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MANAGEMENT BRIEF

Comparing Otoliths and Scales as Structures Used to Estimate Ages of Largemouth Bass: Consequences of Biased Age Estimates

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Abstract
Management agencies often estimate the ages of Largemouth Bass *Micropterus salmoides* based on the examination of scales—a structure that is known to produce biased estimates—without knowing how the associated bias affects management decisions. We sought to understand the effects of this bias by comparing population metrics that were predicted using scale-derived and otolith-derived age data. We collected scales and otoliths from Largemouth Bass that were sampled during standard electrofishing surveys. The age of each fish was estimated independently by three separate readers using both scales and otoliths. We assessed the average coefficient of variation for scale-derived and otolith-derived age estimates, examined the bias of scale-derived age estimates, and estimated von Bertalanffy growth model parameters by using ages estimated from scales and otoliths. These parameter estimates were used in yield-per-recruit simulations that predicted yield and the percentage of individuals in the cohort surviving to 380 mm (proportional size distribution [PSD] 380) or to 470 mm (PSD 470) at several levels of natural mortality and fishing mortality. Otolith-derived age estimates were more precise; scale-derived age estimates showed significant positive bias for fish younger than age 6 and significant negative bias for fish older than age 6. Von Bertalanffy parameter estimates were significantly different when using ages estimated from scales and those estimated from otoliths. Modeling indicated that estimates of yield and PSD 380 resulting from the two structures were similar. However, the use of scale-derived ages resulted in underestimating the impact of fishing mortality on PSD 470 by as much as five times at low levels of natural mortality and fishing mortality. Our estimates of precision and bias were similar to other comparisons of scales and otoliths, and the results of our yield-per-recruit simulations are likely generally applicable for Largemouth Bass management. Trophy fishing is a common management objective, and managers relying on scale-based age data could be less likely to adopt the restrictive harvest regulations that are critical for producing trophy Largemouth Bass.

Estimating the ages of fish can be difficult and often includes substantial error and bias depending on the structure and method used (Tyler et al. 1989). Error and bias in age estimates can result in biased population parameter estimates that misinform management decisions (Beamish and McFarlane 1987). Underestimation of age may lead to the overestimation of growth and mortality and to excessively liberal management strategies and overfishing (Beamish and McFarlane 1987; Lai and Gunderson 1987). Overestimation of age is less common and generally results in overly conservative management (Lai and Gunderson 1987), although Bertignac and de Pontual (2007) found that a stock of European Hake *Merluccius merluccius* was more sensitive to fishing mortality than previously thought because age had been systematically overestimated. Unbiased age estimates provide information for managers to develop strategies that allow full use of stocks while decreasing the likelihood of overfishing.

Although biased age estimates have incurred serious management consequences in large-scale marine fisheries, accurate age information is increasingly important for managing valuable inland recreational fisheries. In many data-poor freshwater fisheries, models that rely on age and growth information, such as yield-per-recruit models (e.g., Maceina et al. 1998; Eder et al. 2016), are widely used to guide length-based management and are easily implemented in fisheries analysis software (e.g., Fisheries Analysis and Modeling Simulator [FAMS]: Slipke and Maceina 2014). Given the availability of these models to inform managers of inland recreational fisheries, it is important to evaluate age data and understand the management consequences of using biased age estimates.

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Scales have historically been the most common structure used to estimate age of Largemouth Bass *Micropterus salmoides* (Quist et al. 2012) because they allow for age estimation without sacrificing the fish. However, age estimates from otoliths are more precise among readers than age estimates from scales (Besler 2001; Long and Fisher 2001), and otoliths have been demonstrated as a valid structure for estimating Largemouth Bass ages (Taubert and Tranquilli 1982; Hoyer et al. 1985) up to 16 years (Buckmeier and Howells 2003). Furthermore, Maceina and Sammons (2006) found that Largemouth Bass ages estimated from scales were greater than the ages estimated from otoliths for age-9 and younger fish but were lower than otolith ages for age-11 and older fish. Biased age information like this would likely result in biased population parameter estimates and erroneous management recommendations. In particular, negative bias in estimating ages of the oldest fish could have serious negative consequences for the management of trophy fisheries—an important goal in many Largemouth Bass fisheries (e.g., Crawford et al. 2002; Wilson and Dicenzo 2002). Despite this, Maceina et al. (2007) found that scales were the most common structure used to age black bass *Micropterus* spp. as recently as 2006, although only 27% of survey respondents believed that scales provided accurate age estimates.

Before 2013, the Ohio Division of Wildlife (ODOW) employed scales when estimating the ages of Largemouth Bass, and only ages up to 3 years were estimated due to low confidence in age estimates derived from scales (Burt 2011). We examined how the choice of otoliths or scales for age estimation could impact management decisions by comparing (1) von Bertalanffy growth model parameters and (2) predicted yield and size structure between the two structures. We assessed bias and precision of our age estimates and conducted comparisons with findings from other studies to evaluate the broad applicability of our results.

METHODS

Personnel of the ODOW conducted standard Largemouth Bass surveys at 11 reservoirs during spring 2013 and at 11 reservoirs during spring 2014. Five of the 11 reservoirs sampled in 2013 were also sampled during 2014, resulting in a total of 22 samples from 17 total reservoirs. The TL of each fish was measured (nearest 1 mm), and sagittal otoliths and scales were collected from a subsample of three fish per 10-mm length class and stored dry. Scales were collected from an area posterior to the tip of the depressed pectoral fin and below the lateral line. Ages were estimated from scales with the existing approach used by ODOW, wherein annuli are either counted directly from scales or from impressions of scales in acetate strips under 10–40× magnification with a dissecting microscope. The edge of the scale was counted as an annulus. Otoliths were heated on a hotplate at a medium setting until they turned dark brown (≈30 s) and were broken near the nucleus. The broken surface was smoothed with 600-grit sandpaper if necessary, and the otolith was inserted into modeling clay so that the broken surface was facing up. The broken surface was covered with glycerin, light was applied to the side of the otolith, and annuli were counted under a dissecting microscope at 10–40× magnification. Annuli were counted along an axis running from the nucleus to the medial surface just ventral to the sulcus. The otolith edge was also counted as an annulus. Ages were estimated with scales and otoliths for all ages of Largemouth Bass.

For each fish, three independent age estimates from scales and three independent age estimates from otoliths were generated. Readers had no knowledge of the age estimates produced by other readers, the ages estimated from the other structure (scale or otolith), or the fish length and weight. In total, 15 different readers estimated ages from both scales and otoliths of Largemouth Bass collected in 2013; ages from scales and otoliths of fish collected in 2014 were estimated by 14 readers, consisting of 13 readers who had examined the 2013 samples as well as one new reader. One of the readers (S. M. Tyszko) aged all scales and otoliths collected during this study; the remaining readers estimated the ages of Largemouth Bass sampled from the reservoirs within their respective management districts. Before this study, three of these readers had received training on estimating ages from otoliths using the method described above but had not used that method to estimate ages of Largemouth Bass. None of the other readers had previous experience in estimating ages with the otolith method. All readers received written and verbal instructions for estimating otolith age. Between 2013 and 2014 sampling, an otolith aging workshop was hosted to improve the precision and accuracy of age estimation by all readers. Experience with scales was variable among readers, but all readers had some basic experience in reading scales.

We used the Fisheries Stock Analysis (FSA) package version 0.7.7 (Ogle 2015) in R version 3.1.2 (R Core Team 2015) to compute the average coefficient of variation (ACV) among readers for each structure, and we tested for bias in scale-estimated ages by creating an age–bias plot (Campana et al. 1995). Because otoliths have been validated as an age estimation structure for Largemouth Bass (Taubert and Tranquilli 1982; Hoyer et al. 1985), estimated otolith ages were treated as the reference age and were plotted on the *x*-axis (Ogle 2016). The FSA package tested for a significant difference between the mean scale-derived age estimate and the mean otolith-derived age estimate with a one-sample *t*-test adjusted for multiple comparisons at α = 0.05 and computed 95% confidence intervals that were unadjusted for multiple comparisons. Wilcoxon's signed rank test with a continuity correction (paired by reservoir; α = 0.05) was used to compare the mean otolith ACV and the mean scale ACV.

With the FSA package in R (Ogle 2016), we constructed age–length keys in 10-mm length bins by using the mean otolith age and mean scale age among the three independent readers of each structure for each fish. Separate age–length keys were constructed for each aging structure from each reservoir in each year. For each structure, ages were then assigned to all unaged fish in each sample by using the age–length key for that year and reservoir via the method of Isermann and Knight (2005). The fish for which ages were estimated were then combined with the fish that were assigned ages based on the age–length key. Each fish therefore had either (1) a mean scale age and a mean otolith age from the three readers for each structure or (2) an assigned otolith age and an assigned scale age from age–length keys.

We used nonlinear mixed-effects models with the "nlme" package (Pinheiro et al. 2014) in R to fit the von Bertalanffy growth function to the combined age-assigned samples (Hart and Chute 2009; English et al. 2012). For each age estimation structure, von Bertalanffy parameters (theoretical age at zero length [t_0], growth coefficient [K], and asymptotic length [L_∞]) were fitted to the combined age-assigned data sets as fixed effects, with reservoir included as a random effect on each parameter to account for spatial differences in Largemouth Bass growth. For von Bertalanffy parameters, fixed effects represented average growth for the 17 study reservoirs, whereas random effects characterized reservoir-specific deviations from the overall average. Samples were pooled between years for the five reservoirs sampled. Starting values for von Bertalanffy parameters were selected for each structure by using the FSA package in R (Ogle 2015). To determine model sensitivities to starting values, we iteratively changed the starting values for each parameter from those selected by the FSA function. We tested starting values ranging from 350 to 650 mm for L_∞, from 0.1 to 0.9 for K, and from −1.0 to +1.0 for t_0 and found that von Bertalanffy parameter estimates were similar across these starting values. Variance in length at age was similar among age-classes; we therefore assumed additive errors in the mixed-effects models.

We conducted yield-per-recruit model simulations in FAMS (Slipke and Maceina 2014) to determine how bias in aging structures could affect the information used to make management decisions. Yield-per-recruit models are commonly used to determine appropriate levels of harvest in fish populations from age and growth information (Slipke and Maceina 2014). Yield-per-recruit models require estimates of the von Bertalanffy growth parameters (L_∞, K, and t_0) and weight–length equation parameters to model yield and size structure indices over a range of conditional natural mortality (*cm*) and conditional fishing mortality (*cf*) estimates.

We compared yield-per-recruit models by using the fixed-effect estimates of von Bertalanffy parameters from scale and otolith nonlinear mixed-effects models. Yield-per-recruit models were constructed under a 305-mm minimum length limit, which is a commonly used regulation for Largemouth Bass fisheries (Wilde 1997) and is currently used statewide by ODOW. All models shared the same length–weight equation developed with FAMS (Slipke and Maceina 2014) based on data from the 1,846 Largemouth Bass that were aged during this study; four estimates of *cm* representing very-low (*cm* = 0.08), low (*cm* = 0.21), intermediate (*cm* = 0.34), and high (*cm* = 0.47) natural mortality selected from instantaneous natural mortality reported by Beamesderfer and North (1995); and *cf* values ranging from 0.05 to 0.70 in increments of 0.05. We compared three model outputs: yield, the percentage of individuals in the cohort surviving to 380 mm (proportional size distribution [PSD] 380), and the percentage of individuals in the cohort surviving to 470 mm (PSD 470). The PSD 380 coincides with the "preferred" length category established by Gabelhouse (1984); PSD 470 was near our estimate of L_∞, and we chose it to represent the largest individuals in a population. Models were run for theoretical cohorts of 100 individuals.

RESULTS

Overall, age estimates were generated for 982 Largemouth Bass collected in 2013 and 864 individuals collected in 2014. Largemouth Bass ages were estimated up to 21 years by using otoliths and up to 16 years by using scales. Scale ACV (mean = 19.0%, SD = 5.2) was significantly greater than otolith ACV (mean = 6.6%, SD = 5.9; Wilcoxon's signed rank test: P < 0.001). A total of 10 reservoir samples had an otolith ACV below 5%, which is a general benchmark proposed by Campana (2001) as suggesting a reliable age estimation structure. All samples had an ACV well above 5% for scale-derived age estimates, and the scale-derived ACV was higher than the otolith-derived ACV for all but two samples (Figure 1). The scale-derived ACV was similar between samples with high and low otolith-derived ACVs (Figure 1). Ages estimated from scales were greater than otolith-based ages for fish younger than age 6 and were less than otolith ages for fish older than age 6 (Figure 2).

Based on scale-derived age estimates, L_∞ was estimated at 530 mm (SE = 20), K was estimated at 0.22 (SE = 0.02), and t_0 was estimated at −0.75 (SE = 0.14) as fixed effects in the nonlinear mixed-effects model. Based on otolith-derived age estimates, L_∞ was estimated at 476 mm (SE = 12), K was estimated at 0.30 (SE = 0.02), and t_0 was estimated at −0.28 (SE = 0.11). The L_∞ estimates were lower and K estimates were higher for otolith-derived age estimates than for scale-derived age estimates in 15 of the 17 study reservoirs (Figure 3). Yield-per-recruit models showed similar estimates of yield and PSD 380 when using scale-derived and otolith-derived fixed-effects estimates (Figure 4), but PSD 470 was overestimated with scale-derived age estimates relative to otolith-derived age estimates, especially at lower levels of *cf* and *cm* (Figure 4). In the most extreme example, when *cm* was 0.08 and *cf* was 0.05, PSD 470 was predicted to be 32% with scale-derived age data, whereas it was predicted to be 6% when otolith-derived ages were used (Figure 4). Furthermore, when *cm* was 0.08 but *cf* was increased to 0.2, PSD 470 was almost 0% with otolith-derived age data but

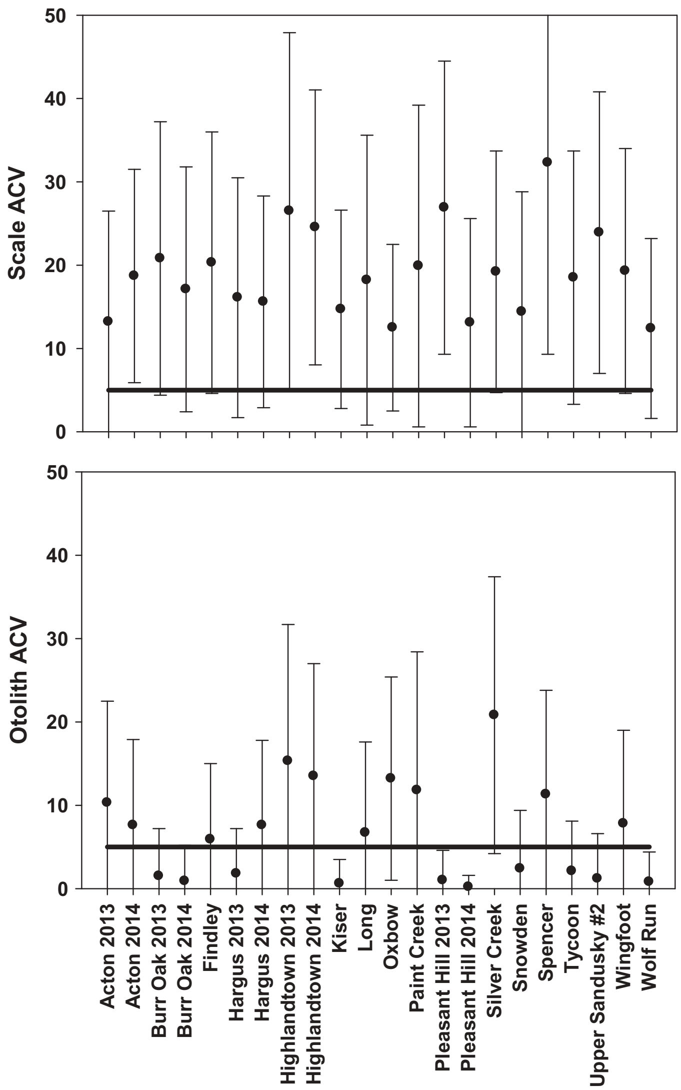

FIGURE 1. Average coefficients of variation (ACVs; %, ±SD) of scale-based age estimates (upper panel) and otolith-based age estimates (lower panel) for Largemouth Bass samples collected from Ohio reservoirs. Samples are labeled by reservoir name. The year when the sample was collected follows the reservoir name for reservoirs sampled in more than one year. In both panels, the solid line represents an ACV value of 5%, the cutoff value for a precise age estimation structure as proposed by Campana (2001).

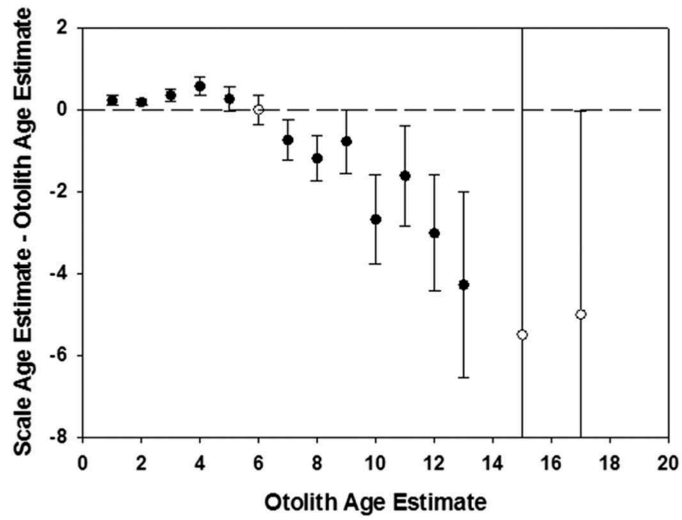

FIGURE 2. Age–bias plot showing the mean difference (±95% confidence interval) in scale-based age and otolith-based age (years) for 1,864 Largemouth Bass sampled across 17 Ohio reservoirs in 2013 and 2014. Black symbols indicate a significant difference between mean scale age and mean otolith age (α = 0.05); open symbols indicate that there was no significant difference. The dashed line represents a difference of zero, which would indicate the absence of bias.

remained relatively high (10%) based on scale-derived age data (Figure 4).

DISCUSSION

In our study, scale-derived age estimates were systematically biased relative to those derived from otoliths, overestimating the ages of young Largemouth Bass (age < 6 years) and greatly underestimating the ages of older fish. Our estimates of bias in scale-derived age estimates relative to those derived from otoliths are similar to those reported previously (Besler 2001; Maceina and Sammons 2006); thus, our modeling and simulation results have broad applicability for Largemouth Bass management. The bias in our scale-derived age estimates resulted in biased von Bertalanffy parameter estimates relative to those derived from otoliths, which in turn led to important differences in predicted population size structure based on yield-per-recruit model simulations commonly used to manage recreational freshwater fisheries. Scale-derived age data overpredicted the proportion of the largest individuals in a population relative to otolith-derived age data because the negative bias in age estimates of old individuals caused overestimation of length at age for large fish.

The use of inaccurate or biased structures to estimate the ages of fish has led to mismanagement of valuable fisheries (Beamish and McFarlane 1987; Lai and Gunderson 1987). Improving or maintaining the size structure of Largemouth Bass populations is often a goal of fisheries managers (e.g., Dotson et al. 2013; Hale et al. 2015), and using age and growth information derived from scales may lead to unrealistic expectations of size structure and improper management. Because our estimates of bias between otoliths and scales are similar to those reported previously the consequences of using scale ages as shown in this study are broadly applicable to Largemouth Bass populations.

Our results have the greatest implications for the management of trophy Largemouth Bass fisheries, which depend on maintaining a high percentage of large individuals in a population. Simulations based on scale-derived age data suggested that a relatively high percentage of large individuals remains

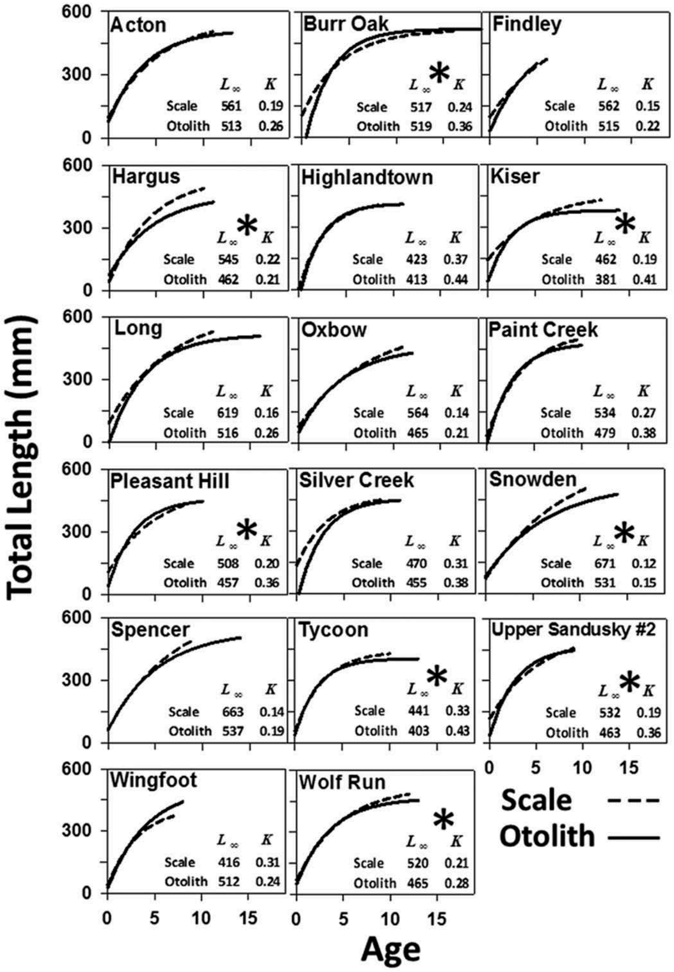

FIGURE 3. Largemouth Bass growth curves plotted with reservoir-specific random-effects estimates of von Bertalanffy growth parameters based on scales and otoliths collected from Ohio reservoirs. Each panel shows the curve resulting from parameters estimated from scale-based age estimates and otolith-based age estimates plotted out to the oldest mean age observed for the respective structure within each reservoir. Mixed-effects modeling estimates from the random effect of reservoir on asymptotic length (L_∞) and the growth coefficient (K) for each structure are displayed for each reservoir. Asterisks indicate reservoirs where the average coefficient of variation for otoliths was less than 5%.

under low levels of fishing mortality, whereas simulations based on otolith-derived age data showed that almost any level of fishing mortality results in a very low percentage of large individuals. Reducing fishing mortality has been shown to be an important factor for producing trophy Largemouth Bass (Crawford et al. 2002; Dotson et al. 2013) and may be accomplished through regulations such as closed seasons (Crawford et al. 2002), catch-and-release-only regulations (Henry 2003), conservative minimum length limits (Dotson et al. 2013), or protected slot limits (Wilson and Dicenzo 2002). Managers relying on age estimates from scales would find less reason to recommend these kinds of restrictive regulations to reduce fishing mortality due to overpredictions of size structure, which in turn would decrease the abundance of (or even eliminate the presence of) large fish in a population. Black bass are the most important inland sport fishes in the United States (USFWS and U.S. Census Bureau 2011), and trophy Largemouth Bass fisheries have major economic impacts on local communities (Chen et al. 2003). Erroneous management decisions that reduce the abundance of large fish can have negative economic consequences.

Biased age information obtained from scales may lead to mismanagement of trophy Largemouth Bass fisheries, yet sacrificing large individuals to obtain otoliths can create public relations concerns for fisheries management agencies. For example, Bulak and Crane (2002) described a sampling protocol used in South Carolina, where otoliths were at first not collected for 475-mm and larger Largemouth Bass and later were not collected for 575-mm and larger individuals. Although we recognize that scales remain an attractive aging structure for fisheries managers because they offer a nonlethal option, such a sampling protocol misses critical information about trophy Largemouth Bass. As an alternative to relying on management surveys to obtain samples of trophy Largemouth Bass, otoliths can be collected by taxidermists to provide age and growth data (Horton and Gilliland 1993; Bulak and Crane 2002; Crawford et al. 2002). This method not only avoids the public relations issue of sacrificing large fish but could provide better access to large fish that may be less vulnerable to standard survey gear than other segments of the population (Bayley and Austen 2002; Tyszko et al. 2017) and that may be more vulnerable to angling than to standard survey gear (Pope et al. 2005).

The utility of scales as an age estimation structure may depend on management objectives. Bulak and Crane (2002) proposed yield as an index of the abundance of "quality" Largemouth Bass. Our results showed no difference between scale-derived and otolith-derived age data in estimates of yield and PSD 380, indicating that scales may be suitable when managing for maximum yield in fisheries where large numbers of quality- to preferred-length fish (Gabelhouse 1984) are more important than the number of trophy fish. The ages that comprise the greatest proportion of a population—and therefore make the greatest contribution to yield—are not those that are most impacted by the bias of scale age estimates (Tyler et al. 1989). Additionally, scales may provide adequate age estimates for use in managing fisheries that are focused on harvest and that are composed of young fish (e.g., Krause 2002). In our yield-per-recruit analysis, little difference existed in predictions made based on otolith-derived versus scale-derived age estimates at high natural mortality and fishing mortality rates. However, Besler (2001) found that scales significantly underestimated mean length at age for 2–5-year-old Largemouth Bass and concluded that the level of bias was biologically significant and could result in erroneous management decisions. We urge caution in using scales to estimate ages of Largemouth Bass for management purposes. Otoliths are known to produce accurate age estimates that are

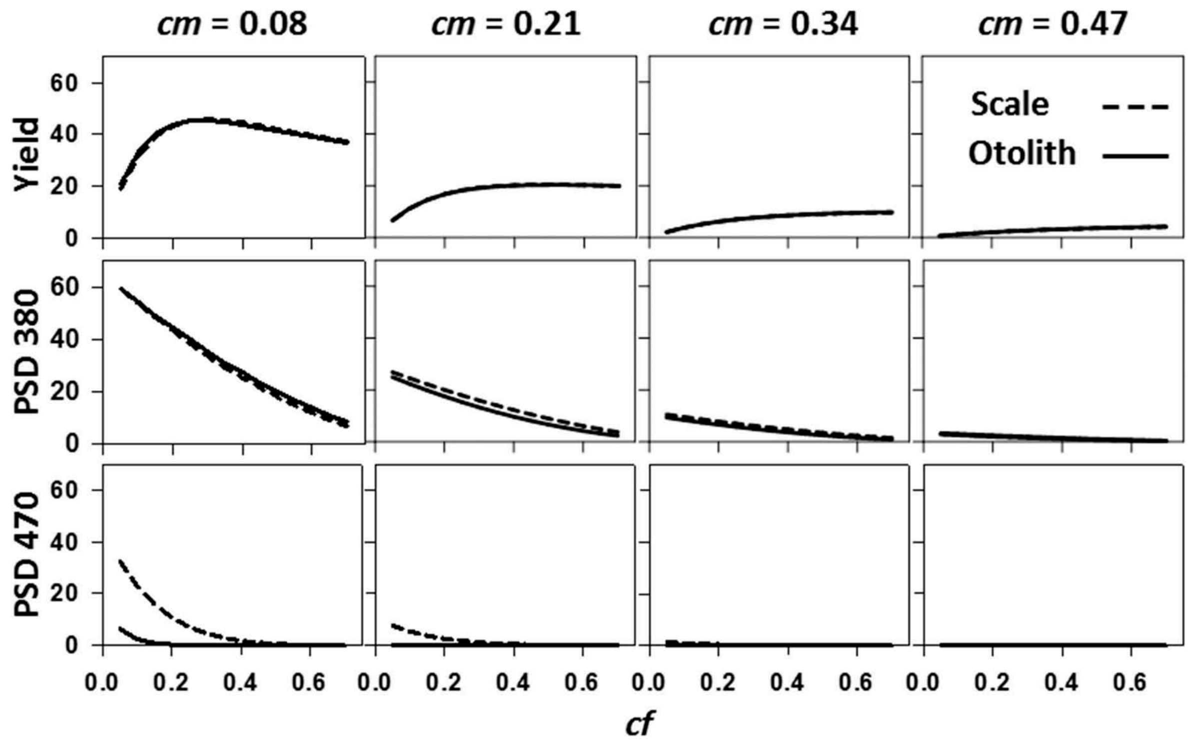

FIGURE 4. Results of Largemouth Bass yield-per-recruit simulations using fixed-effect growth parameter estimates for Ohio reservoirs. Yield (kg) and the percentage of individuals in the cohort surviving to 470 mm (proportional size distribution [PSD] 470) are shown as a function of conditional fishing mortality (*cf*) at very-low, low, medium, and high values of conditional natural mortality (*cm*). Models were run for theoretical cohorts of 100 individuals.

more precise than scale-derived age estimates, and we recommend the use of otoliths to estimate Largemouth Bass age whenever possible.

Our precision results agree with Besler (2001) and Maceina and Sammons (2006), who found that otolith-derived age estimates were much more precise than scale-derived age estimates. However, our results disagree with those of Long and Fisher (2001), who reported similar precision between otolith-derived and scale-derived age estimates for Largemouth Bass. Precision is important for indicating the ease of age estimation from a certain structure and comparing the skill level of readers (Campana 2001). Although our otolith-derived ACV was lower than our scale-derived ACV, there was still some variation in otolith-derived ACV among samples. Buckmeier (2002) found that differences in reader skill generated variability in accuracy of age estimates among readers for Largemouth Bass otoliths, thus demonstrating that age estimates cannot be assumed accurate simply because they were derived from a validated structure. We strongly recommend the thorough training of readers and the monitoring of age estimates' quality by measuring precision and using reference collections (Campana 2001; Buckmeier 2002). Skilled readers should be able to achieve highly accurate and precise age estimates for Largemouth Bass when examining otoliths.

Our results showed that biased growth parameter estimates derived from scales and those derived from otoliths provided very different characterizations of the largest and oldest segment of Largemouth Bass populations. In addition to the direct implications for managing trophy fisheries, caution must be used when interpreting and making comparisons to previous studies that may have included ages estimated from scales. For example, two influential, continentwide comparisons of Largemouth Bass population characteristics (Beamesderfer and North 1995; Helser and Lai 2004) synthesized age and growth data that were likely obtained from a mixture of age estimation structures, including otoliths and scales. Based on our results, these studies likely employed biased values of L_∞ and K to produce generalizations at large geographic scales. In the future, such among-population comparisons should involve consideration of the potential bias introduced by including biased age estimation structures or a mixture of aging structures.

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