FEATURE:
FISHERIES RESEARCH

Current Status and Review of Freshwater Fish Aging Procedures Used by State and Provincial Fisheries Agencies with Recommendations for Future Directions

ABSTRACT: In 2006, the Fisheries Management Section of the American Fisheries Society formed the ad hoc Assessment of Fish Aging Techniques Committee to assess the current status of aging freshwater fish in North America. For seven species groups that included black bass (*Micropterus* spp.), crappie/sunfish (*Pomoxis* spp./*Lepomis* spp.), catfish (Ictaluridae), morinids, percids, salmonids, and esocids, a survey of U.S. and Canadian fisheries agencies (*N* = 51 agencies responding) revealed that scales, otoliths, and spines were the most common structures used to age fish. Latitudinal clines existed for some of the structures that were examined, with scales typically used more in northern latitudes than otoliths. Many agencies conducted some validation of age estimation techniques and most assessed precision at least for some of the age samples collected. Providing personnel with training to age fish was common. Reasons for the structures used and the types of inferences and information generated from age data were reported. Scales were the most common structure used to age esocids, black bass, crappie/sunfish, and moronids, but only 27% of all respondents felt that scales accurately aged fish to the maximum age. Alternatively, most agencies felt that otoliths provided accurate estimates. From a review of published papers, otoliths were more accurate when compared to other aging structures and showed higher precision. Most agencies conducted back-calculation of lengths from annuli that provided additional information on growth, even though back-calculation procedures contain complex and inconsistent interpretation and computation issues. Currently, many studies are being conducted where known-age fish were chemically or physically marked, stocked, then recaptured after a number of years which can furnish data for age validation. Recommendations include the development of a known-age reference database to allow sharing of information, publication of validation studies, and careful considerations for conducting back-calculation of lengths from presumed annuli.

Estado actual y revisión de procedimientos para determinar edad en peces dulceacuícolas, utilizados por agencias estatales y municipales de pesquerías, con recomendaciones para trabajos futuros

RESUMEN: En 2006, La Sección sobre Manejo de Pesquerías estableció de manera expedita el Comité para la Evaluación de Técnicas de Determinación de Edad en Peces con el fin de conocer el estado actual de las técnicas utilizadas para la lectura de edad en los peces dulceacuícolas de Norteamérica. Un estudio prospectivo realizado a las agencias de pesquerías de los Estados Unidos de Norteamérica y Canadá (*N* = 51 agencias respondieron) reveló que las escamas, otolitos y espinas fueron las estructuras más utilizadas para la lectura de edad en siete grupos de especies que incluían a la lobina negra (*Micropterus* spp.), mojarras (*Pomoxis* spp./*Lepomis* spp.), bagre (Ictaluridae), morónidos, pércidos, salmónidos y esócidos. Existe una gradiente (clinal) latitudinal para algunas de las estructuras que son examinadas: las escamas, más que los otolitos, son mayormente utilizadas hacia el norte. Varias agencias hicieron validaciones de técnicas para estimación de edad y la mayoría evaluó la precisión, al menos, de algunas de las muestras colectadas. La capacitación de personal para la lectura de edad, fue un rasgo común. También se reportaron las razones por las cuales se utilizó cierta estructura en lugar de otra, así como los tipos de inferencia e información derivada de los datos de edad. Las escamas fueron las estructuras más utilizadas para determinar la edad en esócidos, lobina negra, mojarras y morónidos, pero solo el 27% de las agencias consideró que la edad máxima podía ser determinada con mayor precisión utilizando las escamas. Alternativamente, la mayoría de las agencias consideró que a través de los otolitos se obtienen estimaciones precisas. Sobre la base de una revisión de trabajos publicados, se encontró que usando otolitos, en comparación a otras estructuras que sirven para determinar la edad, podían derivarse estimaciones más precisas. Casi todas las agencias se valieron del retro-cálculo de longitudes a partir de anillos que podían proveer información adicional sobre crecimiento, pese a que este procedimiento implica interpretaciones intrincadas e inconsistentes y cálculos complejos. Con la finalidad de generar datos útiles para la validación de la edad, actualmente se están realizando muchos estudios en los cuales a peces de edad conocida, se les marca física y químicamente, se les libera y recaptura después de unos años. Se recomienda desarrollar una base de datos de edades conocidas que sirva para compartir información, publicación de estudios sobre validación así como para conocer aspectos fundamentales que deben considerarse al hacer un retro-cálculo de longitudes a partir de anillos.

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INTRODUCTION

Fishery biologists commonly collect and process calcified structures from freshwater fish to estimate age. Age data are regularly used to assess fish population dynamics (growth, mortality, and recruitment) and stock structure, and are an essential component of age-structured population models (Beverton and Holt 1957; Ricker 1975). Many fishery texts devote chapters to discussion of techniques for aging fish and methods to conduct back-calculation to estimate previous lengths-at-age, but few of these texts thoroughly address the need to validate the accuracy of presumed annuli or the importance of assessing the precision of age assignments between or among readers (Beamish and McFarlane 1983, 1995; DeVries and Frie 1996). In addition, few published studies consider age data as estimated values. In this profession, we have typically assumed age data are accurate, and this assumption has been long supported by our text books and publications.

Given the importance of age data in fisheries studies and the increase in published papers on species-specific age estimation and application of age data over the past two decades, a summary of which structures and methods used to estimate age of freshwater fish in North America is warranted. To fulfill this need, the Fisheries Management Section with support of the Fisheries Administration Section of the American Fisheries Society formed the Assessment of Fish Aging Techniques Committee (ad hoc) in 2006. The tasks of the committee were to: (1) survey state and provincial freshwater fisheries agencies regarding the structures and procedures used to age freshwater fish; (2) conduct a literature review on fish aging techniques, primarily examining previous efforts to describe accuracy (validation), precision, and the back-calculation of lengths from presumed annuli; and (3) provide recommendations for aging techniques that will improve accuracy and provide direction for future research. Including federal, tribal, university, and private agencies in the survey was deemed impracticable as identifying all these groups and obtaining a fair representation would be difficult. The results of the tasks assigned to this committee are presented in this article.

PROCEDURES USED BY STATE AND PROVINCIAL FISH AGENCIES TO AGE FRESHWATER FISH

In February 2006, an eight-question survey was sent to state and provincial fisheries chiefs in the United States and Canada via e-mail. The survey contained questions regarding the percentage of sampled fish populations that were aged, the approximate frequency that certain structures were used to age fish, opinions on aging accuracy, precision and validation of different aging structures, training, use of back-calculation, and types of information and analyses generated from age data.

A total of 45 state and 6 provincial agencies responded to the survey; 2 states within this sample reported that they did not routinely estimate the age of freshwater fish. We asked agencies to report frequency of use of scales, otoliths, spines, cleithra, fin rays, vertebrae, and other structures to age seven important recreational and, in some instances, commercial fish groups that included black bass (*Micropterus* spp.), crappie/sunfish (*Pomoxis* spp. and *Lepomis* spp.), catfish (Ictaluridae), salmonids, percids, moronids, and esocids. The relative importance of each structure for each fish group was computed by multiplying frequency of occurrence of use by the percent effort using that structure; thus relative importance values sum to 100% for each species group. Scales and otoliths were the most commonly used structures to age fish (Table 1, Figure 1) and many agencies used more than one structure to estimate ages for the same species group (Table 1). Scales were more commonly (relative importance 58–65%) used to age black bass, crappie/sunfish, and moronids than otoliths (33–41%), but scale and otolith use to age salmonids and percids was nearly equal (Figure 1). The relative importance of pectoral spines was about twice that of otoliths for aging catfish (Figure 1). Scales, followed by cleithra, were the predominant structures used to age esocids (Figure 1).

Significant latitudinal clines in the relative importance of scales and otoliths to age black bass, crappie/sunfish, and moronids were evident, with otoliths more commonly used in southern states and scales used in more northern states and provinces (Figure 2). Similarly, effort directed at aging catfish using otoliths and pectoral spines was negatively and positively correlated, respectively with latitude (Figure 2). For salmonids and percids, the use of otoliths (r = -0.22 to 0.26; $P > 0.1$) and scales (r = 0.05 to 0.07; $P > 0.5$) to age these fish did not vary with latitude. The use of cleithra to age esocids slightly increased with latitude ($r = 0.46$; $P < 0.05$), and otolith use weakly decreased ($r = -0.36$; $P = 0.06$) with latitude.

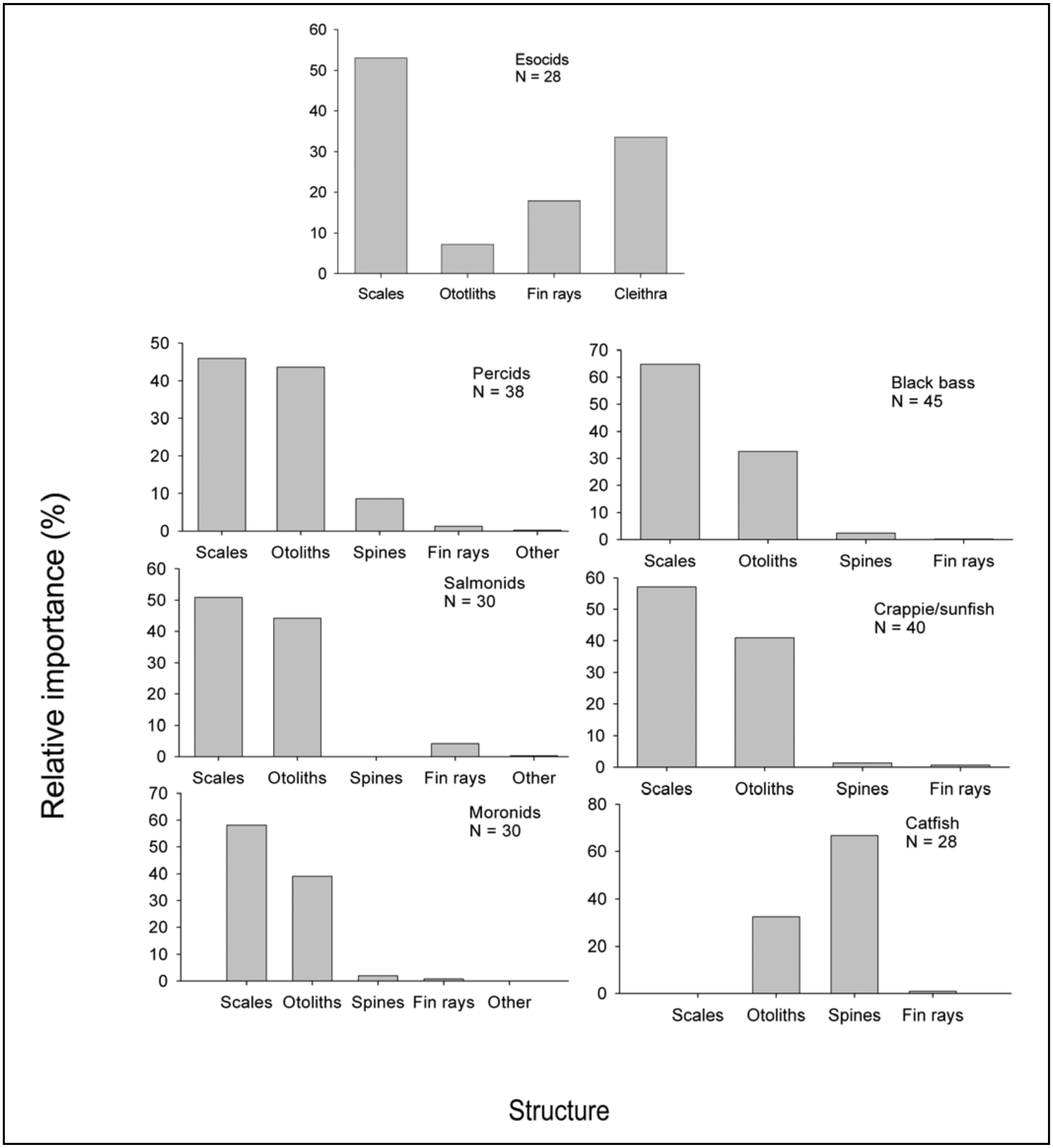
Respondents were asked to indicate the maximum age they believed could be accurately estimated from scales for the applicable species groups. The median maximum age of scale accuracy varied between 5–6 years among 5 species groups (Figure 3). Opinions on maximum ages that could be accurately determined generally ranged from 3 to 9 years for all groups except esocids, where higher maximum reliable ages were more commonly reported. From some of the references listed in Table 4, other references, and our personal observations and communications, maximum age of these North American fish is generally positively related to latitude and some of these species can obtain presumed longevity of 9–15 years for smaller bodied species (Hales and Belk 1992; Soupir et al. 1997; Sammons et al. 2006; Maceina and Sammons 2006) and up to 20–25 years for larger bodied species (Casselman 1974; Erickson 1983; Green and Heidinger 1994).

Table 1. Frequency of aging structures used by 43 U.S. states and 6 Canadian provinces. Number in parenthesis represents the number of states and provinces where this structure was used exclusively.

Structure	Black bass	Crappie/ sunfish	Catfish	Salmonid	Percid	Moronid	Esocid
Scales	34(13)		26(12)	22(10)	25(8)	20(13)	21(9)
Otoliths	27(11)	25(15)	13(7)	20(7)	29(10)	16(9)	4(2)
Fin rays	1	1	1	2	1	1	5
Spines	4	1	21(14)		8	2	
Cleithra							15(5)
Vertebrae				2			
Other				1	1		
Total number of agencies	45	40	28	30	38	30	28

Most agencies (76%) assessed the precision of age estimates either between or among readers for the structures examined and commonly used two blind (independent) readers, with these readers consulting to resolve differences in age assignment (Figure 4). For some agencies, assessment of precision was not standardized, and double-blind, triple-blind, and group reading (simultaneous examination of structures by two or more readers) were commonly-used procedures (Figure 4). However, precision was not assessed for all aging efforts within an agency's jurisdiction (Figure 4). More than half of the agencies (59%) reported conducting some validation of annuli, primarily by stocking fish of known age that were either chemically or physically batch marked and then subsequently recaptured. Not all species groups or structures were

Figure 1. Relative importance of different structures used to age seven species groups of freshwater fish. Relative importance was computed as the occurrence of use for a structure multiplied by the percent effort of use for that particular structure.



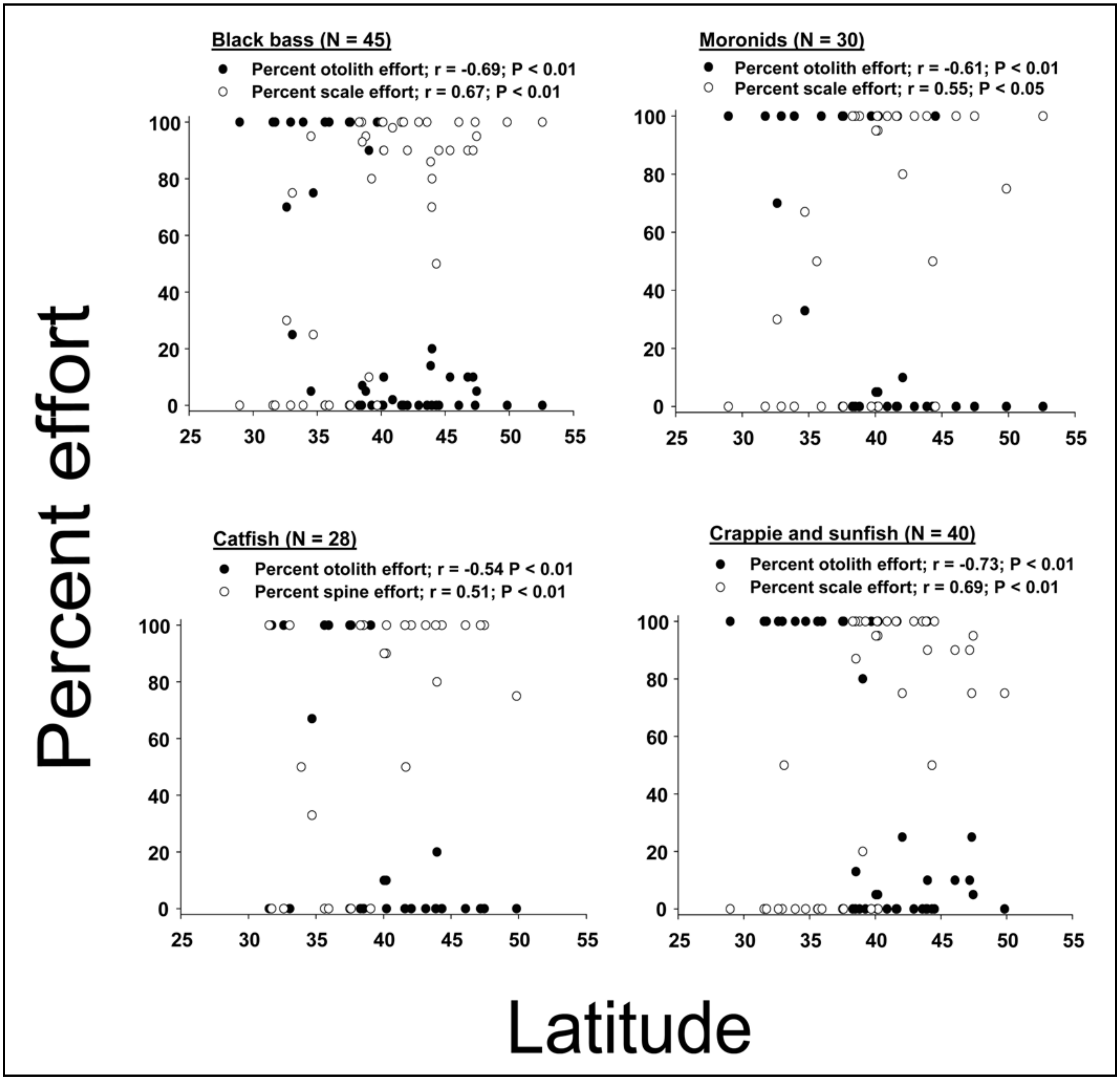
validated as stocking was limited and was species specific.

About 80% of all agencies provided training to personnel to age fish, with 74% of the agencies providing one-on-one training to a single individual through experienced staff. Standardized or formal training and some combination of standardized/individual training was offered to personnel in the remaining agencies. Known-age and reference-aging structures were reported by only 14 of the 38 agencies that offered training.

Nearly every agency that aged fish used this information to assess growth (100%), mortality (86%), and/or recruitment (82%). Analyses of age data were commonly used in the regulation decision-making process (92%) and in research (82%). Additionally, among 49 respondents, 79% conducted back-calculation of lengths from presumed annuli in at least some of the fish populations where age estimates were made. Back-calculation was routine in some agencies as about half (47%) these agencies computed back-calculated lengths for 40 to 100% of the populations that were sampled and aged. Thirty-five of 38 agencies reported that scales (66%) followed by otoliths (43%) were the most common structures used for conducting back calculation.

Finally, for scales, fin rays, and spines, 83% of the agency respondents indicated the non-lethality of collection was a strong consideration for using these structures. However, of these respondents, only 38% acknowledged that these non-lethal structures were accurate for a limited age

Figure 2. The percent effort of using scales, otoliths, and spines to age four major fish species groups plotted against latitude. Latitude was determined from the center of each state and province.



range (primarily young fish). Only 27% of respondents felt scales were accurate aging structures for older aged fish. Most agencies that collected structures that were lethal to fish including cliethra (*N* = 5) and otoliths (*N* = 35) felt these structures provided accurate ages.

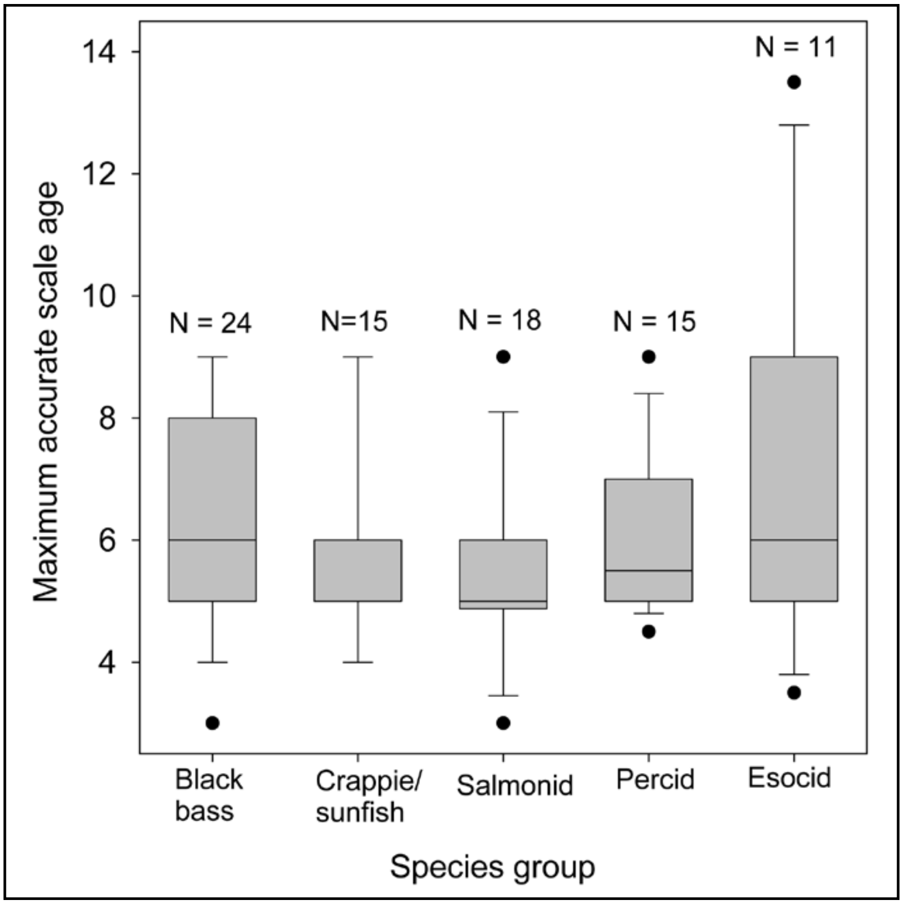
LITERATURE REVIEW: ACCURACY AND PRECISION OF AGES ESTIMATES AND BACK-CALCULATION OF LENGTH

Accuracy and precision of age estimates

Age estimates contain error. Thus, a need exists to assess and understand the magnitude, relevance, and sources of these errors (Beamish and McFarlane 1995; Campana 2001). Campana (2001) separated age estimation error into two components, process error and interpretation error. Process errors occur because some bony structures do not form periodic marks that correspond to annular cycles of growth or, if formed, these annular marks may not be discernible when using a particular technique. Process errors are best assessed through validation (e.g., use of known-age fish) to determine if interpreted annuli are accurate.

Interpretation error is associated with individual subjectivity in identifying annuli. Errors associated with interpretation are best assessed through quality control monitoring, although frequently only precision can be evaluated. Precision simply represents the reproducibility or consistency of repeated measurements on a given structure. Thus, age estimates can be highly reproducible, but inaccurate (Campana et al. 1990; Campana and Moksness 1991). Therefore, estimates of precision cannot be substituted for measures of accuracy. Discussions regarding the consequences of both process error and interpretation error can be found throughout the literature (e.g., Beamish and McFarlane 1983, 1995; Campana 2001). To ensure the accuracy of age estimates, freshwater fisheries biologists should implement techniques to minimize both sources of error. Below, we summarize relevant literature and provide a review of validation and quality control (precision) techniques.

Figure 3. Respondents opinion of the maximum age that could be accurately determined from scales from five major fish species groups where it was recognized that the absolute true maximum age could not be determined. Shaded areas represent the 25th and 75 percentiles, error bars are the 10th and 90th percentile values, and dots represent corresponding minimum and maximum ages. The horizontal line is the median response.

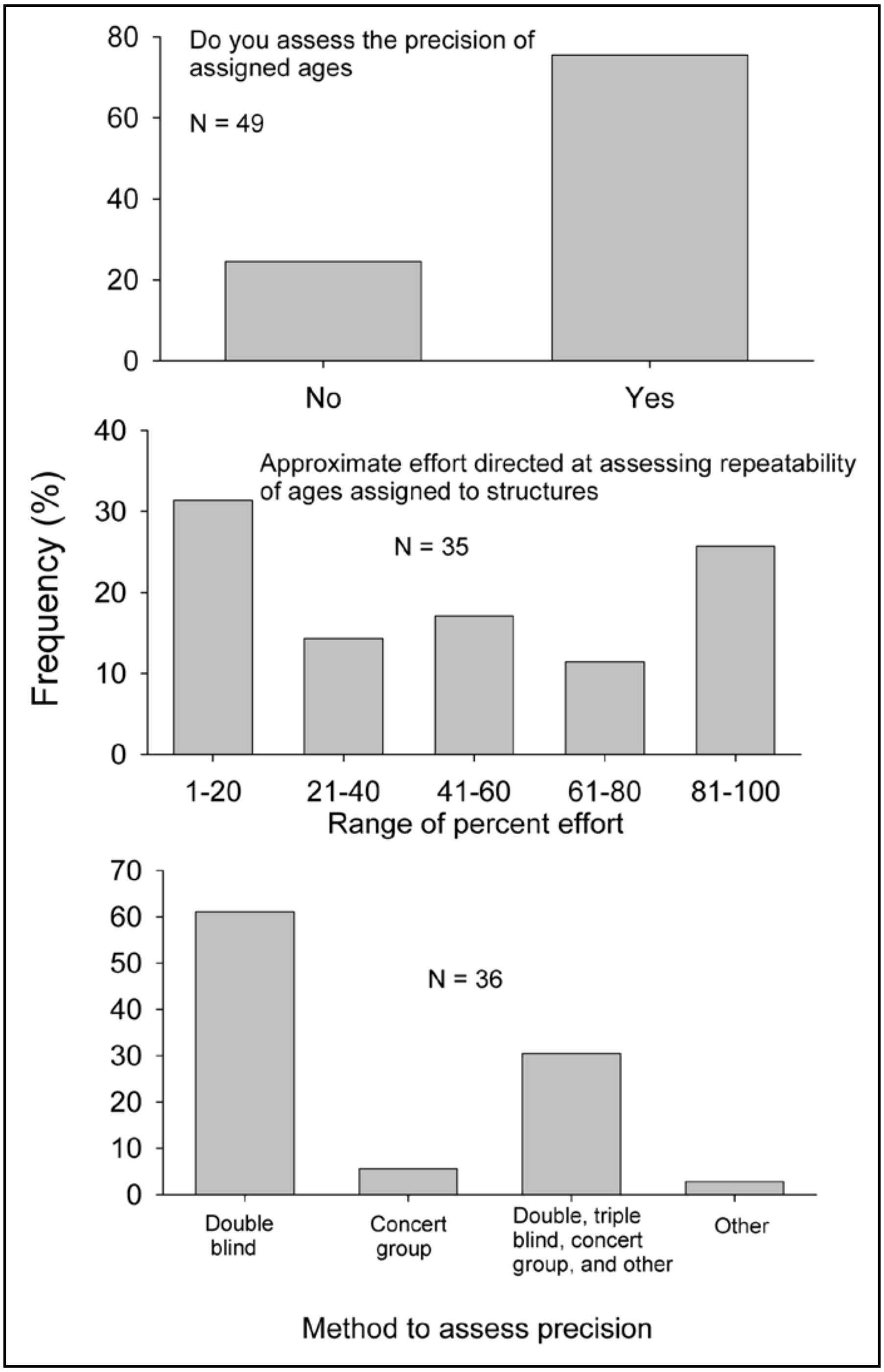


Validation represents an effort to assess process error and often has the objective of "determining the accuracy" of a particular age estimation technique. While many methods have been used to validate age estimation techniques (see review by Campana 2001), we categorize validation techniques into three general types: (1) techniques that validate absolute age and the formation of annular increments as well as a readers' ability to accurately interpret annuli utilizing known-age fish (e.g., Erickson 1983; Heidinger and Clodfelter 1987; Fitzgerald et al. 1997; Buckmeier et al. 2002; Ross et al. 2005); (2) techniques that validate the formation of annular increments and the readers' ability to accurately interpret annuli utilizing marked fish of unknown age that have been at liberty for a known time (e.g., Babaluk and Campbell 1987; Babaluk and Craig 1990; Mantini et al. 1992; Hining et al. 2000) and (3) techniques that attempt to validate the formation of annular increments and the readers' ability to accurately interpret annuli utilizing unmarked fish of unknown age (e.g., marginal increment analysis; Maceina and Betsill 1987). Techniques that validate absolute age are considered optimal; however, techniques that validate annulus formation utilizing marked fish, especially those marked with chemicals (e.g., with tetracycline compounds), can be used as a surrogate if annulus formation is validated for all age groups. Although useful in describing the timing of annulus formation, techniques such as marginal increment analysis rarely offer true validation because few studies have followed the strict protocols recommended by Campana (2001). Techniques including length-frequency analysis, matching back-calculated lengths with previously estimated lengths, and the progression of strong year classes through time, were not considered by Campana (2001) as true methods of validation, but these methods and marginal increment analysis do provide some evidence of annuli accuracy.

Determining the accuracy of a particular technique for all applications may appear to be an impossible standard, as the degree of accuracy associated with a particular technique is almost certain to vary across individual readers and populations. Francis (1995) stated that "the validation of an aging procedure should be aimed at how accurate the procedure is, rather than whether it is accurate." Ideally, a technique that consistently produces a high level of accuracy in at least several evaluations is desirable. However, multiple validation studies for a particular species are rare (Tables 2 and 3). Nevertheless, we attempted to summarize validation studies for freshwater fishes.

We limited the focus of our summary to the seven categories of fishes utilized in our age survey. We recognize that ages are estimated for other species, but suggest that the majority of age estimation occurring in North America is focused on these species. We considered a technique valid for a specified age if the authors reported at least 80% agreement with known age. Although arbitrary, we believe 80% offers a minimum level of quality consistent with many standard fishery assessments. When reported, we also used the 80% level in summarizing those studies validating annulus formation. Large variations in the reporting of techniques and data were evident. In some cases, almost no actual data were reported, while in other instances data were not specifically presented by age class. In addition, it was often difficult to determine how the authors dealt with the bias of knowing the age of the fish in the study. Consequently, variability observed across studies made generalizations difficult and our summary represents our best interpretation of the information as it was presented.

Figure 4. Percent of respondents that assessed precision of ages estimates (top), the effort directed at assessing the repeatability of age assignment (middle), and methods to assess precision (bottom).



Validation of age estimation techniques has been conducted for at least some species in each of the seven categories of fishes we reviewed, though many species commonly aged (e.g., blue catfish *Ictalurus furcatus*, brown trout *Salmo trutta*, white bass *Morone chrysops*, spotted bass *Micropterus punctulatus*, and yellow perch *Perca flavescens*) apparently lack published validation (Tables 2 and 3). In general, most techniques have only been validated for young fish and were based on relatively small sample sizes. Multiple structures have been validated for several species, with otoliths being more accurate than other structures when direct comparisons were conducted (Table 2; e.g., Heidinger and Clodfelter 1987; Secor et al. 1995; Buckmeier et al. 2002; Cooper 2003; Ross et al. 2005). Attempts to validate scales and fin rays for several species apparently failed primarily due to process error (Mann and Beaumont 1990; Rien and Beamesderfer 1994; Fitzgerald et al. 1997; Whiteman et al. 2004; McBride et al. 2005), whereas none of the otolith studies reviewed reported failure. The opinions expressed by the agencies surveyed generally agreed with the published literature. Most (82%) felt otoliths and cleithra provided accurate age estimates whereas only 27% felt scales were accurate. When used, scales were usually only considered accurate for young fish.

To fully assess age estimation error, the accuracy of individual readers must also be assessed due to the subjectivity associated with age estimation. For example, Buckmeier (2002) found variability of age estimates was high among individuals using validated techniques to estimate the age of known-age largemouth bass even after receiving training. Unfortunately, monitoring of this type is rarely conducted due to the relative scarcity of reference collections of known-age fish. As a weak surrogate for this type of quality control, many agencies (76% of those surveyed) do assess the precision of age estimates among readers. Until known-age fish become more readily available, assessing precision may be the only form of quality control that can be conducted.

Traditionally, percent agreement has been used as a measure of precision. This method has inherent problems because of inconsistencies among species and among ages within a species. Percent agreement of 95% can represent poor precision in short-lived species (e. g., 4 years), whereas 95% agreement within 5 years can be good precision in a long-lived species (Beamish and Fournier 1981). Alternative measures of precision have been proposed by Beamish and Fournier (1981) and Chang (1982). These two methods not only assess reader disagreement, but also include the magnitude of reader differences in age assignment.

Precision assessments were more prevalent than validation studies in the published literature for all seven categories of fishes assessed in our survey. Typically, otolith age estimates were more precise than scale age estimates for black basses (Besler 2001; Maceina and Sammons 2006), crappies (Schramm and Doerzbacher 1985; Boxrucker 1986; Hammers and Miranda 1991), salmonids (Sharp and Bernard 1988; Baker and Timmons 1991), percids (Robillard and Marsden 1996; Kocovsky and Carline 2000; Isermann et al. 2003; Maceina and Sammons 2006), sunfish (Hoxmeier et al. 2001), and moronids (Welch et al. 1993). However, precision was similar between otoliths and scales for crappies (Kruse et al. 1993) and white bass (Soupir et al. 1997) in South Dakota and between cleithra and scales for northern pike (*Esox lucius*) in Ontario (Laine et al. 1991). Precision of otolith age estimates was better than spine-based estimates for ictalurids (Nash and Irwin 1999; Buckmeier et al. 2002; Maceina and Sammons 2006) and for walleyes (*Sander vitreous;* Erickson

Table 2. Summary of age ranges that have been validated for common freshwater fishes using known-age fish. Common species and groups of freshwater sport fishes that no validation studies were found are also included to demonstrate need. Only ages that were reported to be at least 80% accurate were included. Superscripted numbers refer to citations in Table 4. Superscripted letters refer to footnotes below table.

Species	Otoliths	Scales	Spines	Fin rays	Vertebrae	Cleithra	Opercula
Bullheads							
Channel catfish[a]	0-3^{4}		0-3^{4,24,29}		0-3^{1}		
Blue catfish							
Flathead catfish			0-5^{31}				
Northern pike		0-1^{10}					0-1^{10}
Muskellunge		0-2,4^{16}		0-7^{16}			
Pickerels							
Rainbow trout[a]	0-3^{7}	0-1^{7}					
Brown trout							
Brook trout							
Lake trout							
Chinook salmon	0-5^{22b}						
Coho salmon							
Striped bass[a]	0-7^{13,28b}	0-4^{13c}					
White bass							
Redbreast sunfish							
Bluegill	0-1^{26}						
Redear sunfish							
Pumpkinseed							
Rock bass							
Smallmouth bass[a]	0-4^{13}						
Spotted bass							
Largemouth bass	0-16^{5,15,30}	0-4^{23c,24}					
White crappie[a]	0-5^{25}	0-5^{25}					
Black crappie[a]	0-5^{25}	0-5^{25}					
Yellow perch							
Sauger							
Walleye[a]	0-4^{9,13}	0-3^{9}					

[a] Studies that examined more than one structure and found otoliths to be more accurate
[b] Validated in saltwater
[c] Average accuracy 80%, not reported for individual age classes

Table 3. Summary of structures that annulus formation has been validated for at least some age classes. Common species and groups of freshwater sport fishes that no annulus validation studies were found are also included to demonstrate need. Methods used for annulus validation include known-age fish (K), mark-recapture(R), and marginal increment analysis (M). Superscripted numbers refer to citations in Table 4.

Species	Otoliths	Scales	Spines	Fin rays	Vertebrae	Cleithra	Opercula
Bullheads							
Channel catfish	K^{4}		K^{4,24,29}		K^{1}		
Blue catfish							
Flathead catfish			K^{31}				
Northern pike		K^{10},R^{10,17},M^{19}		R^{3}		R^{3,6,17}	K^{10}
Muskellunge		K^{16}		K^{16}			
Pickerels							
Rainbow trout	K^{7},R^{14}	K^{7}					
Brown trout							
Brook trout	R^{12}						
Lake trout							
Chinook salmon	K^{22}						
Coho salmon							
Striped bass	K^{13,28}	K^{13}					
White bass							
Redbreast sunfish	R^{20}						
Bluegill	K^{26},R^{20},M^{11}						
Redear sunfish	R^{20}						
Pumpkinseed							
Rock bass							
Smallmouth bass	K^{13}						
Spotted Bass							
Largemouth bass	K^{5,15,30},M^{8,30}	K^{23,24},R^{21}					
White crappie	K^{25},M^{18}	K^{25}					
Black crappie	K^{25},M^{27}	K^{25}					
Yellow perch							
Sauger							
Walleye	K^{9,13}	K^{9}					R^{2}

Table 4. Citations referenced in Tables 2 and 3.

Superscript	Citation
1	Appelget and Smith 1951
2	Babaluk and Campbell 1987
3	Babaluk and Craig 1990
4	Buckmeier et al. 2002
5	Buckmeier and Howells 2003
6	Casselman 1974
7	Cooper 2003
8	Crawford et al. 1989
9	Erickson 1983
10	Frost and Kipling 1959
11	Hales and Belk 1992
12	Hall 1991
13	Heidinger and Clodfelter 1987
14	Hining et al. 2000
15	Hoyer et al. 1985
16	Johnson 1971
17	Laine et al. 1991
18	Maceina and Betsill 1987
19	Mann and Beaumont 1990
20	Mantini et al. 1992
21	Maraldo and MacCrimmon 1979
22	Murray 1994
23	Prather 1967
24	Prentice and Whiteside 1975
25	Ross et al. 2005
26	Schramm 1989
27	Schramm and Doerzbacher 1982
28	Secor et al. 1995
29	Sneed 1951
30	Taubert and Tranquilli 1982
31	Turner 1980

1983; Marwitz and Hubert 1995; Kocovsky and Carline 2000; Isermann et al. 2003).

Back-calculation of length

Many (79%) of the agencies responding to the survey reported using back-calculation procedures to estimate lengths of fish at earlier ages and for many agencies, back-calculation was routinely conducted when age samples were collected. From the survey, scales followed by otoliths were the most common structures used to conduct back-calculation. Back-calculation of lengths from presumed annuli can provide growth information for time periods when no direct sampling occurred, and allows comparison of growth rates among fish populations sampled at different times and/or locations. Growth studies using back-calculated lengths were first published for North American freshwater fish in the 1920s (Carlander 1987). Since then, the methods for back-calculating length-at-annulus have been widely applied, occasionally critiqued, and re-applied to fisheries across North America. Although back-calculated estimates are commonly done, the techniques used are varied and poorly understood, with little agreement on which computational methods are best (Summerfelt and Hall 1987; Francis 1990; Pierce et al. 1996).

The direct proportion method (i.e., the Dahl-Lea method) and the intercept-corrected direct proportion method (i.e, the Fraser-Lee method) are two of the most commonly used back-calculation methods for freshwater fish. These two methods were used in 55 of 94 articles published in American Fisheries Society journals between 1990 and 2005 that used back-calculation. Other techniques for back-calculation, such as regression (Mottley 1942), non-linear (Francis 1990) or polynomial regression (Maceina and Betsill 1987; Secor and Dean 1992) models have been scrutinized and found to perform poorly (Carlander 1981; Gutreuter 1987; Francis 1990; Schramm et al. 1992) or have not been widely applied in North America. Of the 94 articles that we reviewed, only 7 applied the use of regression to back-calculate growth (not including papers that compared regression to other back-calculation techniques). To circumvent the problem of choosing the "correct" back-calculation formula, Weisberg and Frie (1987) introduced the concept of using actual increments measured from structures as a surrogate of growth and incorporated environmental and age effects into a multi-way analysis of variance. Three criteria for the validation of a back-calculation procedure identified by Francis (1990) are: (1) the radius of a structure annulus is the same as the radius of the structure at the time the annulus was formed (2) the time of annulus formation is correct and (3) the formula used accurately relates structure radius and body size for each fish. Campana (1990) found back-calculated lengths consistently underestimated previous lengths-at-age (Lee phenomenon) due to decoupling of somatic and otolith growth in older fish and the application of an incorrect back calculation formula (Fraser-Lee). Because proper validation requires the tracking of individual fish over time, these criteria cannot be met in many instances. Klumb et al. (1999) stated that these three requirements can only be met in mark and recapture, laboratory, or pond studies. Thus for many studies, estimates of back-calculated lengths may be error prone and suspect.

Back-calculated lengths must be recognized as estimates and will possess some inherent level of error. Potential sources of bias and error include: (1) previous lengths are estimated only from surviving fish and may only describe growth of these fish and not the entire cohort; (2) the relation between body length and size of the calcified structure may not be proportional or linear during all or part of the life of an individual, biasing estimates of back-calculated lengths unless the correct relation is applied; (3) annuli may be incorrectly identified; (4) measurements to presumed annuli may not be consistent among readers and for fish within a population, and may vary among collection locations; and (5) fish length measurements at time of capture may be in error.

An underlying assumption for back-calculating is accurately describing the relation between somatic growth and hard part growth. When a linear relationship exists, the body length-to-hard part regression provides the intercept value that is used in the Fraser-Lee equation. The intercept for the Fraser-Lee method has often been interpreted as the length of the fish when the hard part first forms; thus, the Fraser-Lee method is often employed when the hard parts are not present at hatching, such as with scales. This makes biological sense because a fish that develops hard parts after hatching will have some positive length when that hard part develops. However, regressing body length on hard part radius produces an intercept that is statistically, not biologically derived. DeVries and Frie (1996) noted that a statistically-derived intercept (including negative values) can be appropriate for accurately back-calculating growth, but may not have a biological interpretation. Hile (1970) recommended that intercepts be derived for unique stocks of fish, pointing out that a species body-scale curve rarely exists. Carlander (1982) acknowledged Hile's statement, but promoted the use of standard intercepts because body-scale regressions often lack younger age groups, and that "slight variation in estimating the slope from medium to large fish can cause significant deviation in the intercept, and, thus, the calculated lengths of the first few years of life." Standard intercepts, such as those proposed by Carlander (1982) and Beck et al. (1997) have been widely used in back-calculations in North America. Ricker (1992) advocated for the Fraser-Lee method with an intercept that was determined by a symmetrical regression technique, such as geometric mean regression. Campana (1990) demonstrated the computation of a biological intercept in a modified Fraser-Lee back-calculation procedure that corrects for changes in the otolith:body length relation and will approximate otolith size during hatching or fish swim-up. Fish biologists using structures such as otoliths, cleithra, or spines, have reported inconsistent relationships between somatic growth and hard part growth with slow-growing fish having larger otoliths than fast-growing fish of a similar size (Maceina and Betsill 1987; Campana 1990; Casselman 1990).

A single computational method for back-calculating growth does not nor should exist. Fishery biologists should be cognizant of the factors that influence back-calculation and select the most appropriate method for the data. When undertaking a back-calculation study, our committee recommends caution and a suite of questions should be answered:

1. What is the purpose and goal of conducting back-calculation and how are the data to be used?
2. Will the sampling techniques produce a random, unbiased sample?
3. Which hard part will be used to estimate age?
4. Can ages accurately be assigned to that hard part?
5. Can annular increments accurately be measured?
6. Along what axis should measurements be taken?
7. Is the body length-to-hard part relation linear?
8. Which back-calculation formula should be used?
9. Has the chosen formula been validated for the species, age groups, and hard part chosen?

RECOMMENDATIONS AND FUTURE DIRECTIONS

Our survey only included state and provincial agency responses, but obviously a wide variety of other professional fish organizations estimate the age of fish and responses of these groups may vary from our results. However, our survey included a wide geographic sample and based on the regional distribution of the committee, we feel these responses were representative of aging activities in the United States and Canada. Aging of fish is common in our profession and currently the accuracy of annulus formation has not been verified for many species for which ages are estimated. Misconceptions do exist as some structures have been used to age fish for over 50 years, and the accepted and common reference of these structures has been published in fishery texts, reports, and peer-reviewed journals. Yet undoubtedly, inaccurate age assignment still exists due to both process and interpretation errors. In our survey, we observed the conflict (dilemma) fishery biologists face of accepting inaccurate age data to prevent fish sacrifice, but at times some biologists recognize that sacrificing fish is necessary to obtain age structures that they feel are more accurate. Inaccurate age assignment and particularly the underestimation of true age for example, can lead to erroneous population assessment, mismanagement, and the over harvest of an exploited fishery resource (see Beamish and McFarlane 1995).

We recommend a concerted effort be made by all fishery biologists to carefully evaluate the accuracy of their age data, including both age estimates and back-calculations of lengths. The apparent availability of known-age fish detected in our survey should allow for the development of known-age reference data bases containing numerous species groups over different geographic areas. We also recommend that validation studies be continued for both annulus formation as well as back-calculation of length and these results communicated and published in the peer-reviewed literature. Certainly, precision of age estimates also should be assessed in all aging studies and formal, standardized training should be offered to personnel when needed. Aging of fish is a well-established procedure with a long history of application, but improvements and new insights can only be realized if workers continue to consider their own techniques carefully and share their findings.

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