Evaluation of Otoliths and Four Non-lethal Structures for Estimating Age and Population Characteristics of Three Black Bass Species

Austin D. Griffin[1], *Oklahoma Department of Wildlife Conservation, Oklahoma Fishery Research Laboratory, 500 East Constellation, Norman, OK 73072*

Michael J. Porta, *Oklahoma Department of Wildlife Conservation, Oklahoma Fishery Research Laboratory, 500 East Constellation, Norman, OK 73072*

Richard A. Snow, *Oklahoma Department of Wildlife Conservation, Oklahoma Fishery Research Laboratory, 500 East Constellation, Norman, OK 73072*

Abstract: Black bass (*Micropterus* spp.) are the most popular freshwater sportfishes in North America and are intensively managed. Successful management of fish populations relies on dependable age data for estimation of age determined population rate functions (growth, mortality, and recruitment). Otoliths provide accurate age estimates compared to most other aging structures, but otolith removal requires fish to be sacrificed, leading some fisheries managers to rely on alternative, non-lethal methods for estimating ages of fish. However, non-lethal aging structures may produce biased age estimates when compared to otoliths. In this study, we evaluated age-estimate precision for largemouth bass (*Micropterus salmoides*), smallmouth bass (*M. dolomieu*), and spotted bass (*M. punctulatus*) using otoliths, dorsal fin spines, anal fin spines, pectoral fin rays, and scales. Further, we compared growth and mortality parameters derived using age estimates from each structure. For all species, between reader agreement (97.5%–98.2%) and precision (CV = 0.01%–2%) were high using otoliths but were low for the four non-lethal structures. In general, final consensus ages from dorsal fin spines, anal fin spines, and scales overestimated ages of younger fish and underestimated ages of older fish when compared to otolith consensus ages. Using final consensus ages from each aging structure resulted in significant differences in von Bertalanffy growth parameters calculated using non-lethal structures compared to otoliths. Estimated annual mortality rates varied among structures; however, we rarely observed significant differences in instantaneous mortality among structures. Based on these results, fisheries managers should only use otoliths for aging largemouth bass, smallmouth bass, and spotted bass. If for some reason this is not possible, managers should recognize that there may be management consequences due to imprecise and inaccurate age estimates.

Key words: reader agreement, von Bertalanffy, catch curves, *Micropterus* spp.

Journal of the Southeastern Association of Fish and Wildlife Agencies 9: 30–38

Black bass (*Micropterus* spp.) are the most popular freshwater sportfishes in North America (Siepker et al. 2007). As such, these species are intensively managed by many natural resource agencies. Managing black bass populations requires accurate and precise age information for estimation of population rate functions (growth, mortality, and recruitment). Otoliths are well established as the most accurate and precise aging structure for black bass (Heidinger and Clodfelter 1987, Long and Fisher 2001, Buckmeier and Howells 2003, Klein et al. 2017, Phelps et al. 2017, Tyszko and Pritt 2017). Otoliths have also been validated to provide accurate age estimation for largemouth bass (*Micropterus salmoides*; Hoyer et al. 1985, Buckmeier and Howells 2003) and smallmouth bass (*Micropterus dolomieu*; Heidinger and Clodfelter 1987). Use of otoliths requires the sacrifice of fish, and sometimes this may be undesirable due to angler concerns or when managing sensitive or trophy populations (Morehouse et al. 2013, Rude et al. 2013, Porta et al. 2017). In these cases, use of a non-lethal aging method may be justified.

A variety of structures that can be collected non-lethally, including anal fin spines, dorsal fin spines, and scales, have been used for age estimation of black bass, but these structures tend to be less precise when compared to otoliths (Long and Fisher 2001, Maceina and Sammons 2006, Maceina et al. 2007, Rude et al. 2013, Sotola et al. 2014, Klein et al. 2017, Tyzsco and Pritt 2017). Non-lethal structures typically overestimate ages of younger fish and underestimate ages of older fish which can lead to inaccurate population parameters and incorrect management decisions (Porta et al. 2017, Starks and Rodger 2020). For example, age estimates from scales produced von Bertalanffy growth parameter estimates that differed significantly from those using otolith age

1. E-mail: austin.griffin@odwc.ok.gov

estimates for largemouth bass populations in Ohio (Tyszko and Pritt 2017). Despite these known biases, biologists continue to evaluate non-lethal aging structures as an alternative to otoliths for aging black bass, likely hoping to find a non-lethal approach to attain age estimates comparable to those produced by otoliths (e.g., Long et al. 2018, Lindelien et al. 2021). Therefore, the objectives of this study were to 1) evaluate age estimate precision between two readers and among structures for sectioned otoliths, dorsal fin spines, anal fin spines, pectoral fin rays, and scales, and 2) compare growth and mortality parameters derived using each aging method for largemouth bass, spotted bass (*Micropterus punctulatus*), and smallmouth bass in Oklahoma.

Methods

Largemouth bass and spotted bass were collected from Thunderbird Reservoir, Oklahoma, during April 2016. Smallmouth bass were collected at night from Tenkiller Ferry Reservoir during October 2016. All fish were collected using boat electrofishing (pulsed DC, high voltage, 7.5 GPP, Smith Root, Vancouver, Washington) following Oklahoma Department of Wildlife Conservation (ODWC) standardized sampling protocols. Electrofishing sites were randomly selected to ensure that all available habitat types were surveyed to reduce potential biases in size or age for each species.

Each fish was identified and measured for TL (mm) and weight (g). To ensure all age classes were represented, we attempted to collect at least 10 fish per 25 mm TL group for each species. Each fish collected was euthanized using a 1:1 ice water slurry (Blessing et al. 2010) and returned to the lab where sagittal otoliths, dorsal fin spines, anal fin spines, pectoral fin rays, and scales were removed from each fish. Scales were collected from below the lateral line between the pectoral and pelvic fins. Anal spines, dorsal spines, and pectoral rays were removed by cutting as close to the skin as possible using diagonal cutting pliers (i.e., side cutters; Logsdon 2007, Porta et al. 2017). Once removed, all structures were dried for more than 24 h before processing. One otolith from each fish was sectioned in the transverse plane and processed using the methodology of Buckmeier and Howells (2003). Anal spines and dorsal spines were processed using methods of Logsdon (2007). The third pectoral ray from each fish was embedded in epoxy (West System 205-B hardener and 105-B Epoxy resin, Gougeon Brothers Inc., Bay City, Michigan), and processed following the methodology of Koch and Quist (2007) and Morehouse et al. (2013). Five scales per fish were placed between two microscope slides, pressed, and secured with transparent tape prior to age estimation (Long et al. 2018).

Following processing, samples were read in random order by two readers. One reader had extensive experience reading all structure types while the other had previous experience reading otoliths, dorsal spines, and scales. Procedures to read anal spines and pectoral rays are similar to those used for dorsal spines (Fischer and Koch 2017), thus the second reader was considered to be competent to read these structures. Readers had no knowledge of the species, size, or sex of an individual fish or the other reader's age estimates. Anal spines, dorsal spines, and pectoral rays were placed polished side up in a dish containing black modeling clay and a drop of immersion oil was applied to the polished end to improve clarity. Otoliths were placed polished side up in a dish containing black modeling clay and submerged in water. Anal spines, dorsal spines, pectoral rays, and otoliths were viewed with a variable-power Olympus SZX16 stereomicroscope capable of 130× magnification (Olympus Corporation, Lake Success, New York) using a fiber-optic filament attached to an external light source to illuminate annuli. Scales were viewed using a monitor connected to an Olympus DP74 digital camera mounted to the stereomicroscope. If the readers disagreed on the age from a structure, then that structure was read again in concert by both readers until an agreement was made (Hoff et al. 1997). After calculating between-reader precision for each structure, if a structure was deemed unreadable, all structures from that fish were removed from further analysis.

To evaluate between-reader precision between aging structures we used percent reader agreement (Campana et al. 1995), average percent error (APE; Beamish and Fournier 1981), and CV (Chang 1982). Age-bias plots were created to assess consistency between aging structures and readers (Campana et al. 1995).

Growth of each species was described with von Bertalanffy growth models using age estimates from each structure and models were compared with a likelihood ratio test (Kimura 1980, Ogle 2016, Nelson 2019). Weighted catch curves were used to estimate instantaneous mortality (Z) of each species derived using estimated ages from each of the five structures. Total annual mortality (A) was calculated as $1–e^{-Z}$ (Ricker 1975). Growth and mortality analyses were calculated using the Fisheries Stock Analysis R package (Ogle 2017) within the Oklahoma Fisheries Analysis App (Oklahoma Fishery Analysis Application 2018) and the Fishery Science Methods and Models R package (Nelson 2019). Slopes of the catch curves (Z) were compared among structures using ANCOVA in XLSTAT (Addinsoft Inc., New York City, New York). All statistical results were considered significant at $P < 0.05$.

Results

Totals of 122 largemouth bass (119–525 mm TL), 86 spotted bass (90–435 mm TL), and 113 smallmouth bass (89–507 mm TL) were collected for age estimation. Anal spines from three largemouth bass, otoliths from one spotted bass, and pectoral rays from one smallmouth bass could not be read; otherwise, ages were estimated from all other fish using each structure (Table 1). Age estimates for largemouth bass ranged 0–7 years for otoliths and anal spines, 1–8 years for dorsal spines, 0–5 years for pectoral rays, and 0–8 years for scales. Age estimates for spotted bass ranged 0–6 years for otoliths and scales, 0–5 years for dorsal spines and pectoral rays, and 0–8 years for anal spines. Age estimates for smallmouth bass ranged 0–8 years for otoliths and anal spines, 0–7 years for dorsal spines and scales, and 0–6 years for pectoral rays.

Readers agreed on largemouth bass ages 97.5% of the time when using otoliths, about twice as often than when using all other structures other than dorsal spines, for which between-reader agreement was 77% (Table 1). Between-reader agreement was more similar among structures for the other two species, but agreement for otoliths was always 30%–40% higher than the non-lethal structures. Likewise, APE for otoliths ranged 0.44–1.41 across species, and was 13–30, 6–14, and 10–22 times higher for other structures for largemouth bass, spotted bass, and smallmouth bass, respectively (Table 1). Mean CV displayed similar trends among structures and species as the other measures of variability.

Due to high between-reader precision for otolith age estimates, visual inspection of age-bias plots suggested no bias between readers across age classes for all three species (Figure 1). Readers were more likely to underestimate dorsal spine ages for largemouth bass once consensus age was ≥5 years, but this was less likely in the other two species. Anal spine ages showed a similar pattern for largemouth bass and spotted bass, but not smallmouth bass (Figure 1). Aging using pectoral rays of largemouth bass was more precise between readers than any of the other three non-lethal structures, but no fish older than age 5 was detected using this structure. A similar pattern was observed for the other species, although pectoral rays appeared to overestimate ages of young spotted bass (Figure 1). Readers were more likely to underestimate ages from scales once ages reached 5 years for all three species; in addition, readers tended to overestimate ages of young fish using this structure.

Agreement between final otolith consensus age and the four non-lethal structures ranged 13%–40% for largemouth bass, 35%–59% for spotted bass, and 28%–50% for smallmouth bass (Table 2). In all cases, percent agreement for a particular structure was noticeably lower for largemouth bass than the other two species. A similar pattern was observed for APE (Table 2). Within species, pectoral rays always had the highest percent agreement and anal spines the lowest. Similarly, anal spines always had the highest APE within species, but the lowest APE varied among the other three non-lethal structures for each species (Table 2).

Age-bias plots for largemouth bass showed high variability between final consensus age estimates from otoliths and those from all non-lethal structures (Figure 2). For spotted bass, the age-bias plots showed a similar pattern to largemouth bass but only for dorsal spines and scales. Anal spines always overestimated ages compared to otoliths, whereas pectoral-ray ages were comparable to those from otoliths up to age 4 but underestimated ages of older fish (Figure 2). The oldest smallmouth bass (age 8) was always underestimated by all non-lethal structures, but ages of younger fish were overestimated by dorsal spines, anal spines, and scales. However, similar to spotted bass, pectoral-ray ages were comparable to otolith ages for fish up to age 4 (Figure 2).

Von Bertalanffy growth models using otolith ages predicted larger L_∞ for largemouth bass ($L_\infty = 572$) than all other structures

Table 1. Sample size (*n*), percent reader agreement, average percent error (APE), and mean CV for ages estimated by two readers using five aging structures for three species of black bass collected from two Oklahoma reservoirs.

Species	Aging structure	*n*	% Agreement	APE	Mean CV (%)
Largemouth bass	Otolith	122	97.5	0.44	0.01
	Dorsal spine	122	77.1	7.75	10.96
	Anal spine	119	52.1	10.54	14.90
	Pectoral ray	122	59.8	13.21	18.68
	Scale	122	59.8	10.31	14.58
Spotted bass	Otolith	85	97.7	1.41	2.00
	Dorsal spine	86	65.1	15.86	22.43
	Anal spine	86	58.1	11.92	16.85
	Pectoral ray	86	67.4	8.50	12.03
	Scale	86	62.8	13.54	19.15
Smallmouth bass	Otolith	113	98.2	0.59	0.83
	Dorsal spine	113	78.8	6.29	8.90
	Anal spine	113	63.7	11.37	16.08
	Pectoral ray	112	67.0	10.57	14.81
	Scale	113	63.7	12.91	18.25

Table 2. Percent reader agreement and average percent error (APE) for final consensus age estimates from otoliths compared to consensus ages from four non-lethal structures for three species of black bass collected from two Oklahoma reservoirs.

Species	Aging structure	*n*	% Agreement	APE
Largemouth bass	Dorsal spine	119	29.8	32.25
	Anal spine	119	13.2	40.08
	Pectoral ray	119	39.7	21.37
	Scale	119	26.1	27.27
Spotted bass	Dorsal spine	85	57.0	17.27
	Anal spine	85	34.9	26.44
	Pectoral ray	85	59.3	16.30
	Scale	85	53.5	14.65
Smallmouth bass	Dorsal spine	112	49.6	17.32
	Anal spine	112	28.3	27.65
	Pectoral ray	112	50.4	20.50
	Scale	112	48.7	17.52

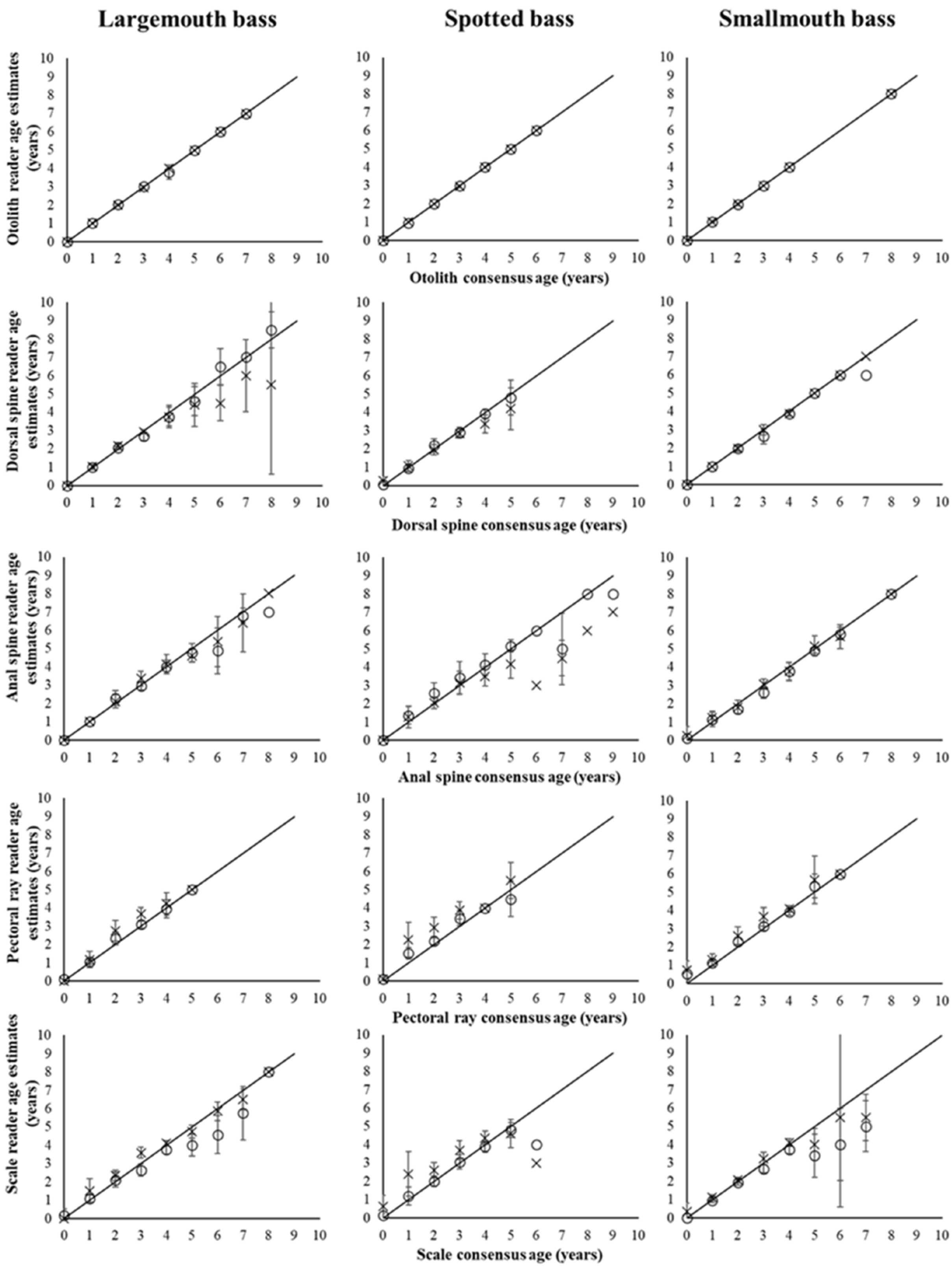

Figure 1. Age-bias plots comparing largemouth bass, spotted bass, and smallmouth bass age estimates from otoliths, dorsal fin spines, anal fin spines, pectoral fin rays, and scales to final consensus age estimates for fish collected from two Oklahoma reservoirs. Error bars represent the 95% confidence interval. The diagonal line represents 100% agreement between consensus and reader 1 (○) and reader 2 (×) age estimates.

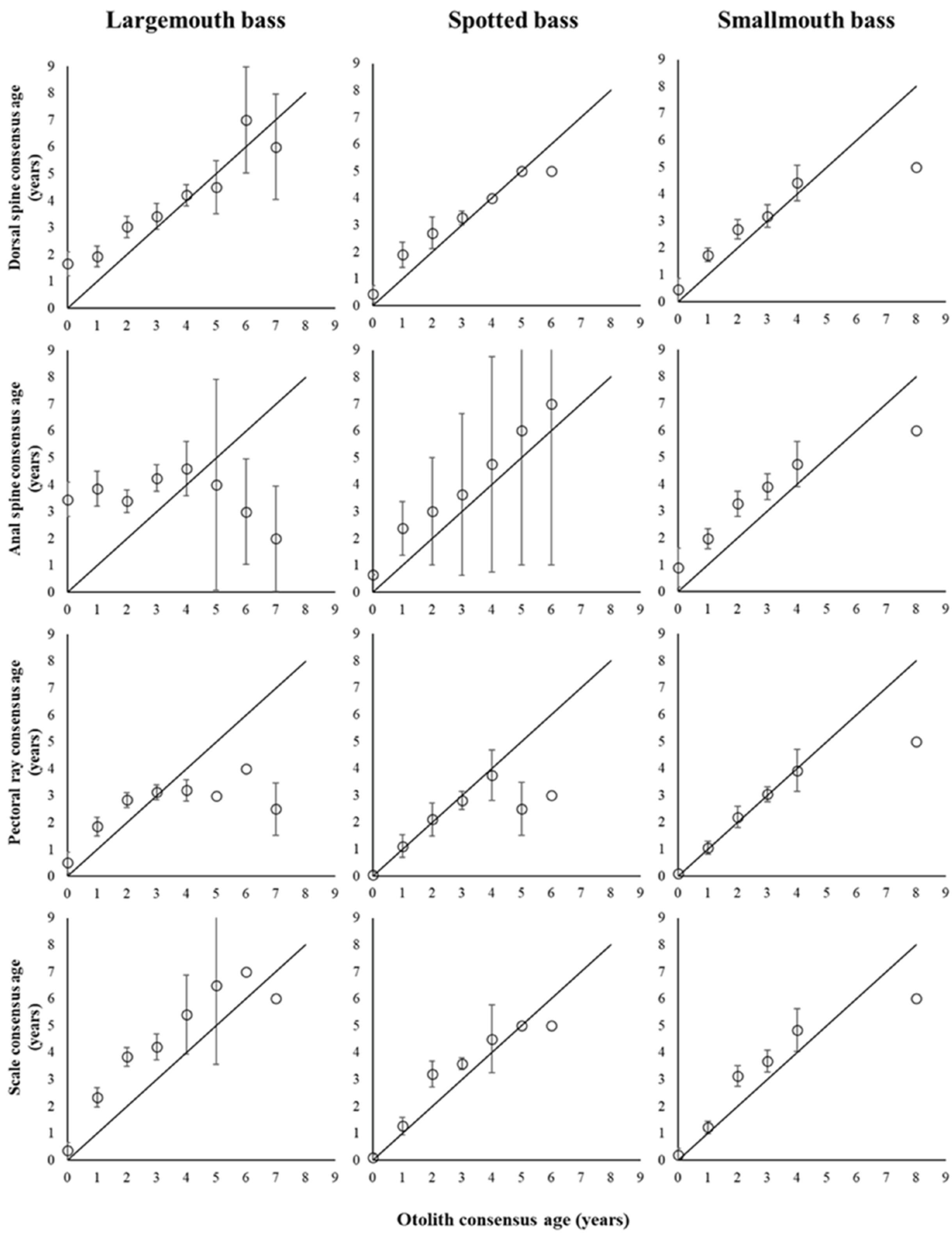

Figure 2. Age-bias plots comparing final consensus age estimates from otoliths to final consensus age estimates from dorsal fin spines, anal fin spines, pectoral fin rays, and scales for largemouth bass, spotted bass, and smallmouth bass collected from two Oklahoma reservoirs. Error bars represent the 95% confidence interval. The diagonal line represents 100% agreement between sectioned otoliths and each of the other aging structures.

($L_\infty = 437–498$), along with associated changes in k and t_0 (Table 3). As a result, von Bertalanffy models differed significantly between growth models derived using otolith ages and those derived using non-lethal structures. Conversely, von Bertalanffy models derived using otolith ages for spotted bass produced a L_∞ that was intermediate to those derived using non-lethal structures (Table 3). Dorsal spine and scale data produced von Bertalanffy models with estimated L_∞ that far exceeded reasonable maximum lengths for this species (>600 mm TL), whereas the other two non-lethal structures produced von Bertalanffy models with estimated L_∞ smaller than fish collected during this study. Not surprisingly, all von Bertalanffy models derived from non-lethal structure ages were different from the one derived using otolith ages (Table 3). A similar pattern was observed for smallmouth bass with otolith data producing the most reasonable von Bertalanffy model; whereas the pectoral ray model produced unreasonable estimates of all model parameters and the dorsal spine and anal spine age data derived von Bertalanffy models with L_∞ that were smaller than fish collected during this study. All non-lethal structure models were different from the otolith model (Table 3).

Less difference was observed among age structures in the catch-curve analyses; however, noticeable differences still occurred. All non-lethal structures underestimated the number of age 0 fish for largemouth bass and additional ages were assigned using dorsal spines, anal spines, and scales when compared with otolith aged fish (Table 4). Similarly, non-lethal structure age estimates resulted in at least one additional age class represented when compared to otoliths for spotted and smallmouth bass (Table 4). Estimates of A ranged 0.40–0.60 for largemouth bass, 0.24–0.38 for spotted bass, and 0.28–0.47 for smallmouth bass (Table 4). The estimate of A derived from otolith data was intermediate to those derived from the four non-lethal structures for largemouth bass and smallmouth bass but not for spotted bass. However, slopes of the catch curve (i.e., Z) were similar between otolith and non-lethal-structure data for all species-structure combinations except for otoliths and anal spines for largemouth bass (Table 4).

Table 3. von Bertalanffy growth parameters for ages estimated using five aging structures for three species of black bass collected from two Oklahoma reservoirs. Likelihood ratio tests compared otolith growth parameters with parameters from four non-lethal structures.

		Growth parameters			Likelihood ratio test		
Species	**Aging structure**	L_∞	K	t_0	X^2	**df**	P
Largemouth bass	Otolith	572	0.32	–1.00			
	Dorsal spine	474	0.44	–0.14	22.68	3	< 0.001
	Anal spine	437	0.41	–0.09	20.10	3	< 0.001
	Pectoral ray	498	0.34	–0.96	17.59	3	0.001
	Scale	463	0.21	–1.36	43.23	3	< 0.001
Spotted bass	Otolith	480	0.34	–0.79			
	Dorsal spine	619	0.17	–1.29	19.23	3	< 0.001
	Anal spine	419	0.31	–0.74	18.82	3	< 0.001
	Pectoral ray	364	0.68	–0.62	25.70	3	< 0.001
	Scale	642	0.14	–1.47	20.76	3	< 0.001
Smallmouth bass	Otolith	563	0.26	–0.89			
	Dorsal spine	482	0.30	–0.96	17.37	3	0.001
	Anal spine	390	0.38	–1.07	34.11	3	< 0.001
	Pectoral ray	911	0.10	–2.03	15.21	3	0.002
	Scale	551	0.22	–1.31	18.69	3	< 0.001

Table 4. Age structure data, instantaneous mortality (Z) and total annual mortality (A) calculated using five aging structures for three species of black bass collected from two Oklahoma reservoirs. ANCOVA compared the slope of the catch-curves (Z) calculated using otoliths to those from four non-lethal structures.

		Ages									Catch-curve results		
Species	**Aging structure**	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	Z	A	**ANCOVA results**
Largemouth bass	Otolith	22	25	38	25	5	2	0	2	0	0.571	0.43	
	Dorsal spine	0	22	28	44	18	2	2	0	3	0.510	0.40	$F = 0.83, P = 0.392$
	Anal spine	1	4	16	48	29	14	4	3	0	0.684	0.50	$F = 10.20, P = 0.015$
	Pectoral ray	14	14	30	42	18	1	0	0	0	0.916	0.60	$F = 0.02, P = 0.887$
	Scale	13	14	16	20	38	6	5	5	2	0.528	0.41	$F = 4.15, P = 0.076$
Spotted bass	Otolith	21	20	11	29	0	3	1	0	0	0.472	0.38	
	Dorsal spine	18	12	18	21	15	1	0	0	0	0.392	0.32	$F = 0.01, P = 0.943$
	Anal spine	10	10	23	14	19	8	0	0	1	0.415	0.34	$F = 3.39, P = 0.108$
	Pectoral ray	26	12	13	27	6	1	0	0	0	0.444	0.36	$F = 0.12, P = 0.739$
	Scale	23	10	10	14	21	6	1	0	0	0.271	0.24	$F = 0.01, P = 0.925$
Smallmouth bass	Otolith	11	41	26	22	11	0	0	0	1	0.438	0.35	
	Dorsal spine	7	23	35	22	18	4	2	1	0	0.627	0.47	$F = 0.04, P = 0.840$
	Anal spine	8	21	16	28	20	12	6	0	1	0.333	0.28	$F = 0.02, P = 0.893$
	Pectoral ray	21	26	26	23	11	3	2	0	0	0.501	0.39	$F = 2.26, P = 0.171$
	Scale	14	27	15	27	18	5	2	4	0	0.360	0.30	$F = 0.22, P = 0.654$

Discussion

We found that age estimates from otoliths were more precise than ages estimated using the four non-lethal aging structures for the three black bass species evaluated in this study. Previous studies also found that anal spines and dorsal spines produced imprecise age estimates compared to otoliths for largemouth bass and smallmouth bass, typically overestimating ages of younger fish and underestimating ages of older fish (Sotola et al. 2014, Klein et al. 2017). We observed similar biases in most cases; however, age estimates from pectoral rays were similar to otoliths for smallmouth bass and spotted bass to age 4. Similarly, Rude et al. (2013) found that pectoral rays provide an adequate non-lethal option for estimating ages of young smallmouth bass (age ≤4). Scale-derived age estimates lacked precision compared to otoliths, generally overestimating ages of younger fish and underestimating ages of older fish, which is consistent with previous studies that compared aging precision between otoliths and scales (Long and Fisher 2001, Maceina and Sammons 2006, Sotola et al. 2014, Tyszko and Pritt 2017). Age estimates from non-lethal structures were unreliable for the black bass populations evaluated in this study; however, otoliths provided a precise and consistent aging method for these species.

Aging precision was high using otoliths in this study, but we did not use known-age fish, so accuracy was unknown. However, aging with otoliths is usually considered more precise and accurate when compared to that using scales and spines, particularly in southern latitudes (Phelps et al. 2017). Further, aging with otoliths has been validated using known-age fish for largemouth bass and smallmouth bass (Heidinger and Clodfelter 1987, Buckmeier and Howells 2003).

Variability in final consensus ages between otoliths and the four non-lethal structures resulted in significant differences in age-based growth parameters. Further, estimated annual mortality rates varied among structures, but this variability did not produce catch curves with different slopes. Differences in age estimates and the resulting estimates of population dynamics have been previously documented. Tyszko and Pritt (2017) found age estimates from scales produced von Bertalanffy growth parameter estimates that differed from those derived using otolith age estimates for largemouth bass populations in Ohio. Similarly, Starks and Rodger (2020) demonstrated differences in growth models produced using age estimates from otoliths and scales of smallmouth bass; these differences resulted in the need to calculate separate growth standards for smallmouth bass aged using otoliths and scales. Fisheries managers should use otoliths to age fish whenever possible to provide the best accuracy and precision.

We found that the non-lethal aging structures evaluated in this study are not acceptable alternatives to otoliths for aging largemouth bass, spotted bass, or smallmouth bass in Oklahoma. Thus, fish need to be sacrificed for otoliths to achieve precise age estimates and accurate population metrics. Concerns about any population-level effects of this practice are almost certainly untenable. Although the high incidence of voluntary catch-and-release practices by black bass anglers likely results in low fishing mortality rates for these populations (Myers et al. 2008, Isermann et al. 2013, Chapagain et al. 2021), natural mortality rates of black bass in southern reservoirs commonly range 15%–30% annually (Beamesderfer and North 1995, Allen et al. 2008, Hakala and Sammons 2015, Sammons et al. 2019). It is highly unlikely that sacrificing fish every few years for an adequate age sample could impact the population, as a robust sample (i.e., 500 fish) would not remove even 1% of the population. Fisheries managers are often concerned about killing large black bass for collection of otoliths which is why managers often select a non-lethal aging approach. However, the traditional electrofishing methods employed by most fisheries managers to sample black bass are often ineffective at capturing an adequate sample size of trophy-sized fish (Hall et al. 2019). Therefore, it is equally unlikely that an age sample of black bass collected using electrofishing will impact the trophy component of these fisheries.

Our results and those of previous studies suggest otoliths are the most appropriate aging structure for most species. Non-lethal structures are not trustworthy for aging purposes and should not be used to estimate population rate functions for these species. If non-lethal structures are the only option available (e.g., because of low abundance or conservation concerns), fisheries managers should be aware that aging inconsistencies associated with these structures could likely affect age-based population metrics and result in inappropriate management decisions (Branigan et al. 2019). Further, this study can be used to advise managers and stakeholders alike that concern over the sacrifice of fish is unwarranted and that sacrificing fish to obtain otoliths is imperative to the process of making informed management decisions.

Acknowledgments

The authors thank Shelby Jeter, Jory Bartnicki, Jon West, Ian Campbell, Micah Waters, Matthew Lyons, and Alexis Whiles for assisting with field and laboratory work. We thank Dr. Daniel Shoup (Oklahoma State University) for assisting with statistical methods. Financial support for this publication was provided by Sport Fish Restoration Program grants [F-86-D-1] and [F-112-D-1] to the Oklahoma Department of Wildlife Conservation.

Literature Cited

Allen, M. S., C. J. Walters, and R. Myers. 2008. Temporal trends in largemouth bass mortality, with fishery implications. North American Journal of Fisheries Management 28:418–427.

Beamish, R. J. and D. A. Fournier. 1981. A method for comparing the precision of a set of age determinations. Canadian Journal of Fisheries and Aquatic Sciences 38:982–983.

Beamesderfer, R. C. P. and J. A. North. 1995. Growth, natural mortality, and predicted response to fishing for largemouth bass and smallmouth bass populations in North America. North American Journal of Fisheries Management 15:688–704.

Blessing, J. J., J. C. Marshall, and S. R. Balcombe. 2010. Humane killing of fish for scientific research: a comparison of two methods. Journal of Fish Biology 76:2571–2577.

Branigan, P. R., K. A. Meyer, N. C. Wahl, M. P. Corsi, and A. M. Dux. 2019. Accuracy and precision of age estimates obtained from three calcified structures for known-age kokanee. North American Journal of Fisheries Management 39:498–508.

Buckmeier, D. L. and R. G. Howells. 2003. Validation of otoliths for estimating ages of largemouth bass to 16 years. North American Journal of Fisheries Management 23:590–593.

Campana, S. E., M. C. Ann, and J. I. McMillan. 1995. Graphical and statistical methods for determining the consistency of age determinations. Transactions of the American Fisheries Society 124:131–138.

Chang, W. Y. 1982. A statistical method for evaluating the reproducibility of age determination. Canadian Journal of Fisheries and Aquatic Sciences 39:1208–1210.

Chapagain, B. P., J. M. Long, A. T. Taylor, and O. Joshi. 2021. Variation in black bass angler characteristics by stream size and accessibility in Oklahoma's Ozark highland streams. North American Journal of Fisheries Management. DOI: 10.1002/nafm.10565.

Fischer, J. R. and J. D. Koch. 2017. Fin rays and spines. Pages 173–187 *in* M. C. Quist and D. A. Isermann, editors. Age and growth of fishes: principles and techniques. American Fisheries Society, Bethesda, Maryland.

Hakala, J. P. and S. M. Sammons. 2015. Exploitation and length-limit evaluation of Alabama bass in a south-eastern USA reservoir. Fisheries Management and Ecology 22:518–529.

Hall, E. P., T. F. Bonvechio, S. L. Shaw, M. S. Allen, and L. Pugh. 2019. Using specialized angling to assess a trophy Florida bass fishery at Calling Panther Lake, Mississippi. North American Journal of Fisheries Management 39:589–595.

Heidinger, R. C. and K. Clodfelter. 1987. Validity of the otolith for determining age and growth of walleye, striped bass, and smallmouth bass in power cooling ponds. Pages 241–251 *in* R. C. Summerfelt and G. E. Hall, editors. Age and growth of fish. Iowa State University Press, Ames, Iowa.

Hoff, G. R., D. J. Logan, and D. G. Markle. 1997. Otolith morphology and increment validation in young Lost River and shortnose suckers. Transactions of the American Fisheries Society 126:488–494.

Hoyer, M. V., J. V. Shireman, and M. J. Maceina. 1985. Use of otoliths to determine age and growth of largemouth bass in Florida. Transactions of the American Fisheries Society 114:307–309.

Isermann, D. A., J. B. Maxwell, and M. C. McInerny. 2013. Temporal and regional trends in black bass release rates in Minnesota. North American Journal of Fisheries Management 33:344–350.

Kimura, D. K. 1980. Likelihood methods for the von Bertalanffy growth curve. Fishery Bulletin 77:764–776.

Klein, Z. B., T. F. Bonvechio, B. R. Bowen, and M. C. Quist. 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.

Koch, J. D. and M. C. Quist. 2007. A technique for preparing fin rays and spines for age and growth analysis. North American Journal of Fisheries Management 27:782–784.

Lindelien, S., A. C. Dutterer, P. Schueller, and C. C. Anderson. 2021. Evidence dorsal spine removal is nonlethal and unharmful for largemouth bass in Florida. Journal of Fish and Wildlife Management 12:190–196.

Logsdon, D. E. 2007. Use of unsectioned dorsal spines for estimating walleye age. North American Journal of Fisheries Management 27:1112–1118.

Long, J. M. and W. L. Fisher. 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.

_____, C. T. Holley, and A. T. Taylor. 2018. Evaluation of ageing accuracy with complementary non-lethal methods for slow growing, northern populations of shoal bass. Fisheries Management and Ecology 25:150–157.

Maceina, M. J., J. Boxrucker, D. L. Buckmeier, R. S. Gangl, D. O. Lucchesi, D. A. Isermann, J. R. Jackson, and P. J. Martinez. 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.

_____ and S. M. Sammons. 2006. An evaluation of different structures to age freshwater fish from a northeastern US river. Fisheries Management and Ecology 13:237–242.

Morehouse, R. L., S. B. Donabauer, and A. C. Grier. 2013. Estimating largemouth bass age: precision and comparisons among scales, pectoral fin rays, and dorsal fin spines as non-lethal methods. Fisheries and Aquaculture Journal 2013:1–7.

Myers, R. A., J. Taylor, M. S. Allen, and T. F. Bonvechio. 2008. Temporal trend in voluntary release of largemouth bass *Micropeterus salmoides*. North American Journal of Fisheries Management 28:428–433.

Nelson, G. A. 2019. fishmethods: fishery science methods and models. R Package version 1.11-1.

Oklahoma Fishery Analysis Application. 2018. Oklahoma fishery analysis application: an R-based application for analysis of standardized fishery samples. Oklahoma Department of Wildlife Conservation. <https://www.odwcfishdata.shinyapps.io/ssp_app/>. Accessed 20 May 2021.

Ogle, D. H. 2016. Introductory fisheries analysis with R. CRC Press, Boca Raton, Florida.

_____. 2017. FSA: Fisheries Stock Analysis. R Package version 0.8.17.

Phelps, Q. E., S. J. Tripp, M. J. Hammel, R. P. Koenigs, and Z. J. Jackson. 2017. Choice of structure for estimating fish age and growth. Pages 81–105 *in* M. C. Quist and D. A. Isermann, editors. Age and growth of fishes: principles and techniques. American Fisheries Society, Bethesda, Maryland.

Porta, M. J., R. A. Snow, and D. E. Shoup. 2017. Comparison of saugeye age estimates and population characteristics using otoliths and dorsal spines. Journal of the Southeastern Association of Fish and Wildlife Agencies 5:23–29.

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

Rude, N. P., W. D. Hintz, J. D. Norman, K. L. Kanczuzewski, A. J. Yung, K. D. Hofer, and G. W. Whitledge. 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.

Sammons, S. M., T. R. Ingram, and J. M. Kilpatrick. 2019. Population and life history characteristics of two *Micropterus* species in the Flint River System, Georgia. Pages 167–192 *in* M. J. Siepker and J. W. Quinn, editors. Managing centrarchid fisheries in rivers and streams. American Fisheries Society, Bethesda, Maryland.

Siepker, M. J., K. G. Ostrand, S. J. Cooke, D. P. Philipp, and D. H. Wahl. 2007. A review of the effects of catch-and-release angling on black bass, *Micropterus* spp.: implications for conservation and management of populations. Fisheries Management and Ecology 14:91–101.

Sotola, V.A., G.A. Maynard, E.M. Hayes-Pontius, T.B. Mihuc, M.H. Malchoff, and J.E. Marsden. 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.

Starks, T.A. and A.W. Rodger. 2020. Otolith and scale-based growth standards for lotic smallmouth bass. North American Journal of Fisheries Management 40:986–994.

Tyszko, S.M. and J.J. Pritt. 2017. Comparing otoliths and scales as structures used to estimate ages of largemouth bass: consequences of biased age estimates. North American Journal of Fisheries Management 37:1075–1082.