Fisheries Research 167 (2015) 13–21

Contents lists available at ScienceDirect

Fisheries Research

journal homepage: www.elsevier.com/locate/fishres

Validation of otolith ages for walleye (*Sander vitreus*) in the Winnebago System

Ryan P. Koenigs[a,*], Ronald M. Bruch[a], Robert S. Stelzer[b], Kendall K. Kamke[a]

[a] *Wisconsin Department of Natural Resources, Bureau of Fisheries Management, 625 East County Road Y, Suite 700, Oshkosh, WI 54901, USA*
[b] *University of Wisconsin Oshkosh, Department of Biology and Microbiology, 800 Algoma Boulevard, Oshkosh, WI 54901, USA*

ARTICLE INFO

Article history:
Received 3 April 2014
Received in revised form 16 January 2015
Accepted 18 January 2015
Handling Editor B. Morales-Nin
Available online 19 February 2015

Keywords:
Age estimation
Age validation
Otolith
Walleye
Recruitment index

ABSTRACT

Although accurate age data are essential when estimating somatic growth and mortality rates required to effectively manage exploited walleye (*Sander vitreus*) populations, aging structures have not been validated for age ranges present in most walleye populations. Otoliths and dorsal spines were collected from 302 walleye considered known age in the Winnebago System, Wisconsin, USA: 142 that were assigned ages via progression of discrete length modes following an individual strong year class (ages 0–3), and 160 (ages 4–10, 12–13, 16, 18) that were initially tagged at lengths small enough to accurately assign age ±1 year (<380 mm) and later recaptured and assigned an age (assigned age at tagging plus number of years at liberty). Paired aging structures were also collected from over 2000 additional walleye sampled during spawning assessments, tournament monitoring, and other surveys to better understand the relationship between spine and otolith age estimates and to compare catch curve residuals from structure and sex-specific catch curves to standard walleye recruitment indices. We found otoliths were accurate for walleye ages 0–10, while dorsal spines yielded relatively accurate age estimates for walleye ages 1–5, but underestimated age of walleye age-6 and older. Age distributions within catch curves constructed from otolith age estimates correlated well with measured year class strength, while age distributions from dorsal spine age estimates correlated poorly. Our results from fish considered known age validate the accuracy of otolith age estimates for walleye up to age-10, with corroborating evidence from catch curves and accurate recruitment indices strongly suggesting that otoliths are valid for all ages of Winnebago System walleye. We recommend the use of otoliths to accurately estimate walleye age, growth, and mortality, and to provide accurate age data for other population analyses.

1. Introduction

Although critical to effective use of fish age data, validation of the accuracy of growth increments counted on boney structures used to estimate age (e.g. scales, fin rays or otoliths) has often been neglected by fisheries biologists (Beamish and McFarlane, 1983; Campana, 2001). Accurate age data are essential for estimating rates of somatic growth and mortality, which are required for effective management of exploited populations. Walleye (*Sander vitreus*) are one of the most popular and actively managed recreational and commercial freshwater game-fish species in North America (Baccante and Colby, 1996; Carlander, 1997). However, walleye age estimates have not been validated for the range of ages present in most walleye populations, and the historic use of inaccurate walleye age data compromises the integrity of population analyses conducted with unacceptable age error (Koenigs et al., 2013).

Historically, scales have been the most common structure used to estimate walleye age as they are easy to collect and removal does not cause long-term damage to the fish. However, extensive peer-reviewed literature has documented that scales underestimate the age of older walleye (Campbell and Babaluk, 1979; Erickson, 1979, 1983; Belanger and Hogler, 1982). Dorsal spines and fin rays have been considered an alternative to scales for estimating fish age as they display annuli that are easier to identify, resulting in more precise age estimates (Campbell and Babaluk, 1979; Frie et al., 1989; Borkholder and Edwards, 2001). Like scales, spines or fin rays can be quickly collected without long-term negative impacts to the fish sampled. However, as with scales, spines display crowding of annuli on the edge of the aging structure when decreases in somatic growth occur following maturation, leading to the underestimation of age for larger, older fish (Erickson, 1979, 1983; Marwitz and Hubert, 1995; Logsdon, 2007; Koenigs et al., 2013).

* Corresponding author. Tel.: +1 920 303 5450.
E-mail addresses: ryan.koenigs@wisconsin.gov (R.P. Koenigs), Ronald.bruch@wisconsin.gov (R.M. Bruch), Stelzer@uwosh.edu (R.S. Stelzer), Kendall.kamke@wisconsin.gov (K.K. Kamke).

http://dx.doi.org/10.1016/j.fishres.2015.01.012
0165-7836/

In contrast to scale and spine growth, otolith growth is not proportional to fish growth. Otoliths grow slower than the body during periods of rapid body growth and quicker than the body during periods of slow body growth, which reduces the crowding of annuli that occurs near the edge of the aging structure, resulting in annuli that are easier to identify (Simkiss, 1974; Casselman, 1990). Subsequently, otoliths tend to yield older age estimates that have generally been found to be more accurate and precise than age estimates from other calcified structures (Erickson, 1979; Heidinger and Clodfelter, 1987; Kocovsky and Carline, 2000; Davis-Foust et al., 2009). For example, Erickson (1983) determined that mean age estimates derived from walleye otoliths were older than estimates from dorsal spines for fish age-11 and older in Eardley Lake and age-10 and older in Obukowin Lake, Manitoba. Similarly, Vandergoot et al. (2008) recommended that otoliths be used to age individuals in populations with a high proportion of older fish when he determined that anal spines from Lake Erie yellow perch *Perca flavescens* underestimated the age of fish older than age-6 relative to otoliths.

Although numerous studies have compared age estimates from calcified structures for walleye (Campbell and Babaluk, 1979; Erickson, 1983; Heidinger and Clodfelter, 1987; Kocovsky and Carline, 2000), few have compared the accuracy of age estimates from the different walleye aging structures. While otolith age estimates have been validated for a number of other fish species including freshwater drum *Aplodinotus grunniens* (Davis-Foust et al., 2009), lake sturgeon *Acipenser fulvescens* (Bruch et al., 2009), striped bass *Morone saxatilis* (Secor et al., 1995), and largemouth bass *Micropterus salmoides* (Taubert and Tranquilli, 1982; Buckmeier and Howells, 2003), we failed to find any studies from the peer-reviewed literature that examined the accuracy of walleye age estimates derived from otoliths, or any aging structure, using known-age fish from a wide range of walleye age classes. Erickson (1983) assessed the accuracy of walleye age estimates derived from scales and otoliths from 100 known-age fish from a single age-3 year class, whereas Heidinger and Clodfelter (1987) investigated the accuracy of various aging structures from 0 to 4 year old known-age walleye. While these studies made valuable contributions to the fisheries literature and expanded the understanding of the accuracy of walleye age estimates, they did not examine a wide range of walleye age groups and thus do not meet the standards required to approach full age validation (Campana, 2001). Validation of age estimates from all age groups is necessary for assessing age group bias and the impacts that aging error can have on management decisions (Buckmeier and Howells, 2003).

Maceina (1997) proposed using residuals from catch curves as a potential recruitment index. However, Quist (2007) proposed that the catch curve residual technique was not a valid measure of recruitment. Annual walleye recruitment data collected during standardized bottom trawl assessments (1986–2012) on the Winnebago System provided an opportunity to examine the use of accurate walleye year class strength indices as corroboratory evidence for the relative abundance and subsequently age estimates of older walleye represented in catch curves.

Our study objectives were (1) to utilize accepted age validation and corroboration techniques to determine the accuracy and precision of age estimates derived from otoliths and dorsal spines for Winnebago System walleye ages 1–18 or older and (2) to examine the usefulness of catch curve residual analysis for corroborating age composition of adult walleye in the Winnebago System.

2. Materials and methods

2.1. Study area

The Winnebago System is a large, shallow (<7 m), eutrophic ecosystem in east-central Wisconsin composed of Lake Winnebago

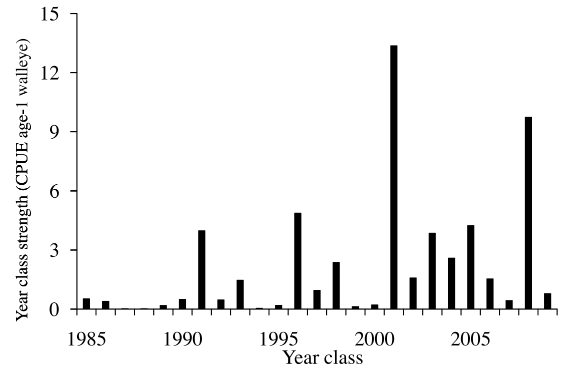

Fig. 1. Year class strength of walleye indicated by catch-per-unit-effort (CPUE) of age-1 walleye captured during August–October standardized bottom trawling assessments conducted on Lake Winnebago, Wisconsin (1986–2010).

(44.0222° N, 88.4231° W) and three smaller lakes (Butte des Morts, Winneconne, and Poygan), which collectively comprise 668 km^2 of surface water. The upper Fox River and the Wolf Rivers (along with their major tributaries) flow into the lakes, draining a 15,540 km^2 watershed. The floodplain of the lower 60 km of the upper Fox River and the lower 200 km of the Wolf River upstream of the lakes contain an extensive network of old river channels, oxbows, and bottomland forest and marsh, which in most years carry spring flood waters over wet meadows, providing spawning habitat for walleye. Walleye are abundant in the Winnebago System and are the primary focus of a high-profile, year-round recreational fishery that has an annual regional economic impact of $234 million (Cook and Neiswender, 2007).

2.2. Collection of known age fish

"Known age" in this study refers to walleye captured or tagged when their age was known or could be reasonably approximated from their size (Campana, 2001). "True age" refers to the age determined from years at large of recaptured known age fish. A very large year class of walleye in the Winnebago System in 2008 (along with very poor year classes in 2007 and 2009) and long-term annual floy tagging of adult walleye, including 10s of thousands of first spawning males from 1993 to 2010, provided a unique opportunity to capture relatively large numbers of walleye whose age at capture could be reasonably approximated for this study. A similar approach for identifying known-age fish was used for validating age estimates of lake sturgeon (Bruch et al., 2009), bluefin tuna *Thunnus thynnus* (Lee and Prince, 1995), and yellow tail flounder *Limanda ferruginea* (Dwyer et al., 2003).

Known age walleye, ages-0–3, from the abundant 2008 year class were sampled monthly during August–October 2008, May–October 2009, April–October 2010, and April 2011 to monitor modal length progression of the year class per Campana (2001). The 2008 walleye year class was the second largest year class documented on the Winnebago System during 1986–2010, preceded in 2007 and followed in 2009 by weak year classes (Fig. 1). Growth of 0–3-year-old walleye in the Winnebago System is rapid, and the 2008 year class could be identified from length frequency plots constructed from data collected during assessments conducted from August 2008 to April 2011, and thus these were considered known age fish. To eliminate any possible sampling overlap with the adjacent weak 2007 and 2009 year classes, known age fish from the 2008 year class were sampled from the central, more abundant size classes observed within length distributions of the fish sampled for this part of the study. Samples of at least 100 walleye ≤380 mm were collected and measured during nighttime electro-fishing surveys conducted on Lake Winnebago during May and June (2009–2010) and April 2010; daytime electro-fishing during spawning assessments conducted on the Wolf River in April 2011; and bottom trawling assessments conducted on Lake Winnebago during 1–2 days (10–15 total trawl hauls) in July (2009–2010) and 5 days (46 total trawl hauls) in each month of August–October (2008–2010). Fish ≤380 mm represented the size range that ensured the 2008 year class would be sampled during all aforementioned surveys. Electro-fishing was conducted with a standard Wisconsin-style boom shocker with pulsed D/C current (5–13 amperes, 50 pulses/s, duty cycle of 25). Trawling assessments were conducted with a balloon trawl, similar to that described by Davis-Foust et al. (2009), towed 5 min per haul at a speed of 6.6 km per hour, resulting in a sampling area of 0.4 ha per haul. Total length of all walleye sampled for age was measured to the nearest mm. A stratified random sample of five fish per 13 mm length class of walleye ≤380 mm was euthanized to collect dorsal spine and otolith samples in May 2009, August 2009, April 2010, and April 2011. Age estimates from dorsal spines and otoliths were compared to known ages assigned from length-frequency plots to determine the accuracy of age estimates from each structure. Sex and maturity were determined for all euthanized fish by visual examination of the shape, color, and development of the gonads (Wisconsin Department of Natural Resources (WDNR), Oshkosh, unpublished data).

Since 1989, the WDNR has used Floy anchor tags (FD-94, Floy Tag Inc., Seattle, WA) to annually mark walleye on the upper Fox and Wolf Rivers during spawning migrations out of the Winnebago Pool lakes. Recaptured adult male walleye that were initially tagged at an age that could be reasonably approximated (age-3 or age-4 ±1 year) based on length were considered known age fish per Campana (2001). Preliminary otolith and dorsal spine age estimates showed that adult male walleye <343 mm were typically estimated to be age-3, while adult male walleye 343–380 mm were age-4. Some overlap of age classes was observed within the established length bins, but all ages were assigned within the accepted error of ±1 year. True ages of recaptured walleye were determined by adding the number of years at large since tagging to the assigned age at tagging. Known age walleye older than age-3 were sampled during April spawning assessments conducted on the upper Fox and Wolf Rivers using electro-fishing (3–6 amperes, all other settings as described earlier) during 2009–2014 and fyke nets (1 m high, 19 mm bar mesh) in 2011. All recaptured walleye that were initially tagged at total lengths ≤380 mm and recaptured during 2009–2014 surveys were considered known-age fish and euthanized for collection of aging structures.

2.3. Otolith and spine paired age analysis

Additional adult male and female walleye were captured during April spawning assessments (2009–2011) to better understand the relationship between spine and otolith age estimates, to estimate the age composition of the adult stock, and to compare residuals from aging structure and sex-specific catch curves to long-term standardized trawling recruitment indices for Winnebago System walleye. All captured walleye were measured to the nearest 0.1 in. and weighed to the nearest 0.02 pounds (field measurements were taken in English and later converted to Metric). Paired otolith and dorsal spine samples were collected from male walleye during spawning assessments (8–16 fish per 0.5 in. (12.7 mm) length class, with increased sampling of larger size classes to account for greater age variability within larger length bins). Due to the high-profile nature of the spring fishery and the value placed on adult female walleye by the public, paired aging structures were collected from walleye mortalities at summer fishing tournaments rather than during spring stock assessments. After weigh in, angler-registered walleye considered un-releasable were measured to the nearest 0.1 in. and weighed to the nearest 0.02 pounds (field measurements were taken in English and later converted to Metric). Sex and maturity of each dead fish was determined using established criteria based on color, shape, and development of the gonads used in the Winnebago walleye management program (WDNR, Oshkosh, unpublished data). Dorsal spines and otoliths were removed from a random sample of female walleye as described earlier.

Dorsal spines and otoliths were also collected from walleye sampled during disease (Viral Hemorrhagic Septicemia) testing conducted on the Winnebago System, 2009–2011. These walleye age estimates supplemented data collected from known age and additional fish sampled during April spawning assessments, summer trawling, and June tournament monitoring.

2.4. Fish age estimation from calcified structures

The second or third dorsal spine was cut as close to the skin interface as possible with a surgical clippers, placed in scale envelopes and allowed to dry for a minimum of 2 weeks. Excess dry tissue was removed before using a Buehler Isomet low speed saw to cut 0.30–0.50 mm sections, using glycerol as a blade lubricant. Reader 1, with 40 years of aging experience, estimated age from spine sections (by counting the number of observed annual growth rings) using a Meiji microscope at 25–45× magnification with dark field transmitted light. Reader 2, with 4 years of experience, estimated age from spine sections with an Olympus SZX7 stereomicroscope at 25–56× magnification using dark field transmitted light. Age estimates from both readers, made without any knowledge of fish sex or size, were used to calculate precision of dorsal spine age estimates. Age estimates from the more experienced Reader 1 were used to compare age estimates derived from dorsal spines and otoliths to ensure consistency between past and present aging techniques for error assessment.

Otoliths were extracted ventrally and placed in perforated vials to minimize breakage and allowed to air dry for a minimum of 30 days. Otoliths were then embedded in Epo-Quick two-part epoxy for a minimum of 24 h before 0.30–0.40 mm sections were cut using a South Bay Technology low speed diamond wheel saw, Model 650, using water as a blade lubricant. Reader 2 estimated age using an Olympus SZX7 stereomicroscope at 25–56× magnification with bright field transmitted light. Isopropyl alcohol (50%) was occasionally used to help clear sections, and no polishing was done. An Olympus DP 71 camera was used to archive photographs of the sections for age assignment from Reader 3 (with 2 years' fish aging experience). Age estimates from both readers were made without knowledge of fish sex and size, and were used to calculate precision of otolith age estimates. Otolith age estimates from Reader 2 were compared to dorsal spine age estimates from Reader 1 to examine structural age bias.

2.5. Assessing accuracy and precision of age estimates

Campana et al. (1995) recommended that age bias plots be used to detect linear and nonlinear biases in age data, and thus were used in this study to assess accuracy of age estimates from otoliths and dorsal spines. Assigned ages from known age walleye sampled during the progression of the length mode procedures and mark-recapture exercises were plotted against mean age estimates derived from dorsal spines and otoliths for each age class. Age estimates from all paired aging structures collected throughout the study (known age fish, April spawning assessments, June tournament monitoring, and other additional sampling) were incorporated into age bias plots (otolith age plotted against mean dorsal spine age estimate) to determine whether systematic differences existed between age estimates derived from otoliths and dorsal spines for male and female walleye (Campana et al., 1995).

Coefficient of variation (CV = 100 × SD/mean) and percent agreement (percent of cases where age estimates were identical between the two readers) were calculated to assess the precision of male and female age estimates derived from dorsal spines and otoliths. Coefficients of variation of age estimates derived from these structures were calculated for each individual fish collected throughout the study. Mean CV was then calculated by sex for each age class to assess whether precision varied with increasing age. Percent agreement between dorsal spine and otolith age estimates derived from different readers was also calculated by sex for each age class to assess whether precision of age estimates varied with increasing age.

2.6. Age corroboration through catch curve analysis

Although age corroboration is not age validation, a well-designed corroboratory study can support and strengthen a properly designed validation study to confirm the accuracy of age estimates (Campana, 2001). Since we were unable to adequately sample known-age walleye older than age-10, we constructed sex-specific catch-curves to corroborate age estimates from older walleye by observing whether estimated strong age classes (age distributions derived from otolith and dorsal spine age estimates) corresponded with strong year classes from empirical catch per unit effort (CPUE) of age-1 walleye during standardized fall trawling assessments on Lake Winnebago (per Campana, 2001). Otolith and dorsal spine age data from adult male walleye collected during April 2009–2011 spawning assessments and adult female walleye collected during June 2009–2010 tournament monitoring were incorporated into structure and sex-specific age-length keys to assign age to all fish sampled during April spawning assessments (Ricker, 1975), and to observe the relative abundances of year classes within each year's sample. Assigned ages from age-length keys were then used to construct structure and sex-specific catch curves for adult male and female walleye collected during 2009–2011 spawning assessments (Robson and Chapman, 1961). The first ages represented in catch curves were age-4 for male walleye and age-5 for female walleye (ages at which >85% of male walleye and >95% of female walleye are mature: WDNR, Oshkosh, unpublished data). Residual values from structure and sex-specific catch curves were calculated to represent relative strength of age classes within the samples (Maceina, 1997). These values were calculated by subtracting the observed value in the catch curve from the predicted value for each age class (inserting the age into the equation from the linear regression $\log_e$ of the number of fish sampled in each age on the age class of walleye). Catch per unit effort values for age-1 walleye captured during standardized trawling assessments on Lake Winnebago (spanning 1986–2010) were used as a measure of year class strength. Residual values from the catch curves and trawling CPUE of age-1 walleye were standardized and scaled to have a mean of 0 and a standard deviation of 1, and then plotted as age vs. standardized year class strength (CPUE age-1 walleye) and age vs. standardized estimates of age class strength (catch curve residuals). Pearson product moment correlation coefficients (r) were calculated to determine the amount of agreement between the standardized CPUE values from trawling assessments and the standardized residual values from otolith and dorsal spine based catch curves. A positive or negative Pearson product moment value of 0.5–1.0 indicates the strength of the association is strong; a value of 0.3–0 indicates strength of association is small to absent (Laird Statistics, 2013). Strong correlation between standardized year class strength and age specific standardized catch curve residuals would provide corroboratory evidence about the accuracy of the age estimates of walleye whose ages were used to develop the catch curves.

Table 1
Age, sample size (n), and mean otolith and dorsal spine age estimates for walleye considered known-age collected on the Winnebago System, Wisconsin (2009–2014). Known-age walleye ages-0–3 were assigned true ages by following modal length of the strong 2008 year class, while known-age walleye ages-4–18 were assigned true ages by adding the number of years at large since tagging to the assigned age at tagging based on length (±1 year).

Age	n	Mean age estimate	
		Otolith	Dorsal spine
1	40	1.00	0.95
2	86	2.02	2.31
3	16	3.00	3.31
4	12	4.23	4.46
5	76	4.63	4.79
6	38	5.66	5.63
7	15	6.50	6.29
8	5	8.00	7.20
9	3	8.67	8.67
10	7	9.67	7.67
12	1	13.00	9.00
13	1	13.00	10.00
16	1	16.00	12.00
18	1	18.00	16.00

3. Results

3.1. Accuracy of age estimates using fish considered known age

A total of 302 walleye considered known-age were collected during the study period (Table 1). Monitoring the modal growth of the 2008 year class was used to assign known age to 142 of these fish (ages-1–3), while mark-recapture techniques were used to assign known age to the remaining 160 fish (ages-4–18) (Campana, 2001). Growth increments were distinct on otolith cross sections from all walleye sampled for age (Fig. 2, upper panel). Inner annuli on dorsal spines were clearly discernible for most fish, but outer annuli were difficult to identify with confidence for older fish due to crowding of annuli at the edge of the structure (Fig. 2, lower panel). Mean age estimates derived from dorsal spines overestimated the age of 2- and 4-year-old known-age walleye, while underestimating the age of known-age fish 6 years of age and older (Fig. 3(A)). In comparison, mean age estimates from otoliths corresponded well with known-age for all ages of walleye sampled (Table 1, Fig. 3(B)).

3.2. Otolith and spine paired age comparisons

Paired aging structures were collected from 2181 walleye (1161 male walleye and 1020 female walleye, known-age fish included). Estimated ages from otoliths ranged from 0 to 20 years for male walleye and 0 to 19 years for female walleye, while age estimates derived from dorsal spines ranged from 0 to 16 years for both male and female walleye (Fig. 4). Age estimates from dorsal spines and otoliths were in close agreement for both male and female walleye ages-0–6, but otoliths yielded significantly older age estimates than dorsal spines for walleye age-7 and older (Fig. 4). Discrepancies between mean age estimates derived from the two structures for individual age classes ranged from −0.31 to 7.40 years for male walleye and −0.22 to 5.00 years for female walleye. Discrepancies between structure-based age estimates increased with increasing age for both sexes (Fig. 4).

3.3. Precision of age estimates

Otolith age estimates were more precise than dorsal spine age estimates for both male (otolith CV = 0.92%, dorsal spine CV = 6.24%) and female walleye (otolith CV = 0.53%, dorsal spine CV = 6.08%). No trends were observed for males or females between age and estimated CV values (Fig. 5 illustrates the relationship between age

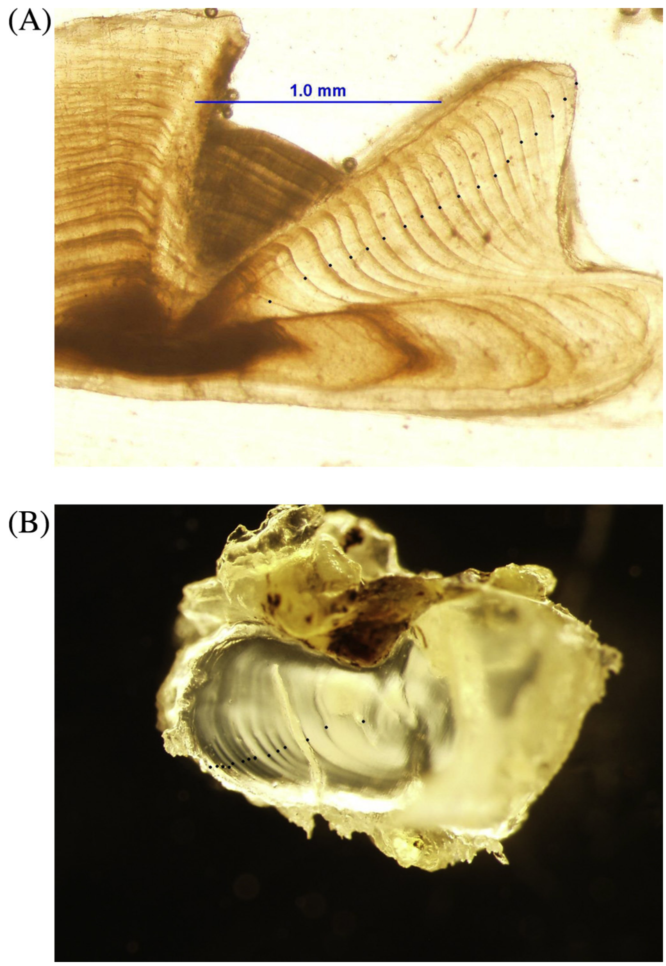

Fig. 2. Growth increments observed on an (A) otolith and a (B) dorsal spine removed from a 554 mm male walleye sampled in April 2010 on the Winnebago System, Wisconsin. Black circles indicate approximate locations of interpreted annuli (18 years from otolith and 14 years from dorsal spine). The edge was counted as an annulus because the fish was sampled in April, and therefore the annulus had not yet formed.

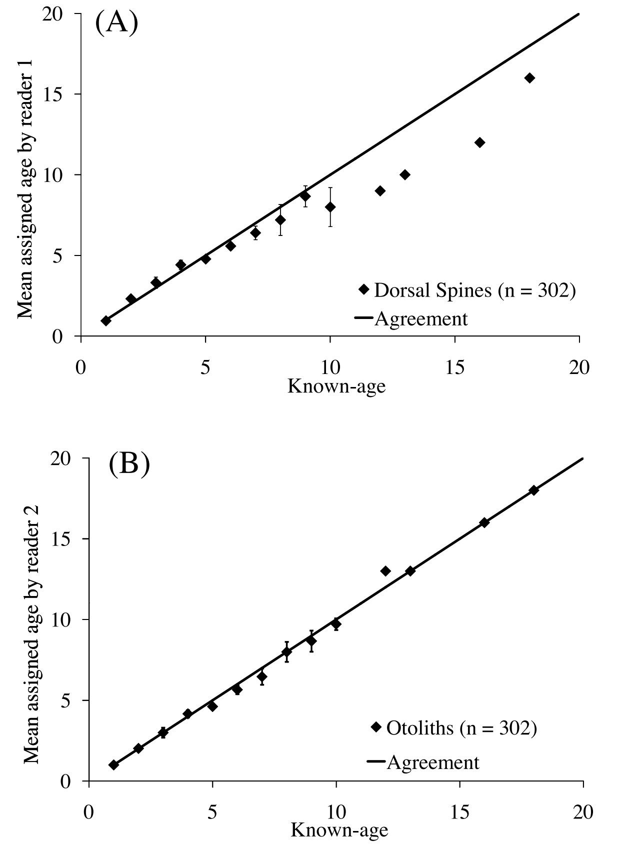

Fig. 3. Age bias plots comparing known-age to mean age estimates from (A) dorsal spines and (B) otoliths for known-age walleye sampled in the Winnebago System, Wisconsin (2009–2014) (solid line represents 1:1 agreement line and error bars represent 95% confidence intervals around the mean, $n = 302$). Per Campana (2001) walleye considered known-age ages-0–3 were assigned true ages by following modal length of the strong 2008 year class, while walleye considered known-age ages-4–18 were assigned true ages through mark-recapture methods where the years at large since tagging was added to the assigned age at tagging based on length (±1 year).

and CV for females). Percent agreement of otolith age estimates between readers was greater than 95% for 15 of the 17 age classes observed in female walleye (Fig. 5) and 13 of the 20 age classes observed in male walleye. Two age classes of male walleye otolith age estimates (age-17 and age-20) were small samples and subsequently exhibited poor precision. Percent agreement of dorsal spine age estimates decreased with increasing fish age (females: Fig. 5).

Mean spine age estimates from Reader 1 were in close agreement with age estimates from Reader 2 for male walleye estimated to be ages-0–9 and female walleye estimated to be ages-0–11. The less-experienced spine reader (2) though typically assigned a younger age, relative to age assignments from Reader 1, for male walleye estimated to be age-10 and older and female walleye estimated to be age-12 and older. No bias was observed in reader agreement for otolith age estimates.

3.4. Age corroboration through catch curve analysis

Standardized catch curve residuals correlated well with standardized age-1 CPUE data for both sexes when otolith age data were used to construct catch curves but not when dorsal spine age data were used to construct catch curves (Table 2, Figs. 6 and 7). Otolith age data indicated that the oldest walleye in the samples were estimated to be age-18 in 2009, age-19 in 2010, and age-20 in 2011. These age classes in the respective years represent the 1991 year class, which was the first strong year class encountered after 5 or more years of non-measurable recruitment (assessment trawling began in 1986) (Fig. 1). No fish were estimated to be older than age-16 with dorsal spines and no relationship was observed between fish from the strong 1991 year class and age compositions developed based on spine age data.

Table 2
Pearson product moment correlation coefficient values between standardized values of age-1 trawl CPUE (August–October assessment trawling) and residuals from catch curves constructed from otolith and dorsal spine age estimates derived from adult male and female walleye sampled during April spawning assessments conducted on the Winnebago System, Wisconsin (2009–2011). A positive or negative value of 0.5–1.0 indicates the strength of the association is strong; 0.3–0 indicates strength of association is small or absent (Laird Statistics, 2013).

	Male		Female	
	Otolith	Dorsal spine	Otolith	Dorsal spine
2009	0.54	0.13	0.62	0.40
2010	0.62	0.17	0.70	−0.17
2011	0.62	−0.29		

4. Discussion

Otoliths provide the most accurate and precise estimates of age for walleye while dorsal spines underestimate true age, and given

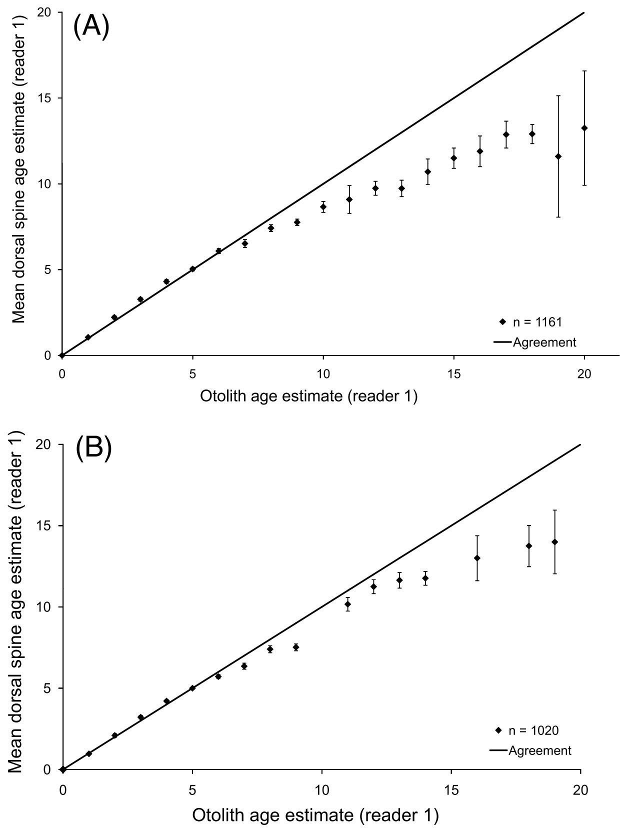

Fig. 4. Age bias plots comparing otolith age estimates to mean dorsal spine age estimates for (A) male (n = 1161) and (B) female walleye (n = 1020) sampled from the Winnebago System, Wisconsin (2009–2011). Solid lines represent 1:1 agreement, and error bars represent 95% confidence intervals around the mean dorsal spine age estimates.

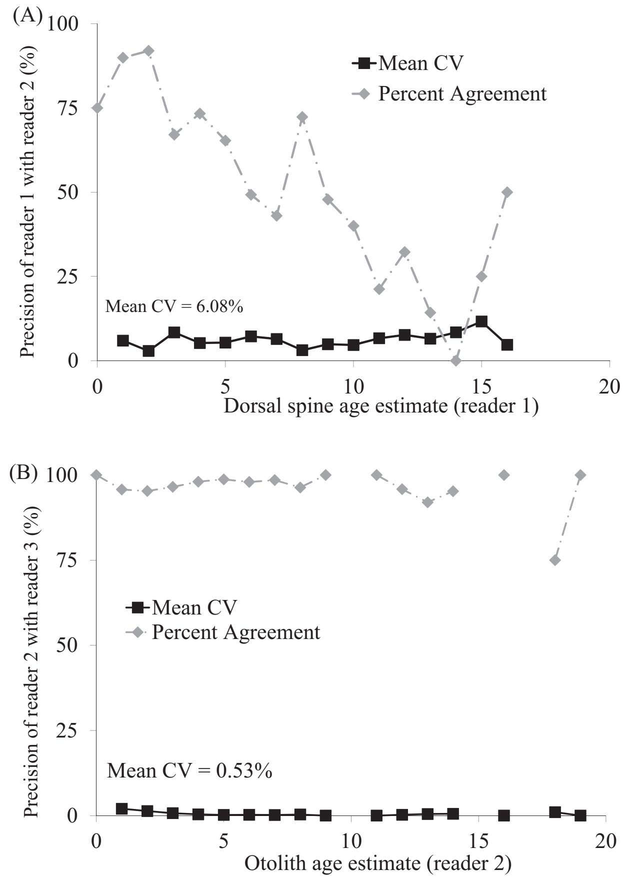

Fig. 5. Precision of mean coefficient of variation (CV) and percent agreement of (A) dorsal spine age estimates and (B) otolith age estimates from female walleye. Walleye were collected during fisheries surveys conducted on the Winnebago System, Wisconsin (2009–2011).

the general acceptance of their overall inaccuracy and imprecision (Erickson, 1983) scales were not evaluated as part of this study. The age validation results for walleye in this study complement results previously reported showing otolith age estimates were accurate for walleye up to age four (Erickson, 1983; Heidinger and Clodfelter, 1987), and expand the range of validated ages using otolith age estimates up to at least age-10, with strong corroboratory evidence from catch curve and year class strength analyses indicating that otolith age estimates are likely accurate for older walleye. These findings add to the growing body of literature reported earlier demonstrating that otolith-based age estimates are accurate, while scale and-spine based estimates are not accurate, especially for older fish. Age estimates from walleye otoliths were also found to be more precise than those from dorsal spines, complementing other studies reporting similar results for walleye age estimates (Marwitz and Hubert, 1995; Kocovsky and Carline, 2000; Isermann et al., 2003; Logsdon, 2007).

The differences between dorsal spine and otolith age estimates were more pronounced for Winnebago System male walleye than for female walleye. Kocovsky and Carline (2000) attributed differences in relative precision of age estimates between male and female walleye to gender-related differences in growth and age at sexual maturity. Female walleye typically have greater asymptotic lengths than male walleye and continue to grow after reaching maturity. Slower somatic growth rates for male walleye, especially after maturity, may result in more extreme crowding of annuli near the edge of the dorsal spine section, making annuli more difficult to identify (Kocovsky and Carline, 2000).

Generally researchers believe that faster growing fish can be more accurately and precisely aged than slower growing fish; and many factors such as trophic status, level of exploitation, and population density can affect fish growth and in turn the accuracy and precision of age estimates (Belanger and Hogler, 1982; Frie et al., 1989; Robillard and Marsden, 1996; Kocovsky and Carline, 2000). Erickson (1979, 1983) estimated similar ages from scales, sectioned dorsal spines, and sectioned otoliths for walleye in Lakes Winnipeg and Winnipegosis, Manitoba, where walleye were heavily exploited and exhibited fast somatic growth rates. In contrast, scales and dorsal spines underestimated the age of older fish relative to otoliths in Lakes Eardley and Obukowin, Manitoba, where walleye experienced little to no exploitation and had slower growth rates (Erickson, 1979, 1983). The Winnebago System is a eutrophic water body with moderate to high levels of exploitation (mean annual exploitation rates of 22.6% for female walleye and 14.7% for male walleye spanning 1993–2011) (Koenigs et al., 2013), which theoretically should contribute to above average growth rates of walleye and increased accuracy of age estimates from dorsal spines. Despite relatively fast growth, our results indicated that age estimates from dorsal spines consistently underestimated the age of walleye age-7 and older relative to otoliths. Given the longevity of walleye within the Winnebago System (20+ years) and the potential for walleye to live even longer in more oligotrophic waters in northern latitudes, it is imperative that the relationship between age estimates from otoliths and dorsal spines (and possibly scales for use of historic age data) is well understood. Changes in lake trophic status, exploitation, densities, forage, or other factors may affect fish growth and structure increment formation (Belanger and Hogler, 1982; Marwitz and Hubert, 1995). Additional or periodic comparisons of age estimates from walleye

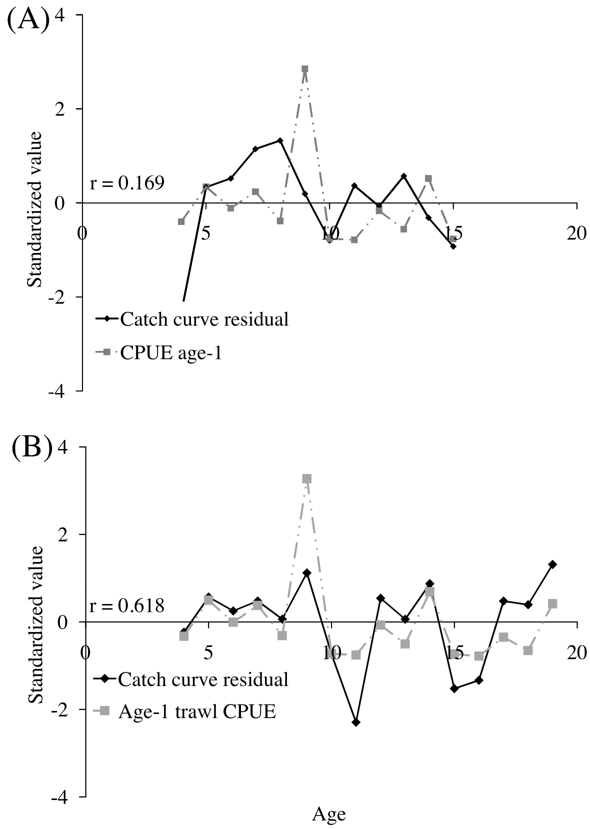

Fig. 6. Plot comparing standardized values of trawl CPUE of age-1 walleye (dashed line) and standardized residual values from a catch curve (solid line) constructed from (A) dorsal spine age estimates and (B) otolith age estimates for adult male walleye sampled during April spawning assessments conducted on the Winnebago System, Wisconsin in 2010.

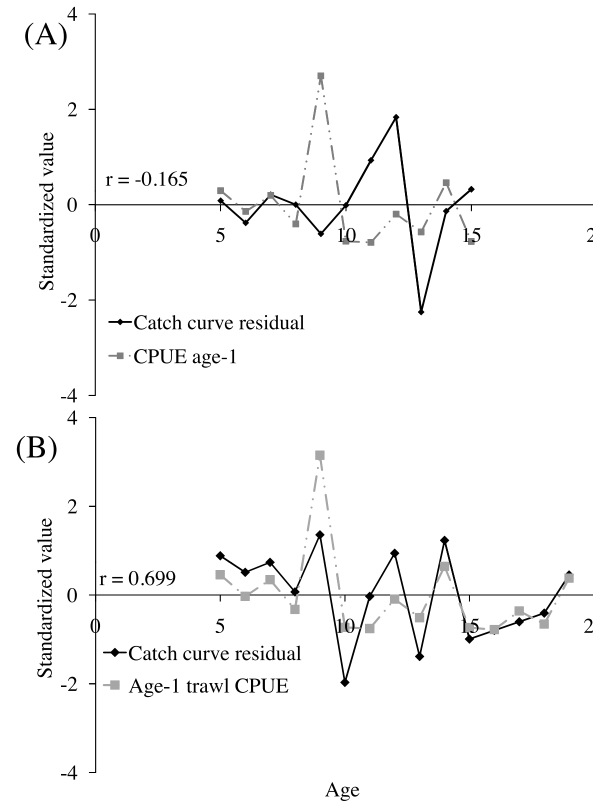

Fig. 7. Plot comparing standardized values of trawl CPUE of age-1 walleye (dashed line) and standardized residual values from a catch curve (solid line) constructed from (A) dorsal spine age estimates and (B) otolith age estimates for adult female walleye sampled during April spawning assessments conducted on the Winnebago System, Wisconsin in 2010.

otoliths and other structures from waters throughout the species' range would greatly contribute to the understanding of the impact of system dynamics on the consistency of growth increments on the structures.

Reader experience along with the type of structure being used can also affect fish age estimation. In this study, the more experienced dorsal spine reader was able to discern older age estimates than the less experienced reader for dorsal spines from larger walleye, while there was no apparent difference in otolith age estimates between the two readers. Vandergoot et al. (2008) observed that scale and anal spine age estimates from a less-experienced reader underestimated age of Lake Erie yellow perch older than age-4 relative to an experienced reader. These trends suggest that less training would be required to accurately and precisely estimate walleye age with otoliths relative to dorsal spines, and that other factors contributing to error would be minimized by using otoliths to estimate age.

Although Quist (2007) argued that residuals from catch curves should not be used to index walleye recruitment due to variation in natural and fishing mortality rates among year classes, the strong correlation between year class strength and age-specific standardized catch curve residuals from otolith age data for Winnebago System walleyes indicate that in some situations residuals can be used to index recruitment and adult stock age composition; and that they can provide strong corroboratory evidence that age estimates from otoliths are accurate for walleye of all ages. Isermann et al. (2002) suggested and Quist (2007) agreed that year class strength indices based on long-term, standardized assessment will provide a good measure of recruitment. The walleye recruitment data we used in our catch curve residual-year class strength analysis to corroborate the accuracy of older walleye otolith ages were produced by extensive standardized assessment trawling on Lake Winnebago designed to measure relative annual walleye recruitment. Further Quist's (2007) evaluation of walleye recruitment indices were based primarily on age estimates from scales, which may have introduced substantial error into his analyses, i.e. the inconsistencies in relationships found by Quist (2007) between the various recruitment indices he evaluated and year class strength, including catch curve residuals, may have been confounded by aging error, although this potential source of error was not addressed in his paper. With a sound age sampling strategy, (i.e. a non-biased sampling scheme where more larger fish are sampled to account for variation in age within length bins) otolith age estimates will accurately represent the age distribution of the sampled stock and the resultant catch curves and estimates of total annual mortality should be valid, along with the resultant residuals as indices of adult stock age composition and year class recruitment. In our study, standardized residuals from catch curves developed using dorsal spine age estimates did not correlate well with standardized year class strength data (similar to Quist's, 2007 results with scale ages), suggesting that spine age estimates, unlike otolith age estimates, were not accurately representing the age distribution of the adult walleye stock in the Winnebago System and subsequently provided inaccurate estimates of total annual mortality and relative recruitment. Quist (2007) raised very important points about the impact of variable mortality among year classes on the validity and applicability of recruitment indices. Some of the noise seen in recruitment indices could very well be due to this factor, but aging error introduces such substantial initial noise into any analyses using age based data and makes any further evaluation of factors affecting recruitment very difficult if not impossible to discern. In the end, the strength and accuracy of the walleye otolith age validation and long-term annual recruitment data from the Winnebago System appears to support the conclusion that the catch curve-recruitment residuals analysis for age corroboration was valid, and that otolith ages of older walleye out to age 20 estimated as part of this validation study are accurate.

Accuracy of otolith age estimates of older fish was also corroborated by the persistent presence of walleye from the strong 1991 year class in each sampling year from 2009 to 2011. Ultimately important insight will be gained into the longevity of walleye in the Winnebago System as the 1991 year class is followed through time via otolith age sampling. A similar phenomenon was observed for the very large 1983 year class of freshwater drum in Lake Winnebago which was consistently strongly represented in otolith based age frequencies sampled between 1986 and 2009 (Davis-Foust et al., 2009).

Based on the results of this study, we recommend that otoliths be used to age walleye as they provide more accurate and precise age estimates than any other structure. Although aging with otoliths does require euthanizing fish, which may be viewed as an obstacle by some fisheries managers, the number of fish that need to be sacrificed in age-structured subsamples from many exploited walleye populations is relatively small compared to the total harvest by anglers (Isermann et al., 2003). In scenarios where euthanization is not possible during fisheries surveys, we recommend collecting paired aging structures (otoliths and spines) from dead walleye whenever possible (e.g. lethal testing, fish kills, and/or harvest by recreational anglers, Native American tribes, and commercial fisherman). By aging paired structures, managers can better understand the relationship between age estimates from these structures and the impacts that aging error may have on estimates of growth and mortality within the population and lead to more effective fisheries management. Aging paired structures also provides an opportunity to develop age sampling strategies utilizing non-lethal structures for younger or faster growing fish to accurately estimate age. For example, Koenigs et al. (2013) reported that dorsal spines yielded relatively accurate age estimates for male walleye <457 mm and female walleye <508 mm, while otoliths were required to obtain accurate age estimates for fish larger than these critical sizes. Error in scale and spine age estimates may also be corrected using an age-error matrix to adjust erred estimates to more accurate estimates of true age (Secor et al., 1995; Bruch et al., 2009). Given the tools available today and the growing body of literature on accuracy and precision (or lack thereof) of estimates from various boney structures of walleye and other important fish species, using only structures that provide accurate and precise age data should be the standard in Fisheries Management programs. Using structures that result in inaccurate age data that underestimate walleye age, overestimate mortality rates and result in inaccurate analyses or assessment of a walleye stock at best leads to inefficient harvest management, and at worst, increases the risk of serious mismanagement or overexploitation.

Acknowledgments

We thank the Oshkosh Fisheries Management Staff of the Wisconsin Department of Natural Resources for collecting data that were included in this analysis. We also thank Jack O'Brien and Eli Felts for their efforts and expertise with age estimation, and Greg Adler, Tim Simonson, and Tom Cichosz for providing critical review of the manuscript. This research was made possible by an education grant donated by Walleyes for Tomorrow, while the technical work was funded by the Federal Aid in Sport Fish Restoration Program.

References

Baccante, D.A., Colby, P.J., 1996. Harvest, density, and reproductive characteristics of North American walleye populations. Ann. Zool. Fenn. 33, 601–615.
Beamish, R.J., McFarlane, G.A., 1983. The forgotten requirement for age validation in fisheries biology. Trans. Am. Fish. Soc. 112, 735–743.
Belanger, S.E., Hogler, S.R., 1982. Comparison of five ageing methodologies applied to walleye (*Stizostedion vitreum*) in Burt Lake, Michigan. J. Gt. Lakes Res. 8 (4), 666–671.
Borkholder, B.D., Edwards, A.J., 2001. Comparing the use of dorsal fin spines with scales to back-calculate length-at-age estimates in walleyes. N. Am. J. Fish. Manag. 21, 935–942.
Bruch, R.M., Campana, S.E., Davis-Foust, S.L., Hansen, M.J., Janssen, J., 2009. Lake sturgeon age validation using bomb-radiocarbon and known-age fish. Trans. Am. Fish. Soc. 138, 361–372.
Buckmeier, D.L., Howells, R.G., 2003. Validation of otoliths for estimating ages of largemouth bass to 16 years. N. Am. J. Fish. Manag. 23, 590–593.
Campana, S.E., Annand, M.C., McMillan, J.I., 1995. Graphical and statistical methods for determining the consistency of age determinations. Trans. Am. Fish. Soc. 124, 131–138.
Campana, S.E., 2001. Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. J. Fish Biol. 59, 197–242.
Campbell, J.S., Babaluk, J.A., 1979. Age determination of walleye, *Stizostedion vitreum vitreum* (Mitchill), based on the examination of eight different structures. Fisheries and Marine Service Technical Report No. 849. Department of Fisheries and the Environment, Winnipeg, MB.
Carlander, K.D., 1997. Handbook of Freshwater Fishery Biology, vol. 3. Iowa State University Press, Ames, IA.
Casselman, J.M., 1990. Growth and relative size of calcified structures of fish. Trans. Am. Fish. Soc. 119, 673–688.
Cook, C., Neiswender, C., 2007. The economic impact of angling on the Lake Winnebago System. University of Wisconsin Extension Winnebago County, Oshkosh, WI.
Davis-Foust, S.L., Bruch, R.M., Campana, S.E., Olynyk, R.P., Janssen, J., 2009. Age validation of freshwater drum using bomb radiocarbon. Trans. Am. Fish. Soc. 138, 385–396.
Dwyer, K.S., Walsh, S.J., Campana, S.E., 2003. Age determination, validation and growth of Grand Bank yellowtail flounder (*Limanda ferruginea*). ICES J. Mar. Sci. 60, 1123–1138.
Erickson, C.M., 1979. Age differences among three hard tissue structures observed in fish populations experiencing various levels of exploitation. Manitoba Department of Natural Resources, MS Report No. 79-77.
Erickson, C.M., 1983. Age determination of Manitoban walleyes using otoliths, dorsal spines, and scales. N. Am. J. Fish. Manag. 3, 176–181.
Frie, R.V., Anderson, J.K., Larson, M.J., 1989. Age verification of walleye from Lake of the Woods, Minnesota. J. Gt. Lakes Res. 15, 298–305.
Heidinger, R.C., Clodfelter, K., 1987. Validity of the otolith for determining age and growth of walleyes, striped bass, and smallmouth bass in power plant cooling ponds. In: Summerfelt, R.C., Hall, G.E. (Eds.), Age and Growth of Fish. Iowa State University Press, Ames, IA, pp. 241–251.
Isermann, D.A., McKibbin, W.L., Willis, D.W., 2002. An analysis of methods for quantifying crappie recruitment variability. N. Am. J. Fish. Manag. 22, 1124–1135.
Isermann, D.A., Meerbeek, J.R., Scholten, G.D., Willis, D.W., 2003. Evaluation of three different structures used for walleye age estimation with emphasis on removal and processing times. N. Am. J. Fish. Manag. 23, 625–631.
Kocovsky, P.M., Carline, R.F., 2000. A comparison of methods for estimating ages of unexploited walleyes. N. Am. J. Fish. Manag. 20, 1044–1048.
Koenigs, R.P., Bruch, R.M., Kamke, K.K., 2013. Impacts of aging error on walleye management in the Winnebago System. N. Am. J. Fish. Manag. 33, 900–908.
March 2013. Laird Statistics. Pearson Product Moment Correlation, Available from: https://statistics.laerd.com/statistical-guides/pearson-correlation-coefficient-statistical-guide.php
Lee, D.W., Prince, E.D., 1995. Analysis of otoliths and vertebrae from nine tag-recaptured Atlantic bluefin tuna (*Thunnus thynnus*). In: Secor, D.H., Dean, J.M., Campana, S.E. (Eds.), Recent Developments in Fish Otolith Research. University of South Carolina Press, Columbia, SC, pp. 361–374.
Logsdon, D.E., 2007. Use of unsectioned dorsal spines for estimating walleye ages. N. Am. J. Fish. Manag. 27, 1112–1118.
Maceina, M.J., 1997. Simple application of using residuals from catch-curve regressions to assess year-class strength in fish. Fish. Res. 32, 115–121.
Marwitz, T.D., Hubert, W.A., 1995. Precision of age estimates of Wyoming walleyes from different calcified structures. Prairie Nat. 27 (1), 41–49.
Quist, M.C., 2007. An evaluation of techniques used to index recruitment variation and year-class strength. N. Am. J. Fish. Manag. 27, 30–42.
Ricker, W.E., 1975. Computation and interpretation of biological statistics of fish populations. In: Fisheries Research Board of Canada. Bulletin., pp. 191.
Robillard, S.R., Marsden, J.E., 1996. Comparison of otolith and scale ages for yellow perch from Lake Michigan. J. Gt. Lakes Res. 22, 429–435.
Robson, D.S., Chapman, D.G., 1961. Catch curves and mortality rates. Trans. Am. Fish. Soc. 90, 181–189.

Secor, D.H., Trice, T.M., Hornick, H.T., 1995. Validation of otolith-based ageing and a comparison of otolith and scale-based ageing in mark-recaptured Chesapeake Bay striped bass, *Morone saxatilis*. Fish. Bull. 93 (1), 186–190.
Simkiss, K., 1974. Calcium metabolism of fish in relation to ageing. In: Bagenal, T.B. (Ed.), Ageing of Fish. Unwin Brothers, London, pp. 1–12.
Taubert, B.D., Tranquilli, J.A., 1982. Verification of the formation of annuli in otoliths of largemouth bass. Trans. Am. Fish. Soc. 111, 531–534.
Vandergoot, C.S., Bur, M.T., Powell, K.A., 2008. Lake Erie yellow perch age estimation based on three structures: precision, processing times, and management implications. N. Am. J. Fish. Manag. 28, 563–571.