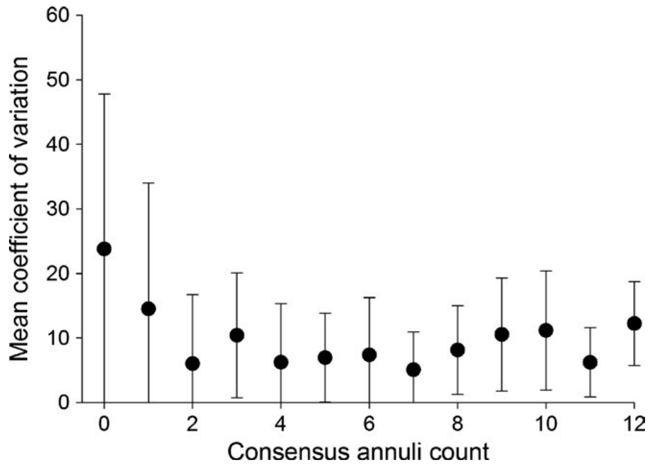

FIGURE 2 Mean coefficient of variation (CV) plots between readers of scale-based annuli counts from shoal bass in the Upper Chattahoochee River basin. Error bars are standard deviations

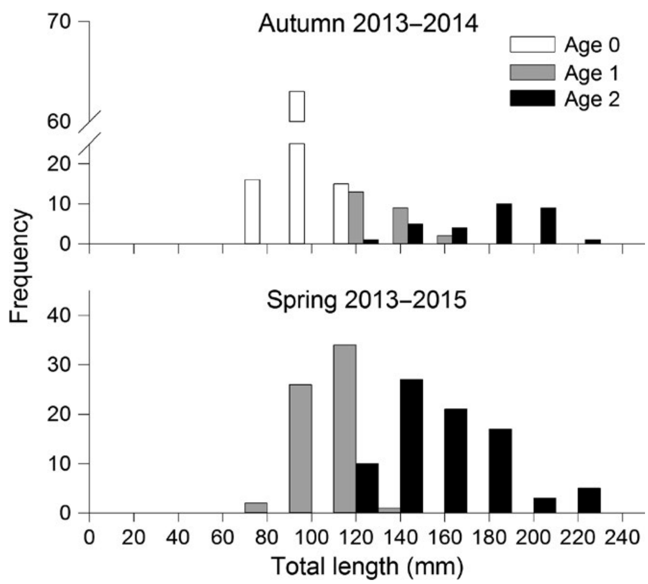

FIGURE 3 Length–frequency of shoal bass from the Upper Chattahoochee River basin as assigned to age 0, age 1 and age 2 in autumn and spring based on analysis of scales. Data are grouped by 20-mm length bins

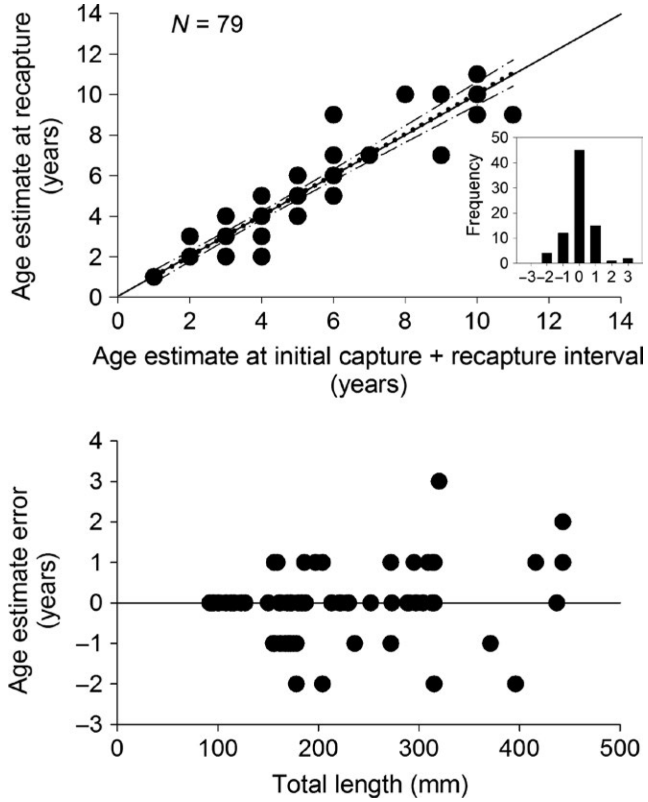

FIGURE 4 Accuracy plots of scale-based age estimates for the consensus age estimate (N = 79) for shoal bass in the Upper Chattahoochee River basin. (top) Solid line indicates 1:1 agreement between the two age estimates, the dotted line represents the linear least square regression results, and the dashed–dotted line is the 95% confidence intervals about the regression line. The inset histogram is the frequency of age estimate differences (annuli count at time of recapture—initial annual count at first capture plus the known elapsed time interval between recapture events). (bottom) Age estimation error, which is the difference between age estimate at recapture minus the sum of age at initial capture plus interval before recapture, plotted against total length of recaptured fish

samples, no fish were assigned age 0 and 63 were assigned age 1. These fish ranged in size from 72 to 123 mm TL, slightly larger than age-0 fish in the autumn.

3.2.2 | Annulus periodicity

Fifty-six PIT-tagged fish recaptured on one or more occasions in spring and autumn samples provided 79 unique capture–recapture comparisons to generate accuracy plots (Figure 4, top). No significant departure from 0 for the y-intercept (0.02 ± 0.38, 95% CI) or 1 for the slope (1.00 ± 0.09, 95% CI) was evident based on 95% confidence intervals. Of the 79 estimates contributing to the age accuracy plot, 45 were in exact agreement (57% accuracy); 16 underestimated age by 1 to 2 years and 18 overestimated age by 1 to 3 years. No age estimation error was detected for fish smaller than 140 mm (N = 16; Figure 4, bottom) and ages tended to be overestimated for fish larger than 400 mm, but sample size was limited to N = 4. For these larger fish, the age error was 0 for one fish, +1 year for two fish and +2 years for one fish. For fish between 140 mm TL and 400 mm TL, ages of 28 were considered accurate and the remaining age estimation error was similarly distributed above (N = 15) and below 0 (N = 16).

3.3 | Length at age and von Bertalanffy growth models

Minimum and maximum age estimates of spring-caught fish used for growth models ranged from 1 to 12 years. The von Bertalanffy parameter estimate for L_∞ and its 95% confidence intervals were above the mean size of 467 mm TL for oldest fish observed in the data set (Table 1) suggesting an effect of age underestimation. By contrast, confidence intervals for the L_∞ estimate (518) from the age-independent data set were relatively narrow and closer to the mean sizes observed at the oldest estimated ages (467 mm at age 12). Compared with von Bertalanffy models from other populations, shoal bass in the three upper Chattahoochee River basin populations in this study, regardless of method of ageing, and the population in the Chattahoochee River below Morgan Falls Dam grew more slowly than more southern populations in the Chipola River, Florida (Woodside et al., 2015) and the Flint River, Georgia (Ingram & Kilpatrick, 2015; Sammons, 2016; Figure 5).

4 | DISCUSSION

Scales have long been regarded as less accurate than otoliths for ageing black bass species (Heidinger & Clodfelter, 1987; Maceina et al., 2007). Ageing fish by otoliths requires sacrificing fish, which was undesirable for the three shoal bass populations investigated in this study. Complementing ages derived from scales with age-independent data from mark–recapture enabled assessment of the

TABLE 1 von Bertalanffy growth parameter estimates (95% confidence intervals) for shoal bass populations in the upper Chattahoochee River basin, Georgia

Data set	N	t_0	k	L_∞
Age dependent	463	−0.848 (−1.169, −0.561)	0.077 (0.054, 0.101)	749.4 (634.4, 957.3)
Age independent	40	0[a]	0.152 (0.112, 0.201)	518.4 (459.2, 613.7)

N = sample size, t_0 is the theoretical length of fish at time 0, k is the Brody growth coefficient and L_∞ is the maximum mean total length estimated from age-dependent and age-independent data.
[a]Not estimable; set at 0.

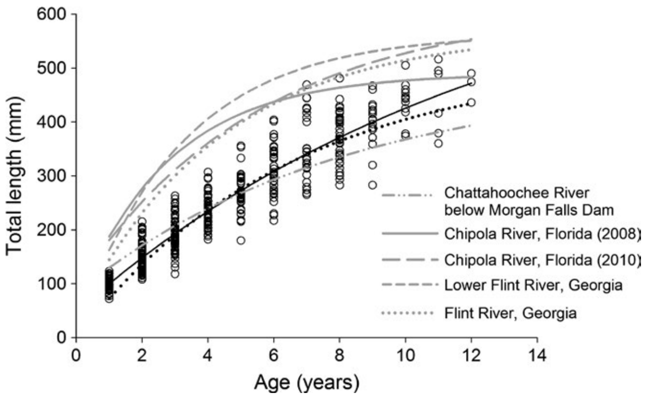

FIGURE 5 von Bertalanffy growth curves for shoal bass in the upper Chattahoochee River (this study) estimated from age-dependent (solid black line) and age-independent (dotted black line) data. Open circles are length and age of the age-dependent data. von Bertalanffy growth curves for shoal bass from other studies are shown in grey: Chattahoochee River below Morgan Falls Dam is from an unpublished analysis of data from Porta and Long (2015); Chipola River, Florida in 2008 and 2010 is from Woodside et al. (2015), Lower Flint River, Georgia is from Ingram and Kilpatrick (2015) and Flint River, Georgia is from Sammons (2016)

accuracy of age estimates and the effect of inaccuracy on growth model estimates. The validation procedure employed was effective at documenting the first annulus and periodicity of subsequent annuli formation. Age accuracy was relatively poor (57%) but unbiased, with over- and underestimates of age for ages 1–11 years.

Although otoliths were not used, ageing precision results from scales used in this study were similar to other studies of black bass that used otoliths (from 0.04% to 15.8%; Besler, 1999; Long & Fisher, 2001; Maceina & Sammons, 2006; Taylor & Weyl, 2012; Rude et al., 2013; Sotola et al., 2014). By contrast, accuracy of scales from shoal bass in the upper Chattahoochee River basin was poor (57%) compared to what has been reported for otoliths from other black bass species [from 92% to 100% (Buckmeier & Howells, 2003; Heidinger & Clodfelter, 1987; Klein et al., 2017); but see Howells, Betsill and Prentice (1997) who reported accuracy from 39% to 47% for known-age 6–8-year-old largemouth bass]. The inaccuracies of the scale-based age estimates affected growth model results as evidenced by comparisons to age-independent data. Age-dependent estimates of L_∞ were inflated (coupled with deflated estimates of k) compared with von Bertalanffy parameters from the age-independent data set, likely due to underestimates of age of older fish, which was up to 2 years in this study and common with scales (Heidinger & Clodfelter, 1987; Maceina et al., 2007). By underestimating age by up to 2 years for larger fish, the von Bertlanffy equation was being fit to data that exhibited a more linear trend, thereby affecting parameter estimates. Shifting data points of larger fish to the right by 1 or 2 years in the length–age plots would produce a more non-linear trend with a lower asymptote (i.e. closer to that calculated from age-independent data). Inaccurate age estimates at both the times of capture and recapture may still document the formation of the annulus but underestimate actual age. Because older fish have more annuli, which become crowded at the edge and less discernible (McInerny, 2017), age inaccuracy would be more likely for older fish. The current method for verifying age estimates through annulus formation did not indicate an age underestimate bias for older fish, but samples sizes were relatively low for fish older than 8 years, masking a bias that appeared evident when the age-independent growth model was compared to the age-dependent growth model.

Even with age estimation error, the results of this study demonstrate that the populations of shoal bass in the upper reaches of their range live longer (up to 12 years) and grow slower than populations at more southern latitudes. Before age and growth data for these populations in the northern extent of the range were available, shoal bass were considered to grow rapidly throughout their range (Sammons, Woodside & Paxton, 2015). The only previous estimates of growth for shoal bass in the upper Chattahoochee River basin came from a stocked population below Morgan Falls Dam in a portion of the river affected by cold-water hypolimnetic discharge from Lake Lanier and was based on otoliths that had been marked at stocking with oxytetracycline (Porta & Long, 2015). This shoal bass population exhibited slow growth and high longevity (14 years), presumably because of the depressed temperature regime. Because that growth curve is similar to that from the present study, which occurs above these cold-water discharges, one may conclude that latitude or other broad factors, such as elevation, may affect growth.

The results of this study demonstrate that northern populations of shoal bass grow more slowly than southern populations, which have been more extensively studied and have served as the basis to generalise about the ecology of this species (e.g. Sammons et al., 2015). Whether growth rates in the northern extent of the range are a response to environmental variation or longer term adaptation to the environment is unknown, but these differences in growth underlie other important demographic parameters such as size- and age-at-maturity, mortality rates, timing of ontogenetic diet and habitat shifts and sportfish management (Beamish & McFarlane,1983; Sammons et al., 2015). The results of the current study suggest a need for regional approaches to management for this species.

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REFERENCES

Beamish, R. J., & McFarlane, G. A. (1983). The forgotten requirement for age validation in fisheries biology. *Transactions of the American Fisheries Society*, *112*, 735–743. https://doi.org/10.1577/1548-8659(1983) 112<735:TFRFAV>2.0.CO;2

Beckman, D. W., & Wilson, C. A. (1995). Seasonal timing of opaque zone formation in fish otoliths. In D. H. Secor, J. M. Dean & S. E. Campana (Eds.), *Recent developments in fish otolith research*, Belle W. Baruch Library in Marine Science Number 19 (pp. 27–43). Columbia, SC: University of South Carolina Press.

Besler, D. A. (1999). Utility of scales and whole otoliths for aging largemouth bass in North Carolina. *Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies*, *53*, 119–129.

Brenden, T. O., Hallerman, E. M., & Murphy, B. R. (2006). Sectioned pelvic ray ageing of muskellunge *Esox masquinongy* from a Virginia river: Comparisons among readers, with cleithrum estimates, and with tag-recapture growth data. *Fisheries Management and Ecology*, *13*, 31–37. https://doi.org/10.1111/j.1365-2400.2006.00469.x

Buckmeier, D. L., & Howells, R. G. (2003). Validation of otoliths for estimating ages of largemouth bass to 16 years. *North American Journal of Fisheries Management*, *23*, 590–593. https://doi.org/10.1577/1548-8675(2003) 023<0590:VOOFEA>2.0.CO;2

Campana, S. E. (2001). Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. *Journal of Fish Biology*, *59*, 197–242. https://doi.org/10.1111/j.1095-8649.2001.tb00127.x

Chang, W. Y. (1982). A statistical method for evaluating the reproducibility of age determination. *Canadian Journal of Fisheries and Aquatic Sciences*, *39*, 1208–1210. https://doi.org/10.1139/f82-158

Cooke, S. J., Hinch, S. G., Lucas, M. C., & Lutcavage, M. (2012). Biotelemetry and biologging. In A. V. Zale, D. L. Parrish, & T. M. Sutton (Eds.), *Fisheries techniques* (3rd ed. pp. 819–881). Bethesda, MD: American Fisheries Society.

Crawford, S., Coleman, W. S., & Porak, W. F. (1989). Time of annulus formation in otoliths of Florida largemouth bass. *North American Journal of Fisheries Management*, *9*, 231–233. https://doi.org/10.1577/1548-8675(1989) 009<0231:TOAFIO>2.3.CO;2

Dakin, E. E., Porter, B. A., Freeman, B. J., & Long, J. M. (2015). Hybridization threatens shoal bass populations in the upper Chattahoochee River basin. In M. D. Tringali, J. M. Long, T. W. Birdsong, & M. S. Allen (Eds.), *Black bass diversity: Multidisciplinary science for conservation*, *Symposium 82* (pp. 491–501). Bethesda, MD: American Fisheries Society.

Fabens, A. J. (1965). Properties and fitting of the von Bertlanffy growth curve. *Growth*, *29*, 265–289.

Harvey, W. D., & Campbell, D. L. (1989). Retention of passive integrated transponder tags in largemouth bass. *The Progressive Fish Culturist*, *51*(3), 164–166. https://doi.org/10.1577/1548-8640(1989)051 <0164:TNROPI>2.3.CO;2

Heidinger, R. C., & Clodfelter, K. (1987). Validity of the otolith for determining age and growth of walleye, striped bass, and smallmouth bass in power plant cooling ponds. In R. C. Summerfelt, & G. E. Hal (Eds.), *Age and growth of fish* (pp. 241–251). Ames, IA: Iowa State University Press.

Howells, R. G., Betsill, R. K., & Prentice, J. A. (1997). Age estimation and length back-calculation for known-age largemouth bass. *Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies*, *49*, 167–177.

Ingram, T. R., & Kilpatrick, J. M. (2015). Assessment of the shoal bass population in the lower Flint River, Georgia. In M. D. Tringali, J. M. Long, T.W. Birdsong & M. S. Allen (Eds.), *Black bass diversity: Multidisciplinary science for conservation*, *Symposium 82* (pp. 157–168). Bethesda, MD: American Fisheries Society.

Isley, J. J., & Grabowski, T. B. (2007). Age and growth. In C. S. Guy, & M. L. Brown (Eds.), *Analysis and interpretation of freshwater fisheries data* (pp. 187–228). Bethesda, MD: American Fisheries Society.

Jelks, J. L., Walsh, S. J., Burkhead, N. M., Contreras-Balderas, S., Diaz-Pardo, E., Hendrickson, D. A., … Warren, M. L. (2008). Conservation status of imperiled North American freshwater and diadromous fishes. *Fisheries*, *33*, 372–407. https://doi.org/10.1577/1548-8446-33.8.372

Klein, Z. B., Bonvechio, T. F., Bowen, B. R., & Quist, M. C. (2017). Precision and accuracy of age estimates obtained from anal fin spines, dorsal fin spines, and sagittal otoliths for known-age largemouth bass. *Southeastern Naturalist*, *16*, 225–234. https://doi.org/10.1656/058.016.0209

Long, J. M., & Fisher, W. L. (2001). Precision and bias of largemouth, smallmouth, and spotted bass ages estimated from scales, whole otoliths, and sectioned otoliths. *North American Journal of Fisheries Management*, *21*, 636–645. https://doi.org/10.1577/1548-8675(2001) 021<0636:PABOLS>2.0.CO;2

Long, J. M., Klein, L. A., & Mauldin, A. C. (2004). Length, weight, age, and growth of young-of-year shoal bass raised in a southwest Georgia hatchery pond. *Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies*, *58*, 40–46.

Maceina, M. J., Boxrucker, J., Buckmeier, D. L., Gangl, R. S., Lucchesi, D. O., Isermann, D. A., … Martinez, P. J. (2007). Current status and review of freshwater fish aging procedures used by state and provincial fisheries agencies with recommendations for future directions. *Fisheries*, *32*, 329–340. https://doi.org/10.1577/1548-8446(2007) 32[329:CSAROF]2.0.CO;2

Maceina, M. J., & Sammons, S. M. (2006). An evaluation of different structures to age freshwater fish from a northeastern US river. *Fisheries Management and Ecology*, *13*, 237–242. https://doi.org/10.1111/j.1365-2400.2006.00497.x

McInerny, M. C. (2017). Chapter 6: Scales. In M. C. Quist, & D. A. Isermann (Eds.), *Age and growth of fishes: Principles and techniques* (pp. 127–158). Bethesda, MD: American Fisheries Society.

Morehouse, R. L., Donabauer, S. B., & Grier, A. C. (2013). Estimating largemouth bass age: Precision and comparisons among scales, pectoral fin rays, and dorsal fin spines as nonlethal methods. *Fisheries and Aquaculture Journal*, *2013*, FAJ–74. Available from http://astonjournals.com/manuscripts/Vol2013/FAJ-74_Vol2013.pdf

Ogle, D. H. (2016). *Introductory fisheries analyses with R*. Boca Raton, FL: CRC Press.

Olmsted, L. L., & Kilambi, R. V. (1978). Age and growth of spotted bass (*Micropterus punctulatus*) in Lake Fort Smith, Arkansas. *Transactions of the American Fisheries Society*, *107*, 21–22. https://doi.org/10.1577/1548-8659(1978) 107<21:AAGOSB>2.0.CO;2

Porta, M. J. (2011). *Effects of environmental variation on stocking success of an endemic black bass species in the Chattahoochee River, Georgia*. Master's thesis. Stillwater, OK: Oklahoma State University.

Porta, M. J., & Long, J. M. (2015). Evaluation of a five-year shoal bass conservation-stocking program in the upper Chattahoochee River, Georgia. In M. D. Tringali, J. M. Long, T. W. Birdsong, & M. S. Allen (Eds.), *Black bass diversity: Multidisciplinary science for conservation*, *Symposium 82* (pp. 169–180). Bethesda, MD: American Fisheries Society.

Quist, M. C., Pegg, M. A., & DeVries, D. R. (2012). Age and growth. In A. V. Zale, D. L. Parrish, & T. M. Sutton (Eds.), *Fisheries techniques* (3rd ed. pp. 677–731). Bethesda, MD: American Fisheries Society.

Ricker, W. E. (1975). Computation and interpretation of biological statistics of fish populations. Bulletin of the Fisheries Research Board of Canada, 191, Ottawa.

Robillard, S. R., & Marsden, J. E. (1996). Comparison of otolith and scale ages for yellow perch from Lake Michigan. *Journal of Great Lakes Research*, *22*, 429–435. https://doi.org/10.1016/S0380-1330(96)70967-X

Rude, N. P., Hintz, W. D., Norman, J. D., Kanczuzewski, K. L., Yung, A. J., Hofer, K. D., & Whitledge, G. W. (2013). Using pectoral fin rays as a non-lethal aging structure for smallmouth bass: Precision with otolith age estimates and the importance of reader experience. *Journal of Freshwater Ecology*, *28*, 199–210. https://doi.org/10.1080/02705060.2012.738253

Sammons, S. M. (2016). Catch and exploitation of shoal bass in the Flint River, Georgia, USA: Implications for harvest restrictions. *North American Journal of Fisheries Management*, *36*, 606–620. https://doi.org/10.1080/02755947.2016.1146178

Sammons, S. M., Woodside, K. L., & Paxton, C. J. (2015). Shoal bass *Micropterus cataractae* Williams & Burgess, 1999. In M. D. Tringali, J. M. Long, T. W. Birdsong, & M. S. Allen (Eds.), *Black bass diversity: Multidisciplinary science for conservation*, *Symposium 82* (pp. 75–81). Bethesda, MD: American Fisheries Society.

Simkiss, K. (1974). Calcium metabolism of fish in relation to ageing. In T. B. Bagenal (Ed.), *The ageing of fish* (pp. 1–12). Surrey, England: Unwin Brothers Limited.

Sotola, V. A., Maynard, G. A., Hayes-Pontius, E. M., Mihuc, T. B., Malchoff, M. H., & Marsden, J. E. (2014). Precision and bias of using opercles as compared to otoliths, dorsal spines, and scales to estimate ages of largemouth and smallmouth bass. *Northeastern Naturalist*, *21*, 565–573. https://doi.org/10.1656/045.021.0411

Taylor, A. T., Papes, M., & Long, J. M. (2017). Incorporating fragmentation and non-native species into distribution models to inform fluvial fish conservation. *Conservation Biology*, *32*, 171–182. https://doi.org/10.1111/cobi.13024

Taylor, A. T., & Peterson, D. L. (2014). Shoal bass life history and threats: A synthesis of current knowledge of a *Micropterus* species. *Reviews in Fish Biology and Fisheries*, *24*, 159–167. https://doi.org/10.1007/s11160-013-9323-9

Taylor, G. C., & Weyl, O. L. F. (2012). Otolith versus scales: Evaluating the most suitable structure for ageing largemouth bass, *Micropterus salmoides*, in South Africa. *African Zoology*, *47*, 358–362. https://doi.org/10.1080/15627020.2012.11407562

Wang, Y.-G. (1998). An improved Fabens method for estimation of growth parameters in the von Bertalanffy model with individual asymptotes. *Canadian Journal of Fisheries Management*, *55*, 397–400. https://doi.org/10.1139/f97-211

Williams, J. D., & Burgess, G. H. (1999). A new species of bass, *Micropterus cataractae* (Teleostei: Centrarchidae), from the Apalachicola River basin in Alabama, Florida, and Georgia. *Bulletin of the Florida Museum of Natural History*, *42*(2), 80–114.

Woodside, K. L., Paxton, C. J., & Kierl, N. C. (2015). Stock assessment of shoal bass in the Chipola River, Florida. In M. D. Tringali, J. M. Long, T. W. Birdsong, & M. S. Allen (Eds.), *Black bass diversity: Multidisciplinary science for conservation*, *Symposium 82* (pp. 139–155). Bethesda, MD: American Fisheries Society.

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