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Abstract
   Mortality, growth, and recruitment are the primary dynamic rate functions that regulate fish populations. Age data obtained from calcified structures can provide direct and indirect information needed for calculations of these metrics; therefore, knowledge of the fish population age structure is often coveted information. Unfortunately, potential sources of error exist in the form of subjectivity in interpretation of growth increments, inconsistent deposition of growth increments, and lack of validation in age-estimation processes. However, many sources of error are either not known or simply ignored, particularly for long-lived fishes. Therefore, we included a level of uncertainty in our age estimates of a periodic life history strategist, the Shovelnose Sturgeon *Scaphirhynchus platorynchus*, by incorporating variability in reader assignment of age. We used a bootstrapping procedure to generate a matrix of new age distributions and demonstrated how calculations of mortality varied as a result of reader assignment variability. Varying mortality rates of adult Shovelnose Sturgeon in a three-stage, female-only population projection model resulted in a wide range of potential responses. Hypothetical population projections after simulating for 30 years ranged from 2,249 to 10,673 individuals, despite mortality estimates varying by only 15% (28–43%). Age-determination errors are an impediment to understanding fish population dynamics using conventional age-based assessments; therefore, consequences of aging error should be considered when attempting to model population dynamic processes and long-term viability.

   Demographic models that use fish population age data have been an integral component used to predict the population viability and responses to management actions (Beverton and Holt 1957; Gedamke et al. 2007; Methot and Wetzel 2013). Further, age-structured models are commonly used for determining fish mortality rates, spawning potential ratios, and recruitment dynamics (Goodyear 1993; Maceina 1997). Age data can provide direct and indirect information needed for

estimating metrics for studying population dynamics; therefore, knowledge of the population age structure is highly valued (Quist et al. 2012). Information on fish age is frequently obtained by inferring ages from growth increments observed on calcified structures (e.g., spines, otoliths). Unfortunately, potential sources of error exist in the form of subjectivity in interpretation of growth increments, inconsistent deposition of growth increments, and lack of validation in

514

estimated ages (Campana 2001). Age validation for respective calcified structures is therefore a prerequisite so that aging accuracy and precision can be quantified. However, absolute age validation is difficult to assess because fish of known age in the population are rare (Beamish and McFarlane 1983; Campana 2001). In the absence of known-age fish, most researchers attempt to verify increment periodicity through various methods (i.e., mark–recapture, marginal increment analysis). If increment periodicity occurs in a consistent manner, those marks are inferred to be an accurate representation of the time scale observed, and age can then be determined. It is important that the validation of increment periodicity occurs throughout the entire age range of interest as growth patterns typically change throughout a fish's life (Campana 2001).

Age estimates are difficult to assign for long-lived fishes because of minimal spacing of growth marks on calcified structures due to slow growth observed after maturity (Hamel et al. 2015a). Without absolute age validation for all ages, age estimates may be grossly underestimated and management decisions may therefore be flawed (Campana 2001). For example, when aged with scales, the Walleye Pollock *Theragra chalcogramma* was thought to be a short-lived fish, and thus their populations can be resilient to high mortality rates from commercial harvest (>40%: Beamish and McFarlane 2000). However, an age validation study revealed that age estimates from otolith cross sections were considerably greater than those from other calcified structures and that a few strong year-classes were responsible for the majority of the harvestable catch. Without these discoveries, the allowable harvest of Walleye Pollock may have been overestimated, leading to a potential collapse of the fishery (Beamish and McFarlane 2000).

Sturgeons (Acipenseridae) represent an extant group of fishes that are long lived and late maturing and have received considerable attention in recent years because of range-wide declines linked to anthropogenic effects such as overharvest, dam construction, and loss of habitat (Boreman 1997). Nearly all European and Asian sturgeon species have experienced population declines and have subsequently been classified as either threatened or endangered (Birstein 1993). Similarly, all eight native North American sturgeons are listed as endangered, threatened, or of special concern (Williams et al. 1989; Jelks et al. 2008). Pallid Sturgeon *Scaphirhynchus albus* was federally listed in the United States in 1990 as endangered (Dryer and Sandvol 1993), and Shovelnose Sturgeon *S. platorynchus* was classified as extirpated or at risk of extirpation in 50% of the states within their native distribution (Koch et al. 2009). These two sturgeons are found throughout the Mississippi and Missouri River basins, and extensive efforts to restore and sustain Pallid Sturgeon and Shovelnose Sturgeon populations have occurred over the past decade.

Prior to reported declines in Pallid and Shovelnose sturgeons, little information was known about the life history, biology, or ecology of *Scaphirhynchus* sturgeons. More recently, there has been an extensive research effort to better understand life history characteristics of these species including estimating abundance and population dynamics (e.g., growth, recruitment, mortality). Age-structured models have commonly been used to estimate sturgeon mortality rates, spawning potential ratios, and recruitment dynamics, particularly for Shovelnose Sturgeon in areas where they are still commercially harvested (Kennedy et al. 2007; Koch et al. 2009). Age data from *Scaphirhynchus* sturgeons are most commonly obtained from interpretation of annuli deposition on pectoral fin rays. This structure can be removed nonlethally and has the highest reported precision compared with other structures (Jackson et al. 2007).

Attempts to validate the accuracy of age estimates for *Scaphirhynchus* sturgeons obtained from fin rays have had little success (Hurley et al. 2004; Whiteman et al. 2004; Koch et al. 2011; Hamel et al. 2014; Rugg et al. 2014). Despite unsuccessful attempts at validating *Scaphirhynchus* sturgeon fin rays for age determination, this structure is still widely used by managers and researchers, particularly for aging Shovelnose Sturgeon as few, if any, known-age fish exist. We hypothesize that those who use fin rays for Shovelnose Sturgeon age estimation perceive aging errors to have minimal deleterious effects, particularly if age estimates are only slightly biased (e.g., 1 or 2 years) for this long-lived species. In addition, information gained (e.g., population dynamics) is vital for this species' management, and fin ray age estimates may be perceived as the only available tool to attain these data. The cumulative effect of using incorrect age estimates to determine metrics of population dynamics is unknown. Therefore, our objective was to assess how variability in age assignments affects calculations of total annual mortality, and ultimately, the trajectories obtained through population demographic models used for recovery or sustainability of long-lived species. We used a case study from the Platte River, Nebraska, where Shovelnose Sturgeon fin ray age validation has been unsuccessful and precision in age assignments between multiple readers is poor, to illustrate how variable age assignments can affect calculations of population dynamics.

METHODS

Data collection.—Shovelnose Sturgeon were collected from the lower Platte River, Nebraska, in 2009. A multigear approach was used to catch a variety of sizes and presumed ages of Shovelnose Sturgeon. An equal number of trotlines and trammel nets were deployed throughout a variety of habitat types during the course of the sampling year (March 1–November 30). All Shovelnose Sturgeon were measured to the nearest millimeter (FL) and weighed to the nearest gram. The leading edge of the left pectoral fin ray was removed from all captured Shovelnose Sturgeon during the spring (March 1–May 31) and fall (September 1–November 30) seasons.

Growth increment deposition was thought to occur during the summer period; therefore, fin rays were not collected during June–August per recommendations by Whiteman et al. (2004). Additional fin rays were collected during 2009–2011 from Shovelnose Sturgeon that were previously tagged in a population assessment study conducted in the early 2000s. These fin rays were used in an attempt to validate annuli deposition on the structure by comparing the known time between capture periods to the number of annuli present on the structure. Fin rays were prepared using methods outlined in Koch and Quist (2007), in which the fin ray is embedded in an epoxy-resin solution and later cross-sectioned. Fin ray cross sections were mounted on microscope slides and photographed using a high-resolution digital camera. Transmitted light was used to enhance the clarity of annuli, and digital images were viewed to determine ages manually.

Three readers independently aged all fin ray sections. Marginal increment analysis revealed no consistent growth increment deposition; therefore, the edge of the fin ray section was considered the outer annulus for all fin rays. Reader agreement for all three readers was low (3% exact agreement) and among-reader comparisons (i.e., combinations of two readers) increased agreement slightly (11–21%). Discrepancies in age determination between readers were re-evaluated by all three readers to develop a consensus age estimate (Figure 1).

The low precision in our study was similar to previous studies for both *Scaphirhynchus* species. For example, the exact agreement between two readers aging Shovelnose Sturgeon fin rays has varied from a low of 13% to a high of 81% (Morrow et al. 1998; Whiteman et al. 2004; Jackson

et al. 2007; Kennedy et al. 2007; Koch et al. 2008). Fewer studies exist regarding precision of Pallid Sturgeon age estimates, and exact reader agreement has varied from 21% to 36% (Hurley et al. 2004; Killgore et al. 2007; Koch et al. 2011; Hamel et al. 2014). Generally, agreement between two readers for *Scaphirhynchus* sturgeon only approaches a high level (~90%) when age estimates are within 3 years among readers. The percent agreement in our study for each combination of two readers varied from 73% to 83% when age assignments among readers were within 3 years.

Data analysis.—The estimated consensus ages of Shovelnose Sturgeon from fin rays were used to determine mortality rate. Total annual mortality was estimated with a weighted catch curve for Shovelnose Sturgeon recruited to the gear (Maceina 1997). A catch-curve analysis is a commonly used procedure to estimate mortality, where the slope of the descending limb of the age frequency histogram corresponds to the instantaneous mortality rate (Z). The antilog of the instantaneous mortality rate corresponds to the annual survival rate (S), and $1 - S$ is the total annual mortality.

Age variability simulations.—The final age estimate used in age and growth studies is often a consensus age agreed upon by multiple readers. A consensus age eliminates the prior variability associated with multiple age estimates, but may not represent the true age and thus bias estimates of total annual mortality. Undue variation in mortality would, in turn, restrict possible population trajectories and ultimately affect our understanding of population viability. Therefore, we maintained a level of uncertainty, which is often overlooked, in our age estimates of Shovelnose Sturgeon by incorporating variability in the assignment of age. We examined the maximum difference in age assignments among readers and calculated the mean maximum difference. A Poisson distribution accurately depicted the variability in age assignments among readers (Figure 2). For each Shovelnose Sturgeon that was aged, a randomly selected measure of age variability was drawn from the Poisson distribution ($\lambda = 3.58$; Figure 2) and added to the original age assignment. An estimate of annual mortality was calculated using catch-curve analysis from the resulting age structure with the randomized reader uncertainty. We generated a distribution of adult mortalities by repeating this process 1,000 times. Catch-curve analysis used regression of the descending limb of the age structure beginning with the modal age-group (Ricker 1975).

Population model.—We developed a three-stage female-only Lefkovitch population matrix model (Lefkovitch 1965) to demonstrate how uncertainty in Shovelnose Sturgeon age estimates and the resulting variability in adult annual mortality would influence simulated population trajectories. We used demographic parameter estimates from previous studies to calibrate our model (Table 1). Survival rates for age-0 and juvenile Shovelnose Sturgeon are not available; therefore,
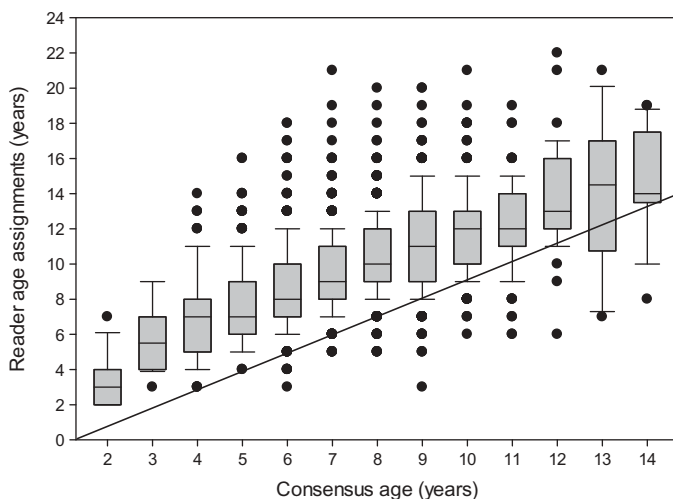

FIGURE 1. Box plots depicting the differences in Shovelnose Sturgeon age assignments among three independent age readers (*y*-axis) in relation to the final consensus age (*x*-axis). The solid line is the 1:1 line, indicating differences between the independent reader assigned ages and the final consensus age.
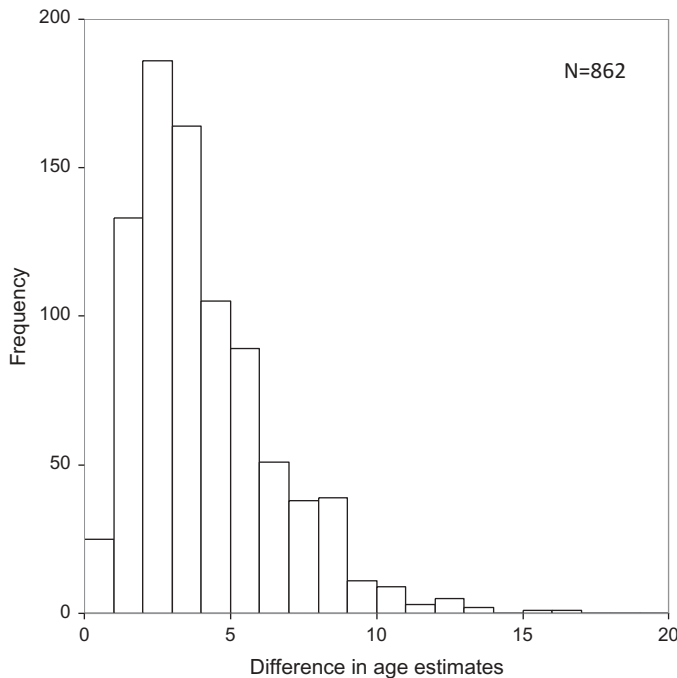
FIGURE 2. Frequency distribution of the maximum difference (years) in age assignment of Shovelnose Sturgeon fin rays among independent readings from three age readers.

previous results published for Pallid Sturgeon (a closely related congener) were used for modelling purposes. All parameter estimates were deterministic except for estimates of adult annual survival, which were randomly selected at the beginning of our simulation from our generated age variability distribution. This enabled us to isolate the effects of variability directly related to uncertainty in the age estimation process on Shovelnose Sturgeon population projections. We categorized the life history of Shovelnose Sturgeon into three stages: age 0 (duration = 1 year), juvenile (duration = 6 years), and adult. All surviving age-0 Shovelnose Sturgeon transitioned to the juvenile stage as the age-0 stage was only 1 year in duration. We calculated the probability of juvenile Shovelnose Sturgeon remaining in the juvenile stage or transitioning into the adult stage using equations from Crouse et al. (1987):

TABLE 1. Input metrics used in the Shovelnose Sturgeon population viability analysis model for the lower Platte River, Nebraska.

Variable	Value	Reference
Age at maturity	Age 6	Hamel et al. (2015b)
Absolute fecundity	16,098	Hamel et al. (2015b)
Survival rates:		
Egg to age 1	0.001	Steffensen et al. (2013)
Age 1	0.686	Steffensen et al. (2013)
Adult	Simulated	This study

$$pi = \left(\frac{1 - pi^{di-1}}{1 - pi^{di}}\right)pi,$$

and

$$gi = \left(\frac{pi^{di}(1 - pi)}{1 - pi^{di}}\right),$$

where stage-specific survival probabilities (pi) and stage duration (di) result in the probability of surviving and remaining in the same stage pi or the probability of surviving and growing to the next stage, gi. No reliable estimate of population size was available; therefore, we set the initial population size at 1,000 individuals and conservatively assumed consistent annual recruitment. Model projections were carried out over 30 years and we ran 10,000 model iterations.

RESULTS

Ages were estimated from fin rays for 862 Shovelnose Sturgeon. Mean consensus age was 7.6 years (±0.07 SE), and there was variation in body lengths associated with each particular age (Figure 3). Fin rays were collected from four Shovelnose Sturgeon that were originally tagged in 2001–2003 and recaptured in 2010 and 2011. Consensus age estimates for these fish ranged from 8 to 12 years, despite these fish being tagged originally as large, presumably older adults (≥590 mm; Figure 4). Total annual mortality estimated from fin ray-generated age assignments using a catch-curve analysis was 36% (Figure 3).

Simulations incorporating aging variability resulted in variable simulated age frequency distributions. The mean age of all simulated age frequency distributions ($n = 1,000$) was 11.1 years and the minimum and maximum ages were 2 and 26 years, respectively (Figure 5). Total annual mortality estimates calculated from each simulated age frequency distribution ranged from 28% to 43% with a mean of 36% (Figure 6). Varying mortality rates of adult Shovelnose Sturgeon in the population model resulted in a wide range of potential responses to the hypothetical population through time (Figure 7). Population projections varied considerably despite mortality estimates ranging by only 15% (i.e., from 28% to 43%). Simulated population size after 30 years was projected to range from 2,249 to 10,673 Shovelnose Sturgeon with a mean size of 4,599 individuals.

DISCUSSION

Our model provided insight into how variability in age assignments can induce ambiguity in population projection models, thereby hindering a manager's ability to assess the impacts that regulations or environmental effects have on a fishery. Estimates of mortality were highly variable when age assignments were subjected to randomized error but were within the range of reported values from previous Shovelnose Sturgeon studies (i.e.,
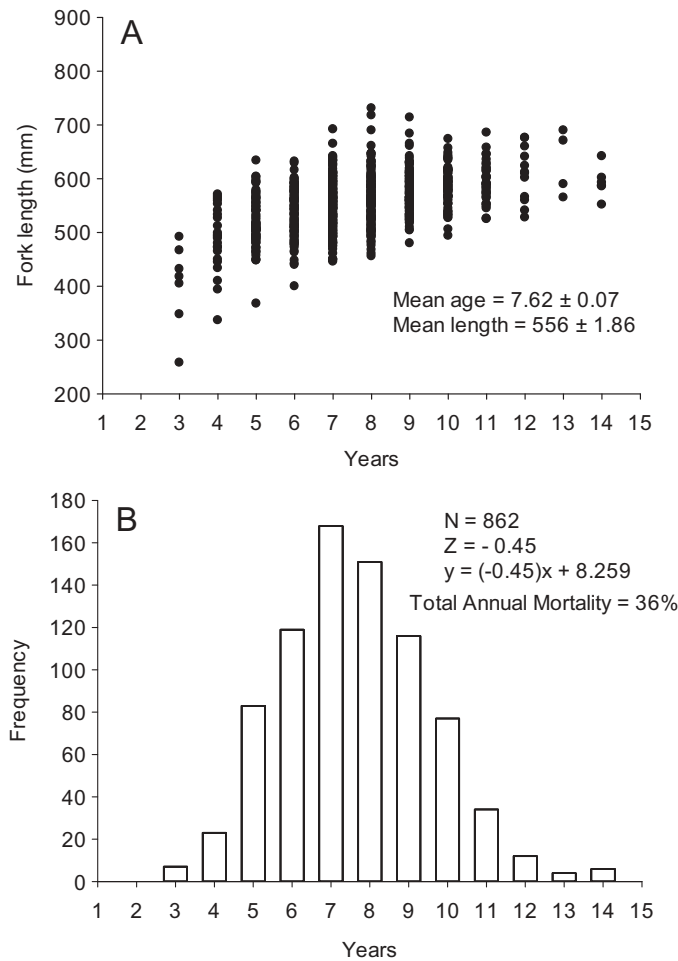
FIGURE 3. (A) Fork length at age and (B) age frequency distribution of Shovelnose Sturgeon in the Platte River, Nebraska, aged with fin rays during 2009. Total annual mortality from catch-curve analysis is reported in panel (B). Ages were determined as a consensus from three independent readers.
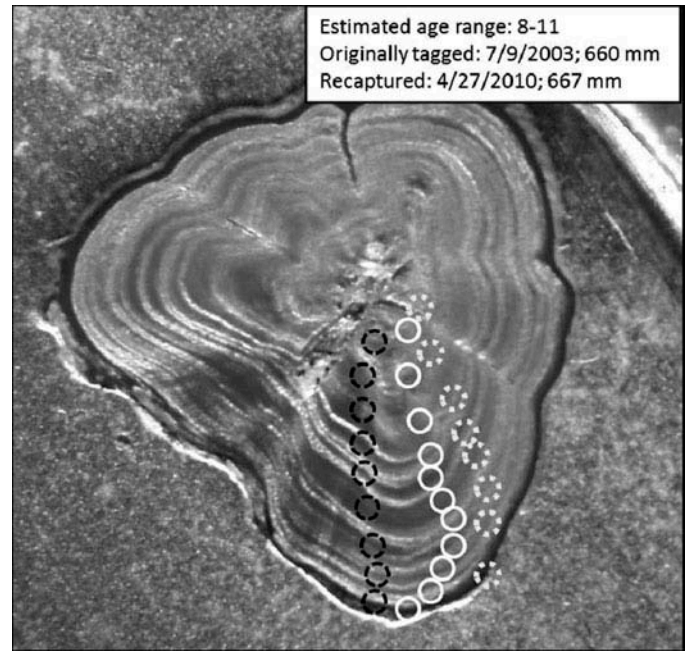

FIGURE 4. Age assignments from three independent readers from a cross section of a fin ray from a Shovelnose Sturgeon that was at large for approximately 7 years. Circles represent the annuli depiction for each individual reader. Tag and recapture dates are given as month/day/year.

age range for particular fish (Spurgeon et al. 2015). This is especially important for long-lived fishes that often exhibit reduced or minimal growth after maturity, making interpretation of closely

20–44%) (Morrow et al. 1998; Colombo et al. 2007; Kennedy et al. 2007; Tripp et al. 2009). Our procedure was unique because the error structure used to assess aging variability was based on actual age estimates from three independent readers. Although precision of age estimates is often reported in the literature, it is difficult to incorporate that variability into the final age assignment. Consensus ages are thought to reduce variability as readers agree on annuli counts in concert, but biases still exist, such as the pressure to defer to more experienced personnel, second-guessing of initial thoughts, human personality differences (e.g., stubbornness), or actual difficulty in reading the structure (e.g., presence of false or incomplete annuli).

The effect of age assignment variability likely varies among species, but is expected to be a function of the aging structure used and whether the structure has been validated. Although there has been an increasing trend in the number of validation studies in recent years (Campana 2001; Maceina et al. 2007), few studies have successfully validated aging structures throughout the entire
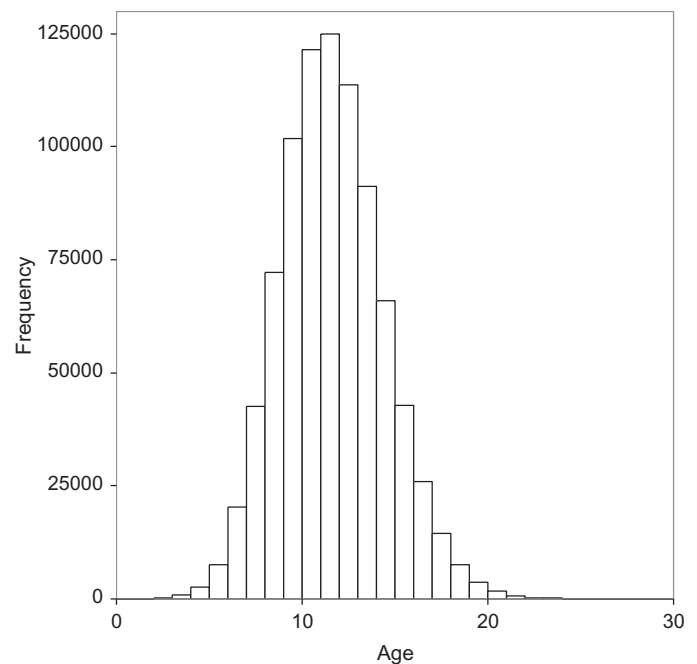

FIGURE 5. Cumulative age (years) frequency distribution after 1,000 iterations of incorporating aging variability to the original age distribution of Shovelnose Sturgeon determined from three readers aging in concert.
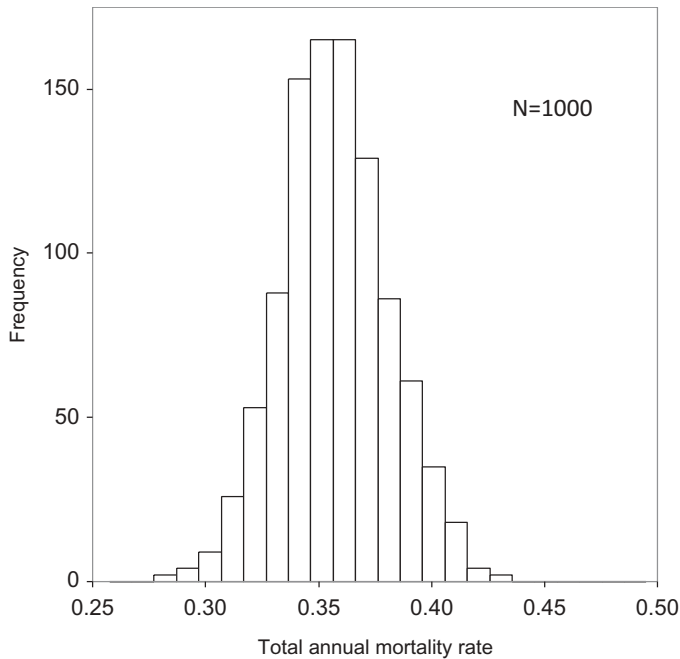
FIGURE 6. Cumulative frequency distribution of total annual mortality rates calculated from each simulated age frequency distribution after incorporating aging variability to the original age distribution of Shovelnose Sturgeon.
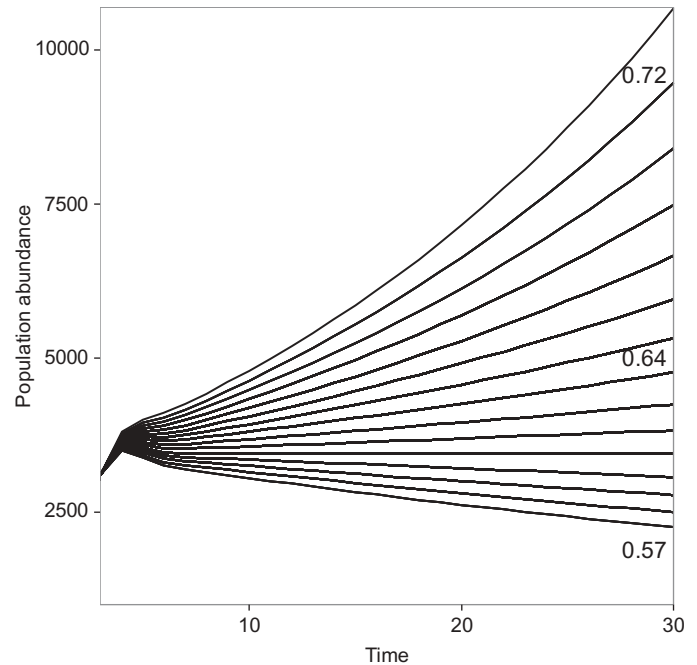

FIGURE 7. Predicted population size of Shovelnose Sturgeon through time (years) under varying levels of the annual survival rate (1 − total annual mortality rate) previously determined through simulation exercises to incorporate aging variability to the original age distribution.

spaced annuli difficult. The four Shovelnose Sturgeon from our study that were at large for 7–9 years displayed negligible growth, suggesting that growth marks on fin rays would have to be spaced very closely if the assumption of proportional somatic growth to annuli spacing is true. Furthermore, Rugg et al. (2014) was unsuccessful in verifying periodicity of annuli deposition of Shovelnose Sturgeon in the Platte River using marginal increment analysis. Hamel et al. (2015a) used mark–recapture information to describe age and growth patterns of Shovelnose Sturgeon and predicted that it would require 20–25 years to attain a length greater than 600 mm. Although the true age at tagging for these four fish in our study was unknown, accounting for the additional number of years at large (7–9 years) indicates that fin rays may drastically underestimate older Shovelnose Sturgeon.

Fin rays from *Scaphirhynchus* sturgeon have been documented as being notoriously difficult to age precisely and accurately, but this aging structure has provided the most precise age assignments among other structures and can be collected nonlethally (Jackson et al. 2007). Multiple studies have urged caution for use of fin rays for aging in determining population dynamics (Whiteman et al. 2004; and others), but several studies have subsequently been published likely because other aging structures were not feasible, other methods were not well understood, or perceived slight inaccuracies were not thought to affect results (Scarnecchia et al. 2006; Tripp et al. 2009; and others). We concede that inaccurate age assignments within 2 or 3 years of the actual age may have fewer consequences when calculating growth and mortality for a long-lived species. This would particularly be true if readers

consistently under- or overaged fish. In this instance, a catch-curve analysis may result in similar estimates because the slope of the descending limb of the age frequency histogram would simply shift to the left or right. However, this assumption would likely only be accurate if discrepancies in age assignments occurred consistently in one way (e.g., only underestimating a couple of years) or if they were toward the later part of life in long-lived species (e.g., Sablefish *Anoplopoma fimbria*: Beamish and McFarlane 2000). This is likely not the case for many species. As in our study example, negligible growth beyond sexual maturity may lead to undetectable annuli. The absence of older individuals in the age frequency histogram likely leads to a different slope trajectory in the catch-curve analysis, resulting in artificially inflated mortality estimates.

The low precision of age estimates in our study was due to the presence of incomplete, closely spaced, and irregularly grouped annuli (Figure 8). A large, shaded band (assumed to be growth during the growing season) often appeared to have several closely spaced growth marks from within. Therefore, some of the largest discrepancies in age estimates among readers were related to the difference in ascertaining these growth marks. Agreement among readers in our study was typically lower than other published studies, and there is likely a variety of factors that influenced these results. Reader experience in this study varied from two to several years, but only one reader had prior experience aging sturgeon. Readers that share a high level of experience aging

FIGURE 8. Cross section of a fin ray from a Shovelnose Sturgeon captured in the Platte River, Nebraska. Circles represent varying interpretations on how readers depicted annuli. White circles show how large dark bands were interpreted as single annuli, whereas black circles attempt to identify many faint marks as multiple annuli.

Shovelnose Sturgeon may have developed a mutual understanding for ascertaining annuli that are difficult to interpret. Another factor that might affect reader agreement is the effect of a large sample size. Readers may spend more time studying a small set of samples knowing they have relatively few fish to age compared with a study with several hundred fish. Furthermore, aging a large sample of fin rays may simply reduce the odds of obtaining a high level of agreement, at least in relation to those studies that examined comparatively fewer samples.

The environment that the fish resides in likely influences both the growth mark deposition and the clarity of aging structures. Hamel et al. (2015a) reported varying growth characteristics of Shovelnose Sturgeon throughout their range, where fish from some populations continued to grow to a very large size (>700 mm), while other populations were characterized by relatively small fish (<600 mm) that experienced minimal to zero growth after presumably attaining sexual maturity. These differences would undoubtedly result in varying degrees of clarity and consistency of annulus deposition in fin rays. We initiated a pilot study in an attempt to further our understanding of age assignment using Shovelnose Sturgeon fin rays. A subset of cross-sectioned fin ray photographs ($n = 6$) were sent to eight Shovelnose Sturgeon biologists from various locations throughout the fish's range for age estimation. We requested that each individual place physical marks on the picture where they thought annuli were located. After collating the results, the mean difference in age estimates among readers for all six fin

rays was 4.66 years (range = 3–7 years), with the number of readers exactly agreeing among each other ranging from one to four agreements per fin ray (mean = 2.5).

Sensitivity analyses are commonly used when developing population viability models to demonstrate how various management decisions and variability in parameter estimates might affect outcomes (Beissinger 1995). A variety of parameter values can be influential in reducing the accuracy of population viability estimates. For example, McLoughlin and Messier (2004) used simulated populations to discover that error in initial population size accounted for the largest source of variability; whereas, Clark (1999) modeled a hypothetical fish population and reported that natural mortality rate had the greatest impact in biasing results. Koch et al. (2009) simulated the effects that variable age and growth estimates would have on yield-per-recruit models for Shovelnose Sturgeon. Those investigators adjusted ages to 2 and 5 years above and below the assigned ages, and similarly, increased or decreased growth estimates by 5% and 10% while holding all other parameters constant. Variable estimates for both age and growth resulted in similar recommendations to implement restrictive harvest regulations to circumvent overfishing. Our sensitivity analysis focused on assessing how a 15% range (28% to 43%) in total annual mortality affected our understanding of Shovelnose Sturgeon viability. Randomly selecting mortality rates within this range of estimates resulted in large discrepancies in estimated population size through time. Depending on the selected value of mortality, the hypothetical Shovelnose Sturgeon population was expected to exponentially rise or substantially decline within a relatively short time frame (30 years). These results are expected to be conservative as all other parameters in our model were deterministic. Including stochasticity in other metrics such as recruitment patterns or initial population size would further distort our understanding of long-term viability.

We have demonstrated the potential inaccuracies of using nonvalidated aging structures in Shovelnose Sturgeon and outlined the ramifications for using these structures to determine population level metrics for long-lived fishes. Age-determination errors are an impediment to understanding population dynamics using conventional age-based assessments; therefore, consequences of aging error should be considered when attempting to model population dynamic processes and long-term viability. In instances where aging structures have not been validated, alternative methods for calculating metrics used in population dynamics should be assessed and conservative estimates should be used to prevent errors in management decisions.

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