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## Comparison of Rainbow Smelt Age Estimates from Fin Rays and Otoliths

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**Abstract.**—Rainbow smelt *Osmerus mordax*, although nonnative, are an important component of the offshore food web in the Laurentian Great Lakes. In Lake Ontario, we estimate ages of rainbow smelt annually to study population dynamics such as year-class strength and age-specific growth and mortality. Since the early 1980s, we have used pectoral fin rays to estimate rainbow smelt ages, but the sectioning and mounting of fin rays are time and labor intensive. Our objective was to assess the feasibility of using otoliths rather than fin rays to estimate rainbow smelt ages. Three readers interpreted the ages of 172 rainbow smelt (60–198 mm total length) based on thin sections of pectoral fin rays, whole otoliths with no preparation, and whole otoliths that had been cleared for 1 month in a 70:30 ethanol : glycerin solution. Bias was lower and precision was greater for fin rays than for otoliths; these results were consistent for comparisons within readers (first and second readings by one individual; three readers were used) and between readers (one reading for each reader within a pair). Both otolith methods appeared to misclassify age-1 rainbow smelt. Fin ray ages had the highest precision and provided the best approximation of age estimates inferred from the Lake Ontario population's length frequency distribution and from our understanding of this population.

Rainbow smelt *Osmerus mordax*, although native to some freshwater lakes of northeastern North America, are nonnative to the Laurentian Great Lakes (Scott and Crossman 1973) and were first reported in Lake Ontario in the late 1920s and early 1930s (Van Oosten 1937; Greeley 1940). Since their introduction into Lake Ontario, rainbow smelt have become well established and are now one of the lake's most abundant species and a major component of the food web (Casselman and Scott 2003; Owens et al. 2003). Naturalized populations of rainbow smelt have been shown to exert food web impacts on both predators and prey in aquatic

systems into which they are introduced (Evans and Loftus 1987). As prey, rainbow smelt are important in the diets of stocked Pacific salmon (Chinook salmon *Oncorhynchus tshawytscha*, coho salmon *O. kisutch*, and steelhead *O. mykiss*) and native lake trout *Salvelinus namaycush* (Brandt 1986; Elrod and O'Gorman 1991; Lantry 2001), which compose the majority of important recreational fisheries on Lake Ontario, valued at over US\$70 million annually (Connelly et al. 1997).

Despite the importance of rainbow smelt in food webs among the Laurentian Great Lakes and elsewhere in their native range, little has been published on techniques for estimating ages for the species. Studies of rainbow smelt populations through the 1980s used scales to estimate ages (Masterman 1913; McKenzie 1958; Jilek et al. 1979; Henderson and Nepszy 1989), whereas more recent papers have generally used length cutoffs based on knowledge of specific systems and populations (Lantry and Stewart 1993; Hoff 2004; Parker-Stetter et al. 2005). The U.S. Geological Survey (USGS) Lake Ontario Biological Station (LOBS), in cooperation with the New York State Department of Environmental Conservation (NYSDEC), has been monitoring the rainbow smelt population in U.S. waters of Lake Ontario since 1978, and age data are used annually to assess important population dynamics including year-class strength and age-specific growth and mortality. The LOBS briefly used scales to estimate ages of rainbow smelt but switched to using a thin section of pectoral fin rays in the early 1980s due to decreased growth rate of rainbow smelt and potential biases associated with the difficulty in obtaining scale samples from small fish (R. Bergstedt, USGS Great Lakes Science Center, personal communication). The primary drawback to using fin rays to estimate rainbow smelt ages is that the sectioning and mounting of fin rays are time and labor intensive. Some researchers have investigated the use of whole rainbow smelt otoliths to estimate ages (S. Parker-Stetter, School of Aquatic and Fishery Science, University of Washington, personal communication; N. Staats, U.S. Fish and

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Wildlife Service, personal communication), but no information on use of this method is available in the published literature. Our objective was to assess the feasibility of using whole otoliths rather than fin rays to estimate rainbow smelt ages by evaluating precision and bias of age estimates within and between readers for three methods: thin sections of pectoral fin rays, whole otoliths, and whole cleared otoliths.

### Methods

We collected rainbow smelt from U.S. waters of Lake Ontario during standard bottom trawl assessments for alewives *Alosa pseudoharengus* and rainbow smelt during April–June 2005 (depth range fished = 8–170 m). The bottom trawl had a 20.4-m headrope and was equipped with a 9-mm, stretch-mesh cod end; additional information on trawl specifications and trawling procedures are described by O’Gorman et al. (2000). We sampled rainbow smelt from the range of lengths available in the catch, and we removed pectoral fins and sagittal otoliths in the field. In the laboratory, fin rays were imbedded in epoxy resin (blackened with carbon powder to enhance contrast). A thin section (0.1524 mm thick) of the fin ray was cut from as near the base of the fin as possible to avoid obscuring the inner annuli. Sections were made with 76.2- × 0.1524-mm diamond wafering blades on a low-speed precision saw (Buehler, Lake Bluff, Illinois; Isomet Model 11-1180), mounted on a clear glass microscope slide (about five per slide) with clear epoxy resin under a cover slip, and viewed with a compound microscope using transmitted light and 100× magnification. Otoliths were prepared in two ways: mounted whole with no treatment (standard) or cleared for 1 month in a 70:30 ethanol : glycerin solution prior to mounting whole (cleared). Otoliths were mounted in clear epoxy resin in black acrylic otolith trays with 50 machined depressions/tray (Sheepscot Machine Works, Newcastle, Maine) and viewed with the same compound microscope at 40–100× magnification (depending on otolith size), but reflected light was used.

Three readers independently estimated ages (two readings per structure per reader) for each of the three methods (sectioned pectoral fin rays, standard otoliths, and cleared otoliths). In some cases, a structure was missing (e.g., we were unable to recover both otoliths, or the first cut of the fin ray was unreadable and no second fin ray was available). Readers estimated ages without knowledge of fish size or of ages previously assigned by themselves or other readers. Each of the three readers had limited, but similar, levels of experience in estimating rainbow smelt ages from fin rays and otoliths. All readers trained with previously aged rainbow smelt fin rays (provided by LOBS) and

cleared otoliths (provided by N. Staats) before the start of this study. If any reader was unable to determine an age for a given fish for each method or if a structure was missing, that fish was dropped from further analyses. For each method, we assigned a consensus age to each fish, defined by agreement of at least four of the six age estimates from the three readers.

Once ages were estimated by all readers for all methods and the consensus age was assigned, we used a combination of analyses to assess bias and precision of rainbow smelt age estimates for each age estimation method as recommended by Campana et al. (1995). We constructed age bias plots to assess bias within readers (comparison of first and second readings by one individual) and between readers (comparison of one reading per individual for each pair of readers) for each method, between each reader and the consensus age for each method, and between consensus ages (comparisons of each pair of methods). When using only one age estimate per reader (bias between reader pairs, reader age versus consensus age), we chose the second of the two readings by each reader, assuming that added experience from the first reading would result in the second reading being the more informed of the two estimates. For each set of comparisons, we used linear regressions (PROC REG in the Statistical Analysis System; SAS Institute 2000) to evaluate whether the intercept ( $b_0$ ) differed from zero and whether the slope ( $b_1$ ) differed from 1.0 (indicating exact agreement between age estimates on x- and y-axes;  $\alpha = 0.05$ ).

We calculated mean coefficient of variation (CV) to evaluate precision within and between readers for each method, and for each method individually. We calculated CV for each fish according to Chang (1982):

$$CV_j = 100 \times \frac{\sqrt{\sum_{i=1}^n \frac{(X_{ij} - X_j)^2}{R - 1}}}{X_j},$$

where  $X_{ij}$  is the  $i$ th age of the  $j$ th fish,  $X_j$  is the mean age of the  $j$ th fish, and  $R$  is the number of times each fish is aged ( $R = 2$  for within-reader comparisons;  $R = 4$  for between-reader comparisons;  $R = 6$  for each method). Mean CV was calculated by averaging  $CV_j$  across all fish. We used analysis of variance (ANOVA; PROC GLM; SAS Institute 2000) to evaluate differences among mean CVs. If differences were detected with the ANOVA, we used pairwise comparisons ( $\alpha = 0.05$ ).

No known-age rainbow smelt were available for use in evaluating accuracy of the three age estimation methods. However, we approximated an evaluation of accuracy by examining the age–length distributions for the population as determined by each of the three methods. Using the consensus age for each method, we first created age–

TABLE 1.—Mean coefficient of variation (CV) and SD for three methods of rainbow smelt age estimation (six estimates per method: 3 readers × 2 readings each). Differences were detected among mean CVs ( $P < 0.05$ ), and letters indicate the results of pairwise comparisons.

Method	N	Mean CV (%)	SD
Fin rays	155	13.7 x	13.5
Standard otoliths	169	24.5 y	13.1
Cleared otoliths	130	19.6 z	12.6

length keys. We then applied the age–length keys to the length frequency distribution observed in our 2005 rainbow smelt assessment (collected late May–early June) by multiplying the percentage of fish in each age category per length group by the total number of fish in each length group as observed in assessment data. We interpreted the results of the length frequency distributions generated from each age estimation method in the context of information known about the Lake Ontario rainbow smelt population.

Results

During April–June 2005, we collected a total of 172 rainbow smelt (60–198 mm total length) for use in this

study. Most (154 of 172) were collected in late April, and 18 additional fish were collected in early June to supplement some length categories from which we did not collect a sufficient number of fish in April. Bottom fishing temperatures were similar (around 4.0°C) during the two sampling events, and we do not expect that any growth occurred between events. For analytical purposes, sample size varied among methods (Table 1). Sample sizes were lower for consensus-age fish because a consensus of four out of six ages did not always occur (no consensus was reached for 37 fin rays, 62 standard otoliths, and 42 cleared otoliths).

We detected bias and imprecision within and between readers for all three structures (Figures 1, 2). For within-reader age estimates from fin rays and cleared otoliths, the mean CV for each reader was relatively low (fin rays: 4.64–8.78%; cleared otoliths: 8.55–11.76%), and we did not detect differences in mean within-reader CV for either method (fin rays:  $P = 0.0823$ ; cleared otoliths:  $P = 0.3735$ ; Figure 1). For standard otoliths, however, mean CVs were higher, and we detected a significant difference in CVs between the least precise (reader 1: CV = 20.71%) and most precise (reader 2: CV = 13.66%) readers ( $P = 0.0041$ ; Figure 1). Age bias plots for within-reader age estimates from

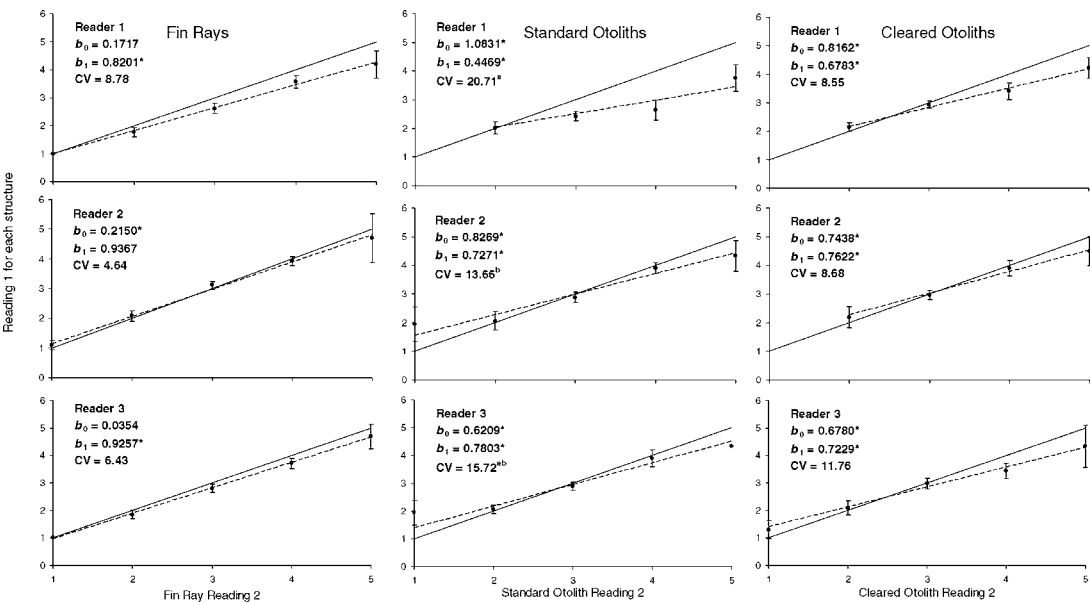


FIGURE 1.—Age bias plots within readers (first and second readings by one individual) for each of three rainbow smelt age estimation methods: fin rays (left panels), standard otoliths (middle panels), and cleared otoliths (right panels). In each graph, the solid line indicates 1:1 agreement between readings on the x- and y-axes, and the dashed line indicates the mean age (95% confidence interval [CI]) estimated on the y-axis for each age on the x-axis (not calculated if  $n < 5$  for a given age). Asterisks indicate that the intercept ( $b_0$ ) was significantly different from zero or the slope ( $b_1$ ) was significantly different from 1.0 ( $\alpha = 0.05$ ). Letters after the CV indicate significant differences (within a method) in pairwise comparisons conducted after a significant ANOVA.

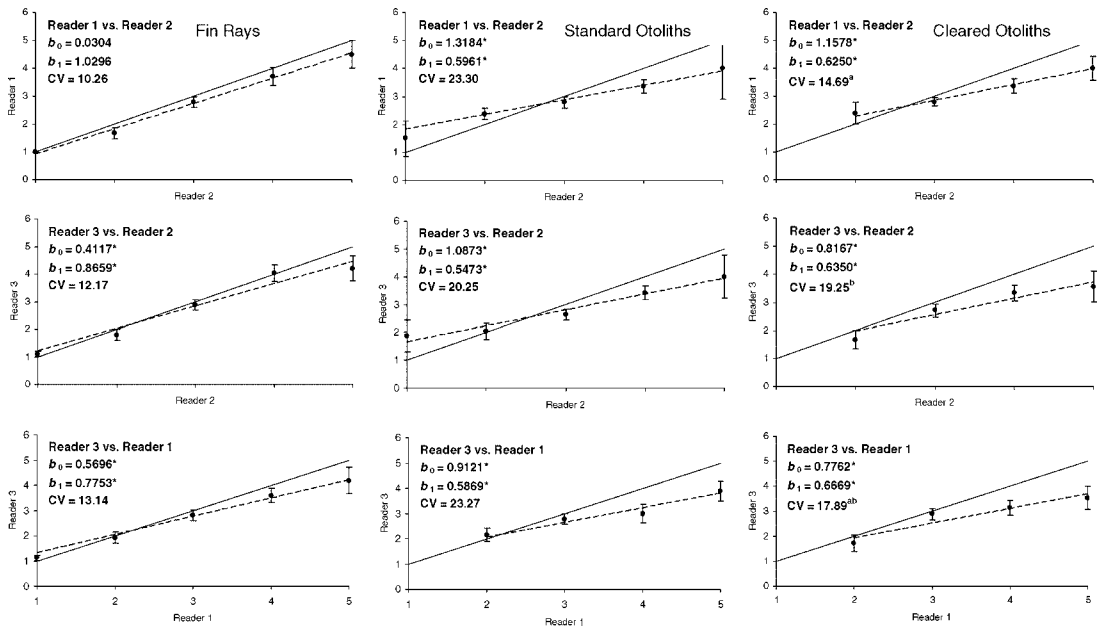


FIGURE 2.—Age bias plots between readers (one reading for each reader within a pair; three readers were used) for each of three rainbow smelt age estimation methods: fin rays (left panels), standard otoliths (middle panels), and cleared otoliths (right panels). In each graph, the solid line indicates 1:1 agreement between readings on the x- and y-axes, and the dashed line indicates the mean age (95% CI) estimated on the y-axis for each age on the x-axis (not calculated if  $n < 5$  for a given age). Asterisks indicate that the intercept ( $b_0$ ) was significantly different from zero or the slope ( $b_1$ ) was significantly different from 1.0 ( $\alpha = 0.05$ ). Letters after the CV indicate significant differences (within a method) in pairwise comparisons conducted after a significant ANOVA.

both otolith methods showed more variation from a 1:1 line (indicates exact agreement between the two readings) than age bias plots for fin rays (Figure 1). For comparisons of age estimates between reader pairs, mean CVs ranged from 10.26% to 13.14% for fin rays, from 20.25% to 23.30% for standard otoliths, and from 14.69% to 19.25% for cleared otoliths (Figure 2). No difference in mean CV between reader pairs was detected for fin rays or standard otoliths ( $P > 0.1357$ ), but for cleared otoliths we detected a difference between the most precise (reader 1 versus reader 2) and least precise (reader 3 versus reader 2) reader pairs ( $P = 0.0100$ ; Figure 2). Age bias plots illustrated more variation from the 1:1 line for age estimates from both standard and cleared otoliths than for estimates from fin rays (Figure 2). We detected significant differences among mean CVs for each age estimation method ( $P \leq 0.0001$ ; Table 1). Fin rays were more precise than both standard and cleared otoliths ( $P \leq 0.0002$ ), and cleared otoliths were more precise than standard otoliths ( $P = 0.0015$ ; Table 1). In consensus age comparisons between method pairs, each otolith method differed from the fin ray method and tended to overestimate age for age-1 fish ( $P < 0.0001$ ; Figure 3). We did not

detect a difference in slope between ages estimated by standard and cleared otoliths ( $P = 0.0511$ ; Figure 3).

When the age-length keys for each method were applied to the length frequency distribution, the resultant age-length distribution generated from the fin ray age-length key showed a trimodal distribution with a peak at age 2 (Figure 4). Only fin rays appeared to correctly identify age-1 rainbow smelt; very few fish were estimated to be age 1 by either of the otolith methods (Figure 4). The distribution derived from standard otolith age estimates also showed highly overlapping size ranges of age-2 and age-3 fish, while the distribution derived from cleared otolith age estimates showed a bimodal distribution dominated by age-3 fish (Figure 4). For all three methods, few fish were estimated to be age 4 or older (Figure 4).

## Discussion

Results from our evaluations of bias, precision, and age-length distributions indicate that sectioned pectoral fin rays are superior to whole otoliths for estimating ages of rainbow smelt. For within- and between-reader comparisons, bias was lower and precision was greater for fin ray age than for otolith age; age estimates from

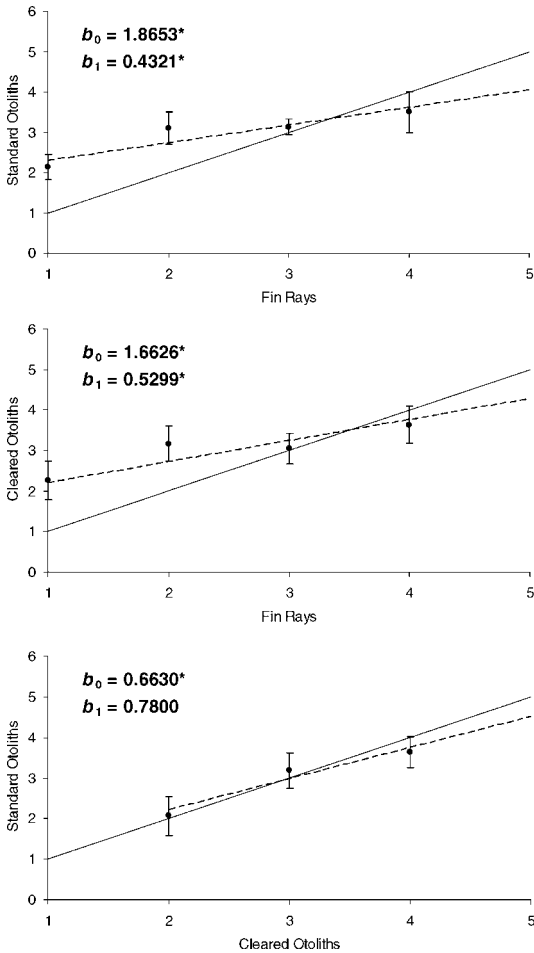


FIGURE 3.—Age bias plots of consensus ages for each pair of rainbow smelt age estimation methods: standard otoliths versus fin rays (top), cleared otoliths versus fin rays (middle), and standard otoliths versus cleared otoliths (bottom). In each graph, the solid line indicates 1:1 agreement between readings on the *x*- and *y*-axes, and the dashed line indicates the mean age (95% CI) estimated on the *y*-axis for each age on the *x*-axis (not calculated if *n* < 5 for a given age). Asterisks indicate that the intercept (*b*<sub>0</sub>) was significantly different from zero or the slope (*b*<sub>1</sub>) was significantly different from 1.0 ( $\alpha = 0.05$ ).

fin rays had overall the highest precision among the three methods evaluated. Validation of age estimation methods is ideal (Beamish and McFarlane 1983), but Campana et al. (1995) stated that when age estimation accuracy cannot be verified, researchers should strive for consistency in age estimation. Of the three methods, fin rays provided the most consistent age estimates.

Corroborating age determination methods with analyses such as length frequency analysis can be valuable in cases when validation is impossible

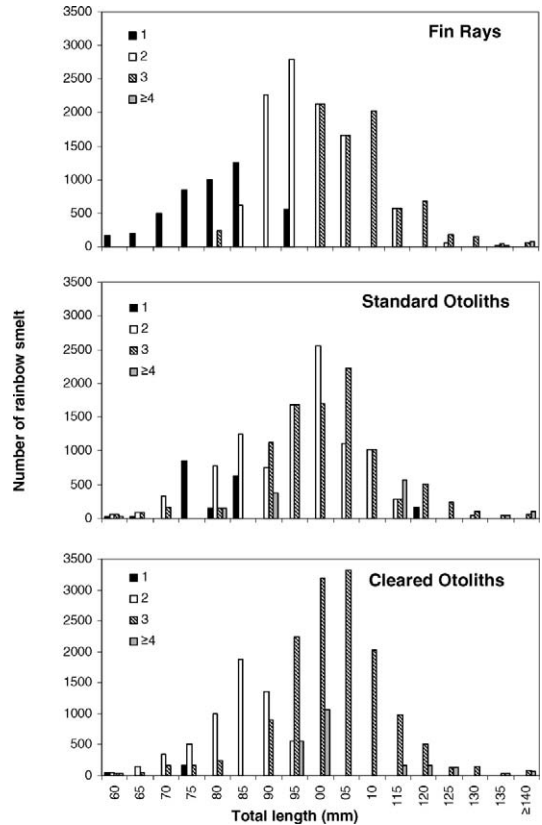


FIGURE 4.—Rainbow smelt age-length distributions derived by applying age-length keys based on three age estimation methods (fin rays, standard otoliths, and cleared otoliths) to the length frequency distribution of fish caught by bottom trawling in southern Lake Ontario during June 2005 (USGS and NYSDEC, unpublished data).

(Kimura et al. 2006). We did not have known-age fish with which to directly measure accuracy of age estimates, but age estimates from fin rays best approximated a realistic age-length distribution based on our field data and our knowledge of the Lake Ontario population. Rainbow smelt in Lake Ontario are under high predation pressure from stocked salmonids (Christie et al. 1987; Owens et al. 2003). When stocking peaked, abundance of 150-mm and larger rainbow smelt declined by 78%; since 1999, abundance of large smelt has been less than 1% of the prestocking peak (LOBS, unpublished data). The predation-abbreviated length distribution suggests that rainbow smelt are short lived in Lake Ontario, and this notion was successfully identified by all three methods of age estimation; fish older than age 4 were rare. However, only the age-length distribution generated from fin ray ages showed the presence of age-1 fish, the youngest fish available to our gear, and the length mode

corresponded to those in length frequency distributions of recent years (generally 80–90 mm; LOBS, unpublished data). The comparison of consensus ages from each method also showed that the two otolith methods overestimated ages for fish designated as age 1 by fin rays. Finally, fin ray ages correctly showed that the 2005 catch was dominated by age-2 rainbow smelt from the 2003 year-class, which was previously identified as a strong cohort at age 1 based on length frequency analysis of the assessment catch in 2004 (LOBS, unpublished data). Cleared otolith ages showed a catch dominated by age-3 fish, which is highly unlikely because of an extremely weak 2002 year-class (LOBS, unpublished data).

Our results collectively indicate that estimation of rainbow smelt ages with otoliths did not represent an improvement over estimation via fin rays and that use of fin rays is the best available method for estimating rainbow smelt ages. However, subjectivity is a source of error inherent to age estimation (Campana 2001), and our results showed that despite the more precise nature of fin rays, systematic bias in age interpretation within and between readers can still pose problems. Therefore, although we will continue to use fin rays to estimate rainbow smelt ages, we have incorporated quality control procedures into our age estimation program to identify and minimize bias and imprecision, as recommended by Campana (2001).

Between standard and cleared otoliths, we found that cleared otoliths provided better age estimates than standard otoliths, but neither performed as well as fin rays. Precision was higher for cleared otoliths both within and between readers, and overall precision of cleared otoliths was higher than that of standard otoliths. Based only on overall mean CVs, cleared otoliths seemed to perform reasonably and would have been identified as a suitable alternative to fin rays. However, in age bias plots within and between readers, both otolith methods varied markedly from a 1:1 line. Additionally, application of the age–length keys from each method to the length frequency distribution revealed some patterns that were not apparent in the analyses of bias and precision. The lack of age-1 rainbow smelt identified with otoliths presents a major problem and occurred because ages of small fish were generally overestimated due to numerous subannual checks on the otoliths. Estimates of rainbow smelt population status in Lake Ontario are provided annually to NYSDEC to aid in management decisions, so failure to adequately characterize year-class strength could result in implementation of an inappropriate management scheme. Overall, the results for the otolith methods verified the perceptions of the three readers in the study, who generally found that estimating ages

was more difficult with otoliths than with fin rays. Estimation of ages for small fish was difficult due to subannual checks, and age estimation for larger fish was often difficult due to otolith thickness. The cleared otoliths sometimes appeared to be excessively cleared, and ages could not be estimated. It is possible that additional processing of the otoliths (sectioning or polishing, rather than just reading whole) could have improved our age estimates. However, this method was not currently in use by any rainbow smelt researchers, so we did not evaluate it.

Age-structured data have become an integral part of most investigations of fish population dynamics and form the basis necessary for understanding the core concepts of fisheries science: recruitment, growth, and mortality (Campana 2001; Campana and Thorrold 2001). After the realization that using scales could lead to underestimation of ages and have significant consequences for the management of fish populations, there was more investigation into using alternative structures such as fin rays (Beamish and McFarlane 1987). However, prevailing thought within the disciplines of fisheries science and management has continued to regard otoliths as universally the best structure for age estimation. Beamish (1981:287) stated that “a popular attitude was (and still is) that if one tries hard enough, the secret of aging a particular fish from scales or otoliths can be found.” At that time, scales were commonly used in studies of freshwater fish and otoliths were more common in studies of saltwater fish (Beamish 1981), but since then numerous comparison studies have found or verified otoliths to be a more precise and less-biased structure for estimating freshwater fish ages as well (Niewinski and Ferreri 1999; Long and Fisher 2001; Maceina and Sammons 2006). Undoubtedly, there are clear advantages to using otoliths in many cases; however, this study, in addition to adding to a surprisingly limited literature base on rainbow smelt, also reminds researchers that in terms of structures used for age estimation, “general applicability ... should never be assumed” (Beamish and McFarlane 1987:22). Selection of aging structures and validation of methods across ages and species should remain important components of age estimation programs (Beamish and McFarlane 1983). A series of recent papers comparing and evaluating age estimation methods (Howland et al. 2004; Ross et al. 2005; LaBay and Lauer 2006; Maceina and Sammons 2006; Sylvester and Berry 2006) highlights the continued interest in this subject and the continued need for evaluation of the most appropriate structures for age estimation based on species, life stage, and life history.



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### References

- Beamish, R. J. 1981. Use of fin-ray sections to age walleye pollock, Pacific cod, and albacore, and the importance of this method. *Transactions of the American Fisheries Society* 110:287–299.
- Beamish, R. J., and G. A. McFarlane. 1983. The forgotten requirements for age validation in fisheries biology. *Transactions of the American Fisheries Society* 112:735–743.
- 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. *Age and growth of fish*. Iowa State University Press, Ames.
- Brandt, S. B. 1986. Food of trout and salmon in Lake Ontario. *Journal of Great Lakes Research* 12:200–205.
- 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. McMillan. 1995. Graphical and statistical methods for determining the consistency of age determinations. *Transactions of the American Fisheries Society* 124:131–135.
- Campana, S. E., and S. R. Thorrold. 2001. Otoliths, increments, and elements: keys to a comprehensive understanding of fish populations? *Canadian Journal of Fisheries and Aquatic Sciences* 58:30–38.
- Casselman, J. M., and K. A. Scott. 2003. Fish community dynamics of Lake Ontario: long-term trends in the fish populations of eastern Lake Ontario and the Bay of Quinte. Pages 349–383 in M. Munawar, editor. *State of Lake Ontario: past, present, and future*. Aquatic Ecosystem Health and Management Society, Ecovision World Monograph Series, Burlington, Ontario.
- Chang, Y. W. B. 1982. A statistical method for evaluating the reproducibility of age determination. *Canadian Journal of Fisheries and Aquatic Sciences* 39:1208–1210.
- Christie, W. J., K. A. Scott, P. G. Sly, and R. H. Strus. 1987. Recent changes in the aquatic food web of eastern Lake Ontario. *Canadian Journal of Fisheries and Aquatic Sciences* 44(Supplement 2):37–52.
- Connelly, N. A., T. L. Brown, and B. A. Knuth. 1997. New York statewide angler survey, report 1: angler effort and expenditures. New York State Department of Environmental Conservation, Albany.
- Elrod, J. H., and R. O’Gorman. 1991. Diet of juvenile lake trout in southern Lake Ontario in relation to abundance and size of prey fishes, 1979–1987. *Transactions of the American Fisheries Society* 120:290–302.
- Evans, D. O., and D. H. Loftus. 1987. Colonization of inland lakes in the Great Lakes region by rainbow smelt, *Osmerus mordax*: their freshwater niche and effects on indigenous fishes. *Canadian Journal of Fisheries and Aquatic Sciences* 44(Supplement 2):249–266.
- Greeley, J. R. 1940. Fishes of the watershed with an annotated list. Pages 42–82 in New York State Department of Conservation. *A biological survey of the Lake Ontario watershed, supplement to the 29th Annual Report* (1939). New York State Department of Conservation, Albany.
- Henderson, B. A., and S. J. Nepszky. 1989. Factors affecting recruitment and mortality rates of rainbow smelt (*Osmerus mordax*) in Lake Erie, 1963–1985. *Journal of Great Lakes Research* 15:357–366.
- Hoff, M. H. 2004. Biotic and abiotic factors related to rainbow smelt recruitment in Wisconsin waters of Lake Superior, 1978–1997. *Journal of Great Lakes Research* 30(Supplement 1):414–422.
- Howland, K. L., M. Gendron, W. M. Tonn, and R. F. Tallman. 2004. Age determination of a long-lived coregonid from the Canadian North: comparison of otoliths, fin rays, and scales in inconnu (*Stenodus leucichthys*). *Annales Zoologici Fennici* 41:205–214.
- Jilek, R., B. Cassell, D. Peace, Y. Garza, and T. Siewart. 1979. Spawning population dynamics of smelt, *Osmerus mordax*. *Journal of Fish Biology* 15:31–35.
- Kimura, D. K., C. R. Kastelle, B. J. Goetz, C. M. Gburski, and A. V. Buslov. 2006. Corroborating the ages of walleye pollock (*Theragra chalcogramma*). *Marine and Freshwater Research* 57:323–332.
- LaBay, S. R., and T. E. Lauer. 2006. An evaluation of the accuracy of age estimation methods for southern Lake Michigan alewives. *North American Journal of Fisheries Management* 26:571–579.
- Lantry, B. F., and D. J. Stewart. 1993. Ecological energetics of rainbow smelt in the Laurentian Great Lakes: an interlake comparison. *Transactions of the American Fisheries Society* 122:951–976.
- Lantry, J. R. 2001. Spatial and temporal dynamics of predation by Lake Ontario trout and salmon. Master’s thesis. State University of New York, College of Environmental Science and Forestry, Syracuse.
- 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.
- Maccina, M. J., and S. M. Sammons. 2006. An evaluation of different structures to age freshwater fish from a northeastern U.S. river. *Fisheries Management and Ecology* 13:237–242.
- Masterman, A. T. 1913. Report on investigations upon the smelt (*Osmerus eperlanus*) with special reference to age-determination by study of scales and its bearing upon sexual maturity. *Fishery Investigations Series I, Salmon and Freshwater Fisheries*, Great Britain Ministry of Agriculture Fisheries and Food 1:115–126.

- McKenzie, R. A. 1958. Age and growth of smelt, *Osmerus mordax* (Mitchill), of the Miramichi River, New Brunswick. *Journal of the Fisheries Research Board of Canada* 15:1313–1327.
- Niewinski, B. C., and C. P. Ferreri. 1999. A comparison of three structures for estimating the age of yellow perch. *North American Journal of Fisheries Management* 19:872–877.
- O’Gorman, R., J. E. Elrod, R. W. Owens, C. P. Schneider, T. H. Eckert, and B. F. Lantry. 2000. Shifts in depth distributions of alewives, rainbow smelt, and age-2 lake trout in southern Lake Ontario following establishment of dreissenids. *Transactions of the American Fisheries Society* 129:1096–1106.
- Owens, R. W., R. O’Gorman, T. H. Eckert, and B. F. Lantry. 2003. The offshore fish community in southern Lake Ontario, 1972–1998. Pages 407–442 in M. Munawar, editor. *The State of Lake Ontario: past, present, and future*. Aquatic Ecosystem Health and Management Society, Ecovision World Monograph Series, Burlington, Ontario.
- Parker-Stetter, S. L., L. D. Witzel, L. G. Rudstam, D. W. Einhouse, and E. L. Mills. 2005. Energetic consequences of diet shifts in Lake Erie rainbow smelt (*Osmerus mordax*). *Canadian Journal of Fisheries and Aquatic Sciences* 62:145–152.
- Ross, J. R., J. D. Crosby, and J. T. Kosa. 2005. Accuracy and precision of age estimation of crappies. *North American Journal of Fisheries Management* 25:423–428.
- SAS Institute. 2000. SAS/STAT user’s guide for personal computers, version 8.1. SAS Institute, Cary, North Carolina.
- Scott, W. B., and E. J. Crossman. 1973. Freshwater fishes of Canada. Fisheries Research Board of Canada Bulletin 184.
- Sylvester, R. M., and C. R. Berry, Jr. 2006. Comparison of white sucker age estimates from scales, pectoral fin rays, and otoliths. *North American Journal of Fisheries Management* 26:24–31.
- Van Oosten, J. 1937. The dispersal of smelt, *Osmerus mordax* (Mitchill), in the Great Lakes region. *Transactions of the American Fisheries Society* 66:160–171.