North American Journal of Fisheries Management 26:571–579, 2006

DOI: 10.1577/M05-098.1

[Management Brief]

An Evaluation of the Accuracy of Age Estimation Methods for Southern Lake Michigan Alewives

STEVEN R. LABAY AND THOMAS E. LAUER
Aquatic Biology and Fisheries Center, Department of Biology, Ball State University, Muncie, Indiana 47306, USA

Abstract.—An evaluation of otoliths, scales, vertebrae, and opercles taken from southern Lake Michigan alewives *Alosa pseudoharengus* was conducted to identify the best structure for estimating age. Based on percent agreement and coefficient of variation analyses, ages estimated from otoliths were significantly more precise than ages estimated from other structures. Mean frequency counts of annuli on scales, vertebrae, and opercles tended to overestimate the relative abundance of young fish and underestimate the relative abundance of older fish more than those of otoliths. Length frequency histogram analysis of alewives collected in 2003 corroborated the accuracy of otolith age estimates. The mean time necessary to estimate alewife ages did not differ significantly between structure types. Based on their precision, accuracy, and time efficiency, otoliths are recommended for estimating ages of southern Lake Michigan alewives.

Precise and accurate estimates of fish age are often a primary goal of fisheries managers when assessing population demography. Fish age is typically estimated with one of three methods: (1) direct observation, such as mark–recapture, (2) length frequency analysis, and (3) structure analysis (Devries and Frie 1996). However, researchers are often limited in their choice of methodology because of time, logistic, or economic constraints and may find it difficult or impossible to assess the accuracy of structure analysis (Casselman 1982). In response to these limitations, age estimation methods are typically chosen to provide a high degree of precision. Corroborative attempts based solely on precision can yield incorrect age estimates (poor accuracy). Avoiding such a result requires age estimates to be validated by use of known-age fish in the population (Beamish and McFarlane 1987), a task that can be impractical or unattainable. Because age validation is rarely possible, corroborative attempts at validation can be used as an alternative (Campana 2001).

Alewives *Alosa pseudoharengus* are the primary prey of adult salmonids (Jude et al. 1987; Stewart and Ibarra 1991; Miller and Holey 1992; Madenjian et al. 1998) and adult yellow perch *Perca flavescens* (Truemper and Lauer 2005) in Lake Michigan, and these sport fisheries have multimillion-dollar economic impacts on the region (Francis et al. 1996; Bence and Smith 1999). Proper management of the alewife population is essential for sustaining the viability of the fish community and for satisfying the recreational demand. Thus, appropriate alewife age estimation methodology is necessary to provide growth, recruitment, and mortality statistics for this fish.

Although scale and otolith age estimation methodologies for alewives have been previously investigated, information on precision is lacking, as is an assessment of alternative structures such as opercles and vertebrae. In the only known validation of alewife age estimates, O'Gorman et al. (1987) used a natural marker on scales to determine the minimum age of 12 Lake Ontario alewives and found that scales considerably underestimated the true age. Other studies evaluating alewife scale and otolith comparisons concluded that age estimates from otoliths were more precise than age estimates from scales, based on exact percent agreement (Kornegay 1978; Libby 1985). However, none of the studies incorporated tests of significance into their study designs.

Alewife otoliths have shown great potential in age estimation precision and have been used to assess mean length, weight, and condition at various ages (Madenjian et al. 2003). Otoliths may also be as equally precise as scales for estimating age in other clupeid species (Messieh and Tibbo 1970; Chilton and Stocker 1987). Despite these numerous reports of otolith precision, many agencies continue to use scales for routine management because scales are more convenient to sample, easier to prepare, and nonlethal (Norden 1967; Brown 1972; Daniel 1984; Isermann et al. 2003). However, scale loss and contamination with scales from other fishes during the use of bottom trawls or seines are problematic (Messieh and Tibbo 1970; Kornegay 1978; Fletcher and Blight 1996).

Opercles have provided precise age estimation in a variety of fishes (European perch *P. fluviatilis*: Le Cren 1947; common carp *Cyprinus carpio*: McConnell 1951; goldeye *Hiodon alosoides*: Donald et al. 1992; and yellow perch: Baker and McComish 1998) but have not been evaluated in alewives. Similarly,

* Corresponding author: tlauer@bsu.edu

Received June 16, 2005; accepted January 9, 2006
Published online July 24, 2006

vertebrae have not been used in making age determinations in alewives but have been used for other species, including Arctic char *Salvelinus alpinus* (Baker and Timmons 1991), bluefin tuna *Thunnus thynnus* (Prince et al. 1985), and lake trout *S. namaycush* (Sharp and Bernard 1988). Moreover, vertebrae have been shown to be the most reliable structure for age determinations of the congeneric Pontic shad *A. pontica* when scale, vertebra, otolith, opercle, and subopercle structures were compared (Yilmaz and Polat 2002).

Extraction, preparation, and viewing times for the various age estimation structures have not typically been evaluated. According to Isermann et al. (2003), whole otoliths of walleyes *Sander vitreus* required the least amount of total processing time, followed by scales and dorsal spines. Ihde and Chittenden (2002) similarly found that preparation and reading times for each structure were lowest for sectioned otoliths, followed by scales, dorsal fin spines, and pectoral fin rays of spotted seatrout *Cynoscion nebulosus*. For striped bass *Morone saxatilis*, Welch et al. (1993) found that mean viewing times were lowest for otoliths and highest for scales. Others have only provided anecdotal evidence that otoliths required less preparation and viewing time than scales (Schramm and Doerzbacher 1985; Hammers and Miranda 1991; Krause et al. 1993), and Boxrucker (1986) found that otoliths could be removed in less than 1 min after workers became proficient. We know of no other studies that have evaluated processing (collection and preparation) or viewing times for alewife vertebrae or opercles.

Our objectives were to (1) determine whether otoliths, scales, vertebrae, or opercles were more precise for estimating the ages of alewives from southern Lake Michigan; (2) compare the time needed to estimate ages from otoliths, scales, opercles, and vertebrae; and (3) corroborate the accuracy of age estimates using length frequency analysis.

Methods

Field collection procedures.—Fish were collected with bottom trawls and gill nets at depths of 5, 10, and 15 m in the Indiana waters of Lake Michigan from 27 May to 7 July 2003 and from 7 to 21 July 2004 following methods described by Lauer et al. (2004). Fish were placed on ice immediately after capture and were stored at 4°C overnight. Within 12 h of capture, alewife total lengths (TL; mm) were measured and scales were removed. All fish were then preserved in 95% ethyl alcohol for laboratory removal of opercles, otoliths, and vertebrae. Fish were tallied in 10-mm length-groups ranging from 60 to 239 mm, which spanned the length range of alewives collected. If 10 or fewer fish were captured in a length-group, then all fish were included in the analysis. If more than 10 fish were collected, then 10 fish were selected randomly for analysis. Alewives collected at the same sites with the same gears from 1998 to 2003 were used to estimate the length frequency of the alewife population in the area sampled.

Structure preparation.—Scales were removed from the fish's left side, below the lateral line and posterior to the insertion of the pectoral fin. Scales were scraped from the fish's side with a knife, wiped clean with a cloth to prevent contamination, and placed in a coin envelope. In the laboratory, 10–15 scales from each fish were cleaned with soap and water and mounted between two glass slides in preparation for viewing. Otoliths were extracted up to 3 weeks after capture and were stored in glass vials. The first anterior vertebra was extracted in the laboratory with a knife and forceps, boiled in water with a household detergent for approximately 3 min, brushed free of any fleshy materials, and placed in a coin envelope. When the first vertebra was lost or broken, the next vertebra in the spinal column was substituted. Opercles were removed in the laboratory with a scalpel, were boiled and brushed to remove fleshy materials, and were placed in coin envelopes.

Aging procedures.—Opercles, otoliths, and vertebrae were viewed under reflected light through binocular microscopes with 6.5–50 (magnification. Scales were viewed under a binocular microscope with transmitted light. Otoliths, vertebrae, and opercles were all viewed whole in Type B immersion oil against a black background. An exterior fiber-optic light source was used for additional illumination of all structures except scales.

Three readers estimated the age of each fish from all four structures. Age was estimated three times by each reader for each structure (replicates). None of the readers had experience in estimating ages of alewives. Fish were viewed in random order in each replicate to prevent memorization biases. All structures of a particular type were viewed together, and all viewings were completed before the viewing of a different structure or replicate viewings of the same type of structure. Readers were not provided with information on fish length or date of capture but were allowed to view both left and right otoliths and opercles.

All readers had practice materials at their disposal and were given an instructional session before the first reading. Readers were also instructed to assign an age to a fish only if five scales were in agreement (Robillard and Marsden 1996) to minimize the risk of contamination of scales from other fish. Criteria for identifying annuli on scales followed DeVries and Frie (1996), where incomplete circuli and "cutting over" constituted an annulus. For otoliths, the criteria for identifying annuli were defined as the translucent (hyaline) zones between opaque zones (Beamish 1979). A vertebra annulus was defined as one complete concentric, translucent ring. Criteria for identifying opercle annuli followed those of Le Cren (1947), who defined an annulus as the transition between a broad, opaque zone (summer growth) and a narrow, translucent zone (winter growth). Each reader recorded the time(s) used to estimate the age of each fish for each structure.

Fish that were caught in May and June for this study typically had large growth areas beyond the last observed annulus, whereas fish caught later in the summer generally had well-defined annular rings on or near the edge. Based on our observations and those of others (Rothschild 1963; Norden 1967), we concluded that alewife annulus formation did not occur until after our sampling period was completed and that all structures formed the annular ring at the same time. Therefore, age estimates for all structures in this study were defined as the number of annuli identified by the reader plus 1.

Structure analysis.—Percent agreement, as used in this study, was the proportion of fish in a sample that were assigned the same age by three readers for each structure (Hoenig et al. 1995), that is,

$$\text{Percent agreement} = A/n \times 100,$$

where A = the number of fish with ages that were agreed upon (same age) and n = the total number of fish in the sample.

The mean and variance of the three replicates for each structure were tested in a single-factor analysis of variance (ANOVA) based on an α level of 0.05 to determine significance. Prior to analysis, percentages were arcsine transformed (Zar 1999).

The coefficient of variation (CV) was also used to assess precision among structures. A low CV is indicative of a high degree of precision, whereas a high CV is indicative of low precision. The CV was included in the analysis because percent agreement is a poor measure of precision when only a few year-classes are present within a population (Beamish and Fournier 1981). The CV corrects for this by incorporating the averaged year-class (Chang 1982), thereby allowing for a more-robust statistic. The CV was defined as

$$\text{CV} = \text{SD}/\text{mean} \times 100,$$

where CV = the CV of individual age estimates, SD = the standard deviation of individual age estimates (in this study, $n = 3$), and mean = the mean value of $n = 3$ readings.

In this analysis, one CV was calculated for three age estimates, each from a different reader but from the same replicate and the same structure. For example, if on the first reading of an otolith for a single fish, reader 1 gave an age of 5, reader 2 gave an age of 5, and reader 3 gave an age of 6, then the CV for the first replicate would be 10.8 (SD/mean $\times$ 100 = 0.577/5.333 $\times$ 100 = 10.8). The otolith CV was also computed for all other fish in the replicate and was averaged ($n = 123$ total). Similarly, the mean CV was then computed for the other two replicates of otoliths. Applying this procedure to opercles, scales, and vertebrae generated a mean and variance for all three replicates and all four structure types. A single-factor ANOVA was then used to determine whether significant differences existed among structure types based on an α level of 0.05. If the ANOVA was significant, specific pairwise differences were tested by use of a Tukey–Kramer multiple comparison test.

Age bias plots (Campana et al. 1995) were used to visually detect systematic bias between structures. For age bias plots, mean ages from the most precise structure were plotted on the x-axis and those of the less precise structure were plotted on the y-axis. Mean ages of the less precise structure were calculated based on the same fish in the age-groups for the more precise structure. Age bias plots were constructed with age estimates from all three readers for the third replicate.

Processing and viewing times were quantified for selecting the most useful method. Mean viewing time was defined as the average amount of time(s) used by a reader to estimate the age for one structure type and was compared among the four structures by means of a single-factor ANOVA. An α level of 0.05 was used to determine statistical significance. Processing time was defined as the amount of time(s) used by a reader to remove, clean, boil, and mount one structure. Processing and mean viewing times were added together for a total age determination time.

Corroboration of accuracy.—To determine whether length frequency distributions collected from 1998 to 2003 could be used to corroborate the identification of the large 1998 (age-5) year-class, fish with a TL of 140–159 mm ($n = 18$, identified as age-5 fish from the length frequency distribution) were compared with age estimates from our structure analysis ($n = 111$; the 12 fish collected in 2004 were not included in this analysis). Structure ages were taken from the third replicate of each of the three readers and were averaged. Because the fish in the length frequency distribution were presumed to be age 5, variance could not be estimated, thereby preventing statistical comparison.

An age frequency distribution for the entire 2003 alewife sample ($n = 2{,}691$) was created based on ages estimated from the third replicate of each reader ($n = 111$; the 12 fish collected in 2004 were not included in this analysis). Mean (SE) age proportions for each structure were calculated for each length interval to provide the age frequency distributions.

Results

Ages from opercles, otoliths, scales, and vertebrae were estimated for 123 alewives from southern Lake Michigan. Fish ranged in length from 68 to 231 mm (Table 1). Fish with any one unreadable structure were discarded, thereby equalizing sample sizes. Twelve fish were collected during summer 2004 to fill voids in the length distribution. A total of 4,428 readings were used in the data set (3 readers × 3 replicates × 4 structures × 123 fish).

Percent agreement varied among structures. Ages estimated from otoliths had the highest percent agreement (55%), followed by scales (43%), vertebrae (33%), and opercles (24%). However, only otoliths and opercle percent agreement means differed statistically ($F = 8.10$, df = 3, $P = 0.008$).

The CV analysis showed that otoliths were significantly more precise than the other three structures, while opercles were least precise ($F = 33.16$, df = 3, $P < 0.001$; Table 2).

Otoliths yielded the most precise ages; therefore, otoliths were used as the standard by which other structures were measured in age bias plots (Figure 1). Scale ages overestimated otolith ages for age-2 fish, whereas they underestimated otolith ages for fish older than age 5. Vertebra ages consistently overestimated otolith ages for ages 1–4 and underestimated otolith ages for fish older than age 5. No consistent patterns of bias for opercles were evident among the three readers.

Viewing times did not vary significantly among structures ($F = 1.07$, df = 3, $P = 0.347$) (Table 3) and ranged from 79 to 103 s/structure. Although processing time (extraction, cleaning, boiling, and mounting) differed somewhat among structures, variability was not estimated, thereby preventing statistical comparison. Processing time for scales was approximately twice as long as that of other structures.

Length frequency histograms for alewives in southern Lake Michigan showed modal progression from 1998 to 2003. In 1998, alewife length frequency was unimodal and had a median value of 153 mm (Figure 2), although the specific year-class was unknown. In 1999, this same cohort had grown by 10–20 mm TL. Although evidence of this cohort was indicated in subsequent years, the frequency was low. Beginning in 1999, a new cohort was identified that progressed in size through 2003 (Figure 2) and dominated the population after the disappearance of the cohort identified in 1998. If we assume that these new fish were recruited to the trawl at age 1 (T. S. McComish, personal communication), then most fish in this cohort would have been age 5 (1998 year-class) in 2003, and the most common age-5 fish ranged in size from 140 to 159 mm. The average estimated age of the fish sampled from this size was 4.85 years (SE = 0.07) for otoliths, 4.51 years (SE = 0.08) for scales, 4.78 years (SE = 0.14) for vertebrae, and 4.44 years (SE = 0.17) for opercles.

After applying the age–length key to the 2003 length frequency distribution, we determined that most of the fish in the population in 2003 were age 5 (Figure 3). However, the proportion of age-5 alewives in the

TABLE 1.—Total number of Lake Michigan alewives (within 10-mm length increments) collected in 2003 ($n = 111$) and 2004 ($n = 12$) for which age was estimated from otoliths, scales, vertebrae, and opercles.

Length interval (mm)	Number of fish aged (n)
60–69	1
70–79	4
80–89	9
90–99	10
100–109	10
110–119	10
120–129	10
130–139	10
140–149	10
150–159	10
160–169	10
170–179	10
180–189	10
190–199	4
200–209	4
210–219	0
220–229	0
230–239	1
Total	123

TABLE 2.—Mean (SE) coefficients of variation (CVs) of ages assigned by three readers in three replicate readings for otoliths, scales, vertebrae, and opercles taken from Lake Michigan alewives in 2003 and 2004. A Tukey–Kramer multiple comparison test was used to indicate which structures were not significantly different from each other in terms of the overall CV (same lowercase letter; $P > 0.05$).

Replicate	Otoliths	Scales	Vertebrae	Opercles
1	11.99 (1.20)	13.9 (1.49)	18.2 (1.59)	24.68 (1.64)
2	10.61 (1.57)	15.2 (1.73)	17.9 (1.78)	22.17 (1.79)
3	7.23 (1.78)	14.4 (1.73)	15.3 (1.78)	20.75 (1.74)
Overall CV[a]	9.95 (0.79) x	14.5 (0.91) y	17.1 (0.95) y	22.54 (1.00) z

[a] General linear model ANOVA ($F = 33.16$, df = 3, $P < 0.001$).

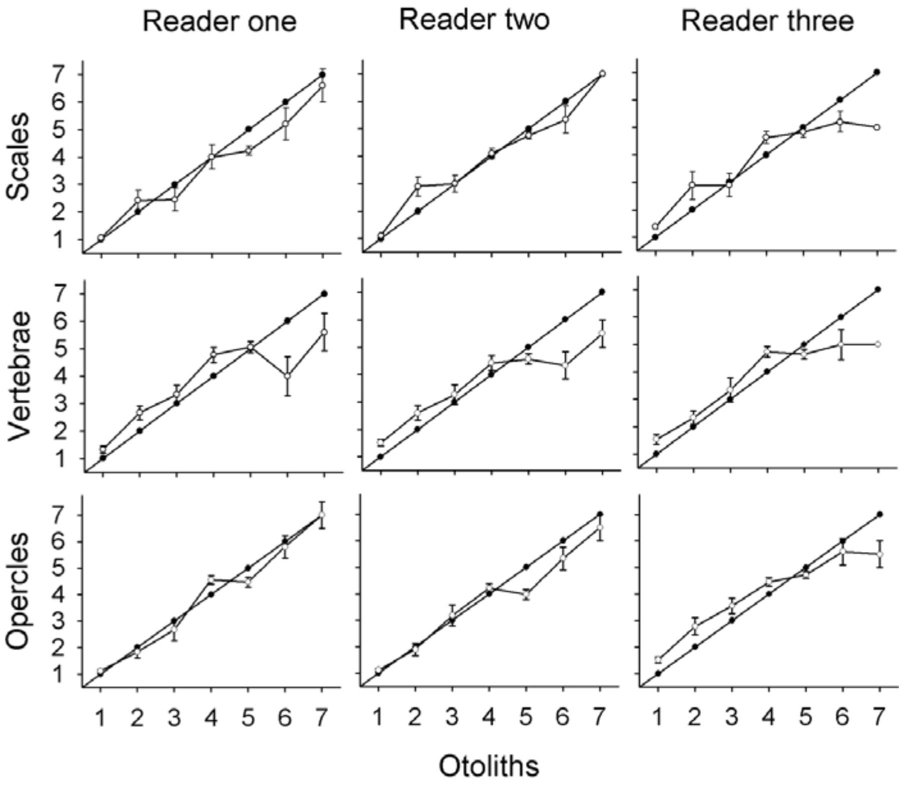

FIGURE 1.—Age bias plots for otolith, scale, vertebra, and opercle mean ages (±SE) determined by three readers in the third of three replicate readings for Lake Michigan alewives collected in 2003 and 2004. The diagonal lines represent perfect agreement between mean ages estimated from scales, vertebrae, and opercles (*y*-axes) and mean ages estimated from otoliths (*x*-axes).

population was highest for otoliths (88%), followed by vertebrae (67%), opercles (52%), and scales (46%).

Discussion

Our finding that alewife otoliths were the most precise structure for estimating the ages of Lake Michigan alewives was not surprising because otoliths have been shown to be more precise than scales for both anadromous and land-locked alewife populations (Kornegay 1978; Libby 1985; O'Gorman et al. 1987), gizzard shad *Dorosoma cepedianum* (Weathers et al. 1993), yellow perch (Robillard and Marsden 1996), bluegills *Lepomis macrochirus* (Hoxmeier et al. 2001), largemouth bass *Micropterus salmoides*, smallmouth bass *Micropterus dolomieu*, and spotted bass *Micropterus punctulatus* (Long and Fisher 2001). Annuli on otoliths were more recognizable and easier to interpret than annuli on other structures, a finding previously identified by Libby (1985). Clarity of annuli on otoliths probably contributed to the greater precision of otolith ages than ages based on other structures. Therefore, we conclude that alewife otoliths are the most precise structures for estimating alewife ages.

TABLE 3.—Mean viewing, processing (extraction, cleaning, boiling, and mounting), and total age determination times (s) for ages estimated from otoliths, scales, vertebrae, and opercles of alewives collected in Lake Michigan in 2003 and 2004. For viewing time, SDs are shown in parentheses; variances were not available for processing time or total age determination time.

Structure	Viewing time	Processing time	Total age determination time
Otoliths	86 (28)	307	393
Scales	103 (37)	600	703
Vertebrae	82 (32)	187	269
Opercles	79 (27)	307	386

Our finding that ages estimated from vertebrae were greater than ages estimated from scales (Figure 1) for younger fish agrees with the results of Prince et al. (1985). However, identification of annular rings may depend on several factors, including slow growth, which makes scale annuli less detectable and less precise (Madenjian et al. 2003), and situations where readers have difficulties in identifying the translucent

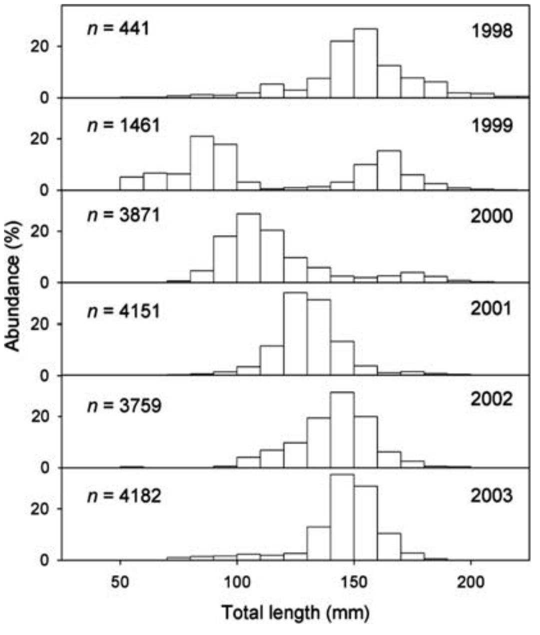

FIGURE 2.—Length frequency histograms of Lake Michigan alewives collected by bottom trawl during June–August of 1998–2003.

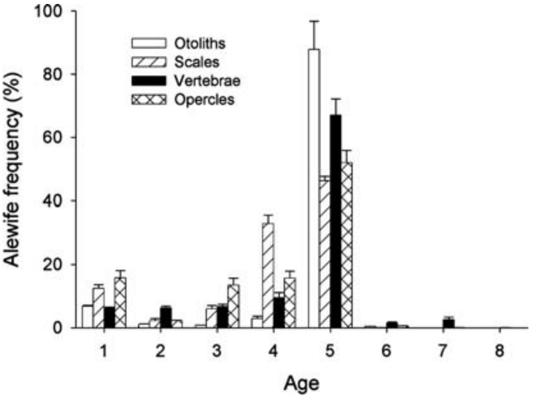

FIGURE 3.—Mean (SE) age frequency distribution of Lake Michigan alewives collected during 2003 ($n = 2{,}691$) and used for age estimation based on otoliths, scales, vertebrae, and opercles. Values were expanded from fish ages ($n = 111$) estimated by three readers on the third of three replicate readings for each structure.

zones (Weathers et al. 1993). Lastly, individual fish may lay down marks on some structures that are inherently more identifiable than marks on other structures (e.g., otoliths versus opercles).

The total processing time for structures can be important, particularly when estimating the ages of many fish, but is less important than precision or accuracy. Regardless of their processing times, opercles and vertebrae should not be used to estimate alewife age because of their poor precision. Although the use of scales for estimating age of many species has the advantage of being nonlethal, alewife mortality is high during sampling, thereby negating this advantage. Thus, the mortality required to extract alewife otoliths may not be a consideration when choosing between scale and otolith structures for age estimation. Moreover, the processing time for scales was nearly twice that of otoliths, mainly due to the longer cleaning and mounting time. Our findings agreed with those of Isermann et al. (2003), who found that whole-view otoliths were significantly lower in mean viewing time and processing time than scales.

True age or accuracy validation can only be determined by direct observation based on such techniques as mark–recapture (DeVries and Frie 1996). Unfortunately, a mark–recapture study on Lake Michigan alewives would be of enormous cost in money and manpower. Moreover, alewives may not be able to physiologically withstand the handling stress that would be required during marking. Although not a true validation, our study utilized the two other common methods of fish age estimation, length frequency and hard-structure analysis (DeVries and Frie 1996). Monitoring the progression of length frequency modes through time is one of the most basic forms of age estimation and can be reliable for young, fast-growing fish (Campana 2001) or in cases where a single year-class dominates the population for several years. In our study, the length frequency distribution modes of the alewife population were distinct and provided corroboration of ages estimated from otoliths. Although these two methods of age estimation cannot be used for validating true age, even if the results are combined, their concurrence in identifying the 1998 year-class was not coincidental. Moreover, the high abundance of the 1998 alewife year-class in Lake Michigan was also noted by Madenjian et al. (2005), further corroborating our otolith age estimates. The suggestion in our study that scales underestimated otolith ages of older fish (e.g., age 5) has also been observed by O'Gorman et al. (1987) and supports the use of otoliths for estimating alewife age. Lastly, validation studies have shown otoliths to be accurate for estimating age in several other species, including Chinook salmon *Oncorhynchus tshawytscha* (Murray 1994), channel catfish *Ictalurus punctatus* (Buckmeier et al. 2002), and largemouth bass (Buckmeier and Howells 2003).

Since the alewife invasion of Lake Michigan in the 1940s, predation by alewives has altered the size structure, abundance, and distribution of zooplankton

(Wells 1970) and is thought to be responsible for declines in the abundance of native fishes, including emerald shiners *Notropis atherinoides,* deepwater sculpin *Myoxocephalus thompsonii*, yellow perch, bloaters *Coregonus hoyi* (Madenjian et al. 2002), and lake trout (Krueger et al. 1995). Alewives have also been the principal prey of Great Lakes salmonids (Stewart and Ibarra 1991; Madenjian et al. 2002), a situation that has both improved sport fishing (Bence and Smith 1999) and controlled the alewife nuisance levels found in the 1960s (Bence and Smith 1999; Madenjian et al. 2002). Because the alewife plays such a vital role in the Lake Michigan ecosystem, managing the fish without a full knowledge of its demographics, including precise age estimates, may limit effective stewardship of the Lake Michigan fish community and ecosystem by natural resource professionals. We recommend the use of whole otoliths to estimate ages of land-locked alewives because otoliths had the highest degree of precision and because their accuracy was corroborated by length frequency analysis. Additionally, processing time was minimal, and less-skilled readers became quickly experienced in estimating age from otoliths and were more confident when identifying otolith annuli.

Acknowledgments

This research was supported by Federal Aid in Sport Fish Restoration funds through the Fisheries Section, Division of Fish and Wildlife, Indiana Department of Natural Resources. Ball State University provided matching funding, equipment, and facilities. We thank Paul Allen, Heath Headley, Cassandra May, Rod Edgell, and Bridget Sullivan for field collection and laboratory assistance. We also thank three anonymous reviewers for their insightful comments that improved the manuscript.

References

Baker, E. A., and T. S. McComish. 1998. Precision of ages determined from scales and opercles for yellow perch *Perca flavescens*. Journal of Great Lakes Research 24:658–665.

Baker, T. T., and L. S. Timmons. 1991. Precision of ages estimated from five bony structures of Arctic char (*Salvelinus alpinus*) from the Wood River System, Alaska. Canadian Journal of Fisheries and Aquatic Sciences 48:1007–1014.

Beamish, R. J. 1979. Differences in the age of Pacific hake (*Merluccius productus*) using whole otoliths and sections of otoliths. Journal of the Fisheries Research Board of Canada 36:141–151.

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

Beamish, R. J., and G. A. McFarlane. 1987. Current trends in age determination methodology. Pages 15–42 *in* R. C. Summerfelt and G. E. Hall, editors. The age and growth of fish. Iowa State University Press, Ames.

Bence, J. R., and K. D. Smith. 1999. An overview of recreational fisheries of the Great Lakes. Pages 259–306 *in* W. W. Taylor and C. P. Ferreri, editors. Great Lakes fisheries and policy management: a bi-national perspective. Michigan State University Press, East Lansing.

Boxrucker, J. 1986. A comparison of otolith and scale methods for aging white crappies in Oklahoma. North American Journal of Fisheries Management 6:122–125.

Brown, E. H. 1972. Population biology of alewives, *Alosa pseudoharengus*, in Lake Michigan, 1949–1970. Journal of the Fisheries Research Board of Canada 29:477–500.

Buckmeier, D. L., E. R. Irwin, R. K. Betsill, and J. A. Prentice. 2002. Validity of otoliths and pectoral spines for estimating ages of channel catfish. North American Journal of Fisheries Management 22:934–942.

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

Campana, S. E. 2001. Accuracy, precision, and quality control in age determination, including a review of the use and abuse of age validation methods. Journal of Fish Biology 59:197–242.

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

Casselman, J. M. 1982. Age and growth assessment of fish from their calcified structures–techniques and tools. Pages 1–17 *in* E. D. Prince and L. M. Pulos, editors. Proceedings of the international workshop on age determination of oceanic pelagic fishes: tunas, billfishes, and sharks. NOAA Technical Report NMFS 8.

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

Chilton, D. E., and M. Stocker. 1987. A comparison of otolith and scale methods for aging pacific herring. North American Journal of Fisheries Management 7:202–206.

Daniel, K. L. 1984. Food habits, age and growth, and forage value of the alewife in Watauga Reservoir, Tennessee. Master's thesis. University of Tennessee, Knoxville.

DeVries, D. R., and R. V. Frie. 1996. Determination of age and growth. Pages 483–512 *in* B. R. Murphy and D. W. Willis, editors. Fisheries techniques 2nd edition. American Fisheries Society, Bethesda, Maryland.

Donald, D. B., J. A. Babaluck, J. F. Craig, and W. A. Musker. 1992. Evaluation of the scale and operculum methods to determine age of adult goldeyes with special reference to a dominant year-class. Transactions of the American Fisheries Society 121:792–796.

Fletcher, W. J., and S. J. Blight. 1996. Validity of using translucent zones of otoliths to age the pilchard *Sardinops sagax neopilchardus* from Albany, Western Australia. Marine and Freshwater Research 47:617–624.

Francis, J. T., S. R. Robillard, and J. E. Marsden. 1996. Yellow perch in Lake Michigan: a multijurisdictional challenge. Fisheries 21(2):18–20.

Hammers, B. E., and L. E. Miranda. 1991. Comparison of methods for estimating age, growth, and related population characteristics of white crappies. North American Journal of Fisheries Management 11:492–498.

Hoenig, J. M., M. J. Morgan, and C. A. Brown. 1995. Analyzing differences between two age determination methods by tests of symmetry. Canadian Journal of Fisheries and Aquatic Sciences 52:364–368.

Hoxmeier, R. J., D. D. Aday, and D. H. Wahl. 2001. Factors influencing precision of age estimation from scales and otoliths of bluegills in Illinois Reservoirs. North American Journal of Fisheries Management 21:374–380.

Ihde, T. F., and Chittenden E Jr. 2002. Comparison of calcified structures for aging spotted seatrout. Transactions of the American Fisheries Society 131:634–642.

Isermann, D. A., J. R. Meerbeek, G. D. Scholten, and D. W. Willis. 2003. Evaluation of three different structures used for walleye age estimation with emphasis on removal and processing times. North American Journal of Fisheries Management 23:625–631.

Jude, D. J., F. J. Tesar, S. F. Deboe, and T. J. Miller. 1987. Diet and selection of major prey species by Lake Michigan salmonines, 1973–1982. Transactions of the American Fisheries Society 116:677–690.

Kornegay, J. W. 1978. Comparison of aging methods for alewife and blueback herring. North Carolina Department of Natural Resources and Community Development, Special Scientific Report 30, Morehead City.

Krause, C. G., C. S. Guy, and D. W. Willis. 1993. Comparison of otolith and scale characteristics for black crappies collected from South Dakota waters. North American Journal of Fisheries Management 13:856–858.

Krueger, C. C., D. L. Perkins, E. L. Mills, and J. E. Marsden. 1995. Predation by alewives on lake trout fry in Lake Ontario: role of an exotic species in preventing restoration of a native species. Journal of Great Lakes Research 21:458–469.

Lauer, T. E., P. J. Allen, and T. S. McComish. 2004. Changes in mottled sculpin and johnny darter trawl catches after the appearance of round gobies in the Indiana waters of Lake Michigan. Transactions of the American Fisheries Society 133:185–189.

Le Cren, E. D. 1947. The determination of the age and growth of the perch (*Perca fluviatilis*) from the opercular bone. Journal of Animal Ecology 16:188–204.

Libby, D. A. 1985. A comparison of scale and otolith aging methods for the alewife, *Alosa pseudoharengus*. Fishery Bulletin 83:696–701.

Long, J. M., and W. L. Fisher. 2001. Precision and bias of largemouth, smallmouth, and spotted bass ages estimated from scales, whole otoliths, and sectioned otoliths. North American Journal of Fisheries Management 21:636–645.

Madenjian, C. P., T. O. Hook, E. S. Rutherford, D. M. Mason, T. E. Croley, E. B. Szalai, and J. R. Bence. 2005. Recruitment variability of alewives in Lake Michigan. Transactions of the American Fisheries Society 134:218–230.

Madenjian, C. P., J. D. Holuszko, and T. J. DeSorcie. 2003. Growth and condition of alewives in Lake Michigan, 1984–2001. Transactions of the American Fisheries Society 132:1104–1116.

Madenjian, C. P., G. L. Fahnenstiel, T. H. Johengen, T. F. Nalepa, H. A. Vanderploeg, G. W. Fleischer, P. J. Schneeberger, D. M. Benjamin, E. B. Smith, J. R. Bence, E. S. Rutherford, D. S. Lavis, D. M. Robertson, D. J. Jude, and M. P. Eberner. 2002. Dynamics of the Lake Michigan food web, 1970–2000. Canadian Journal of Fisheries and Aquatic Sciences 59:736–753.

Madenjian, C. P., T. J. DeSorcie, and R. M. Stedman. 1998. Ontogenic and spatial patterns in diet and growth of lake trout in Lake Michigan. Transactions of the American Fisheries Society 127:236–252.

McConnell, W. J. 1951. The opercles as an indicator of age and growth of the carp, *Cyprinus carpio* Linnaeus. Transactions of the American Fisheries Society 81:138–149.

Messieh, S. N., and S. N. Tibbo. 1970. A critique on the use of otoliths for aging Gulf of St. Lawrence herring. Journal du Conseil, Conseil International pour l'Exploration de la Mer 33:181–191.

Miller, M. A., and M. E. Holey. 1992. Diets of lake trout inhabiting nearshore and offshore Lake Michigan environments. Journal of Great Lakes Research 18:51–60.

Murray, C. B. 1994. A method for preparing Chinook salmon otoliths for age determination, and evidence of its validity. Transactions of the American Fisheries Society 123:358–367.

Norden, C. R. 1967. Age, growth, and fecundity of the alewife, *Alosa pseudoharengus* (Wilson), in Lake Michigan. Transactions of the American Fisheries Society 96:387–393.

O'Gorman, R., D. H. Barwick, and C. A. Bowen. 1987. Discrepancies between ages determined from scales and otoliths for alewives from the Great Lakes. Pages 203–210 *in* R. C. Summerfelt and G. E. Hall, editors. The age and growth of fish. Iowa State University Press, Ames.

Prince, E. D., D. W. Lee, and J. C. Javech. 1985. Internal zonations in sections of vertebrae from Atlantic bluefin, *Thunnus thynnus* and their potential use in age determination. Canadian Journal of Fisheries and Aquatic Sciences 42:938–946.

Robillard, S. R., and J. E. Marsden. 1996. Comparison of otolith and scale ages for yellow perch from Lake Michigan. Journal of Great Lakes Research 22:429–435.

Rothschild, B. J. 1963. A critique of the scale method for determining the age of the alewife, *Alosa pseudoharengus* (Wilson). Transactions of the American Fisheries Society 92:409–413.

Schramm, H. L. Jr., and J. F. Doerzbacher. 1985. Use of otoliths to age black crappie from Florida. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 36(1982):95–105.

Sharp, D., and D. R. Bernard. 1988. Precision of estimated ages of lake trout from five calcified structures. North American Journal of Fisheries Management 8:367–372.

Stewart, D. J., and M. Ibarra. 1991. Predation and production by salmonine fishes in Lake Michigan, 1978–1988. Canadian Journal of Fisheries and Aquatic Sciences 48:909–922.

Truemper, H. A., and T. E. Lauer. 2005. Gape limitation and piscine prey size selection by yellow perch in the extreme southern area of Lake Michigan with emphasis on two exotic prey items. Journal of Fish Biology 66:135–149.

Weathers, K. C., M. J. Newman, and F. Hamilton. 1993. An assessment for aging techniques for gizzard shad (*Dorosoma cepedianum*). Alabama Department of

Conservation and Natural Resources, Research Project Number F43-I-8, Montgomery.

Welch, T. J., M. J. Van Den Avyle, R. K. Betsill, and E. M. Driebe. 1993. Precision and relative accuracy of striped bass age estimates from otoliths, scales and anal fin rays and spines. North American Journal of Fisheries Management 13:616–620.

Wells, L. 1970. Effects of alewife predation on zooplankton populations in Lake Michigan. Limnology and Oceanography 15:556–565.

Yilmaz, S., and N. Polat. 2002. Age determination of shad (*Alosa pontica* Eichwald, 1838) inhabiting the Black Sea. Turkish Journal of Zoology 26:393–398.

Zar, J. H. 1999. Biostatistical analysis. Prentice-Hall, Upper Saddle River, New Jersey.