North American Journal of Fisheries Management
Publication details, including instructions for authors and subscription information:
http://www.tandfonline.com/loi/ujfm20

A Comparison of the Scale and Otolith Methods of Age Estimation for Lake Whitefish in Lake Huron

Andrew M. Muir [a b], Mark P. Ebener [c], Ji X. He [d] & James E. Johnson [d]

[a] Chippewas of Nawash Unceded First Nation, Rural Route 5, Wiarton, Ontario, N0H 2T0, Canada

[b] Department of Forestry and Natural Resources, Pfendler Hall, Purdue University, 715 West State Street, West Lafayette, Indiana, 47907-2061, USA

[c] Chippewa Ottawa Resource Authority, 179 West Three Mile Road, Sault Ste. Marie, Michigan, 49783, USA

[d] Michigan Department of Natural Resources, Alpena Fishery Research Station, 160 East Fletcher, Alpena, Michigan, 49707, USA

Published online: 08 Jan 2011.

North American Journal of Fisheries Management 28:625–635, 2008

DOI: 10.1577/M06-160.1

[Article]

A Comparison of the Scale and Otolith Methods of Age Estimation for Lake Whitefish in Lake Huron

ANDREW M. MUIR*

Chippewas of Nawash Unceded First Nation, Rural Route 5, Wiarton, Ontario N0H 2T0, Canada; and Department of Forestry and Natural Resources, Pfendler Hall, Purdue University, 715 West State Street, West Lafayette, Indiana 47907-2061, USA

MARK P. EBENER

Chippewa Ottawa Resource Authority, 179 West Three Mile Road, Sault Ste. Marie, Michigan 49783, USA

JI X. HE AND JAMES E. JOHNSON

Michigan Department of Natural Resources, Alpena Fishery Research Station, 160 East Fletcher, Alpena, Michigan 49707, USA

Abstract.—We compared sagittal otolith and scale age estimation methodologies for lake whitefish *Coregonus clupeaformis* collected in Georgian Bay and the main basin of Lake Huron between 2002 and 2004 in terms of the age, growth, and mortality estimates generated by the two methodologies. In general, otolith age estimates were higher than scale age estimates. Forty-nine percent of the fish aged by otoliths were judged to be greater than 10 years of age, compared with 5% of the fish aged by scales, and more age-classes were found when otoliths were used. Otolith and scale ages agreed for 16% ($n = 60$) of Georgian Bay fish and only 9% ($n = 27$) of main-basin fish. The overall coefficients of variation for the otolith and scale age estimation methodologies pooled across years and basins were 5.52% and 2.68%, respectively. Mean length at age based on otoliths was significantly lower than mean length at age based on scales. Variation in the mean length at age was greatest for fish age 7 and older. Otolith-based catch-curve estimates of total instantaneous mortality (Z) were 1.26 in Georgian Bay and 0.57 in the main basin. In contrast, scale-based estimates of Z were 0.98 for Georgian Bay and 0.85 for main-basin lake whitefish. This study has demonstrated that estimates of age, growth, and mortality for lake whitefish in Lake Huron vary according to aging methodology. Therefore, we recommend that mark–recapture studies be undertaken to validate the spatiotemporal variation in lake whitefish age estimates in Lake Huron.

Fisheries biologists depend on calcified structures to estimate the age, growth, and mortality of lake whitefish *Coregonus clupeaformis*, and these parameters are used to model the dynamics of their populations (Ebener et al. 2005). Based on the work of Van Oosten (1923, 1939), scales have been the primary structure used to estimate age of lake whitefish in the Laurentian Great Lakes. Van Oosten (1923) reported that the number of "annuli" that developed on the scales of laboratory-reared lake whitefish was the same as the number of winters through which these fish had lived; therefore, accurate ages could be estimated from the scales. However, since that time, many authors have presented evidence challenging the validity of the scale method for aging wild lake whitefish (Neth 1955; Ovchynnyk 1962; Power 1978; Mills and Beamish 1980; Barnes and Power 1984; Mills and Chalanchuk 2004; Mills et al. 2004).

* Corresponding author: ammuir@purdue.edu

Received June 7, 2006; accepted November 16, 2007
Published online April 10, 2008

While scales continue to be the preferred structure to use for estimating the age of lake whitefish in the Laurentian Great Lakes, Casselman (1983) warned that food web disruptions or large shifts in abundance can affect fish growth, thereby making age estimation a challenge. Since the early 1990s substantial changes in growth and condition have been observed in lake whitefish stocks in three of the five Great Lakes (Mohr and Nalepa 2005). These declines and their effects on age estimation have probably been most pronounced in Lake Huron. Mohr and Ebener (2005) reported that mean scale age of harvested lake whitefish from Ontario waters of Lake Huron's southern main basin increased by 5 years from 1983 to 2000. Based on scales, the mean weight of lake whitefish age 10 and older in Ontario's southern main basin declined about 168% from 1987 to 2000, while in the northern main basin the mean weight of the same ages declined about 120% from 1980 to 1987 and only 13% from 1987 to 2000 (Mohr and Ebener 2005). Similarly, condition of lake whitefish in Ontario's southern main basin declined at a rate of 21 g/year (mean slope of decline

TABLE 1.—Mean ages (years) and numbers of age-classes of lake whitefish caught by the Saugeen Ojibway commercial fishery in the main basin of Lake Huron and Georgian Bay during 2002–2004 based on otoliths and scales. The last two columns provide test statistics for paired *t*-tests and significance values for the hypothesis that the mean otolith- and scale-based age estimates are equivalent.

Basin	Year	Sample size	Otoliths Mean age	Otoliths Age-classes	Scales Mean age	Scales Age-classes	t	P
Georgian Bay	2002	110	9.4	11	7.7	8	6.64	<0.001
	2003	141	9.2	12	7.4	8	7.60	<0.001
	2004	137	7.8	13	6.1	7	7.87	<0.001
Main basin	2002	77	10.9	13	8.3	9	8.24	<0.001
	2003	98	10.6	11	7.7	10	10.59	<0.001
	2004	125	9.8	12	6.7	7	8.40	<0.001

in mean weight at age plotted against year) compared with 6.5 g/year in the northern main basin of Lake Huron (Mohr and Ebener 2005). These changes in growth have led managers to question the reliability of the scale method of age estimation and have led to uncertainty associated with modeling the dynamics of lake whitefish populations within the Laurentian Great Lakes.

The goal of our research was to describe and quantify the variation in ages estimated from scales and otoliths in Lake Huron lake whitefish and to assess the potential effects of that variation on the estimation of growth and mortality. Although several authors have examined the variation in age estimates between scales and other calcified structures for lake whitefish, with the exception of Mills and Beamish (1980) and Mills et al. (2004) these studies have not focused on the magnitude of the effects those differences can have on our understanding of the dynamics of exploited lake whitefish populations. Our specific objectives were to (1) compare scale- and otolith-based age estimates of lake whitefish, (2) quantify differences between scale and otolith ages, and (3) compare growth and mortality estimates derived from scale and otolith age estimates.

Methods

Fish collections.—Scale and otolith samples were randomly taken from 688 lake whitefish harvested in the Saugeen Ojibway commercial fishery during 2002–2004 (Table 1) and their total lengths (mm) and weights (kg) were recorded. This is a year-round aboriginal fishery that is concentrated in the Lake Huron waters of Ontario extending from Kincardine north to Tobermory in the main basin, around the tip of the Bruce Peninsula, and south to Meaford in Georgian Bay (Figure 1). All fish were captured in 114- to 133-mm-stretch-mesh, bottom-set, monofilament gill nets. Gear length and depth of capture ranged from 0.09 km to 9.14 km (mean $\pm$ SE = 2.19 $\pm$ 0.001 km) and from 1.83 to 152.5 m (30.23 $\pm$ 2.16 m), respectively.

Age estimation.—Ages of individual lake whitefish were estimated from both scales and otoliths. Scales were collected from the region of the fish below the insertion of the dorsal fin and above the lateral line. A subsample of three nonresorptive scales of similar shape and size from each fish was cleaned using a soft brush, dried with paper towel, and mounted between two 76-mm $\times$ 25-mm microscope slides with the mediolateral (shiny) side of the scale facing up. Otoliths from 12 individuals were mounted with the sulcus side down in a polyester mold (Ted Pella, Inc., Redding, California) and embedded in epoxy resin (System Three; Auburn, Washington, D.C.) to form a block for sectioning. Each otolith was labeled for later identification. To ensure that the nucleus was captured, two 0.3-mm-thick transverse sections through each otolith were made using a modified lapidary saw (0.33-hp motor [1 hp = 746 W] at 1,725 revolutions per minute) equipped with a 0.23-mm, diamond-impregnated Blue Blazer blade (Raytech Industries, Middletown, Connecticut). Otolith sections were lightly polished using wetted 1,500-grit silicon carbide sandpaper. Sections were air-dried for 24 h, labeled and mounted between two 76-mm $\times$ 25-mm microscope slides using epoxy resin. With this method, the otoliths from 6 individual fish were sectioned simultaneously and 18 individuals could be processed per hour.

Image Pro Express 4.0 software (Media Cybernetics, Inc., Silver Spring, Maryland) was employed to capture, store, and enhance the calcified structure images and to quantify and identify growth features on the structures. Scale images were acquired using a color digital camera attached to a 0.4$\times$ magnification stereomicroscope. Otolith images were captured using the same camera that was attached to a 4, 8, 10, and 20$\times$ magnification compound microscope. All images were captured at a resolution of 100 dots per inch, and

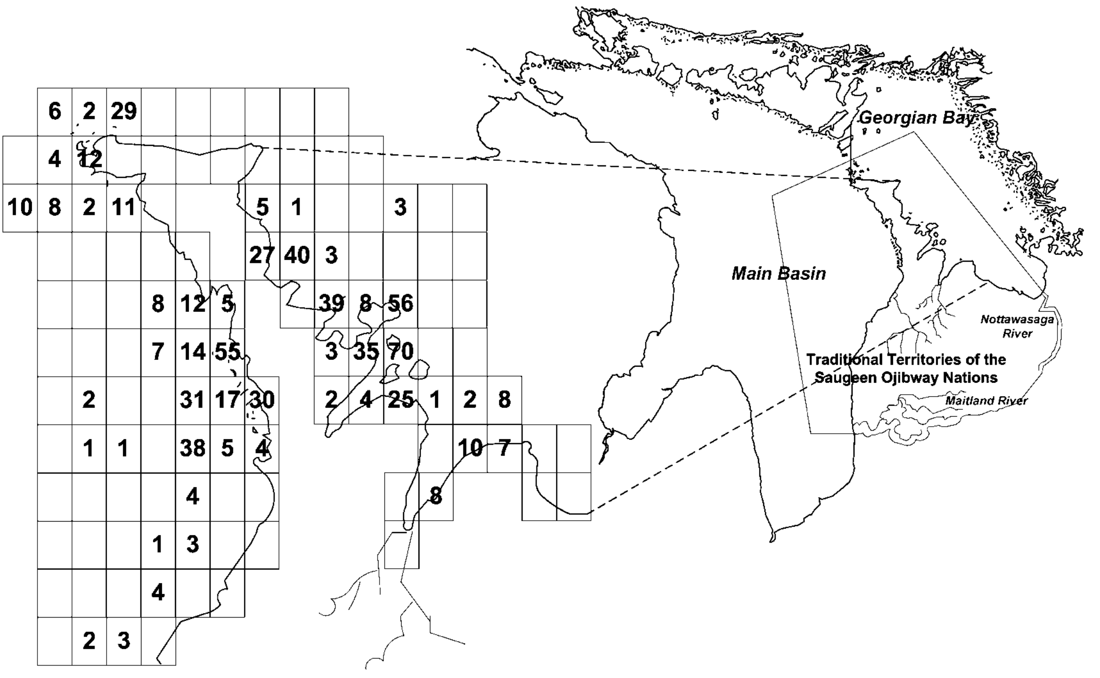

FIGURE 1.—Study area and traditional territories of the Saugeen Ojibway. Each rectangle represents a 5-min × 5-min grid of latitude and longitude. The number within each grid is the number of scale and otolith pairs sampled from that grid across all sampling years ($n = 685$).

whole-structure and best-quadrant images were captured for each of the three scales examined per individual. The otolith section that was nearest to the nucleus was selected for image acquisition.

Two experienced analysts (i.e., 10 years combined) interpreted the scale and otolith images using a blind protocol; the analysts were unaware of the season or basin of capture and lacked any biological data regarding the size of the fish. At the beginning of an interpretation session approximately 50 scale or otolith images were selected from the entire pool of images, displayed on a monitor, randomized, and presented to the analyst for interpretation. The procedures used to select images for interpretation are described below. Using the manual tagging tool available in Image Pro Express 4.0, analysts annotated annuli and what we termed "potential annuli" on each image, stored the annotations as a separate file, and exported the interpretation data to a Microsoft Excel spreadsheet. A scale annulus was defined as the first complete ridge (i.e., circulus) that cuts across or crosses over a region of incomplete ridges and may be associated with a narrow band of hyaline material or sometimes marked by changes in ridge spacing (Tesch 1971; Bagenal 1978; Chilton and Beamish 1982; Beamish and McFarlane 1983; Casselman 1983, 1987; Allen 1985; Johnson 1986; Casselman and Scott 2000). An otolith annulus was defined as the sharp line of transition between the translucent zone and the next broad opaque zone (i.e., transmitted light). For otoliths, annuli had to exist along the entire otolith section. We defined potential annuli, as those features present in the calcified structure, which met some, but not all of the criteria used to identify annuli. The purpose for the potential annuli designation is detailed later. Edge condition was interpreted based on a modification of the methods described by Casselman and Scott (2000). Scale edges were interpreted as follows: 0 = no growth on the edge; 1 = growth in the anterior region; 2 = growth in the lateral regions; and 3 = growth in the anterior and lateral regions. Otolith edge condition was interpreted as either 0 (no growth on the edge) or 1 (growth present on the edge).

Interpretations from each age estimation session were transcribed to a separate spreadsheet that was programmed to estimate age based on the precision of the replicate interpretations and to correct age estimates for growth on the edge of the structure and month of capture. The precision of the age estimates (D) was derived from the coefficient of variation (CV =

100•SD/mean) and the percent error contributed by each observation, that is,

$$D = \mathrm{CV}/\sqrt{R},$$

where R is the number of replicate interpretations (Chang 1982). Because most fish species can be aged with a CV of less than 10% (Campana 2001), we conservatively set the threshold level of D at 6% for which our spreadsheet would estimate age. A D-value of 6% with three replicate interpretations is equivalent to a CV of 10.4%. For example, if two interpretations resulted in a value of D that was less than 6%, the spreadsheet was programmed to accept these data and estimate an age. In contrast, if D was greater than 6%, the spreadsheet was programmed to prompt the analyst to provide more replicate interpretations. Once the interpretation data resulted in a precision value less than 6%, the spreadsheet was programmed to notify the analyst that the data were acceptable and an age could then be automatically estimated. Depending on the variation associated with replicate interpretations, from 2 to 12 replicate scale or otolith interpretations were required for the spreadsheet to accept the data and provide an age estimate. As a result of this methodology, the number of images interpreted by each analyst for each fish varied based on the spreadsheet's requirement for replicates. Furthermore, the specific images to be presented to the analyst were selected based on the spreadsheet's demand for data.

Our spreadsheet was programmed to use two data sets in an attempt to objectively distinguish between true and false annuli. The first set of data included only annuli identified on each image, whereas the second data set included both annuli and potential annuli. The spreadsheet was programmed to select the data set with the lowest D-value to calculate an age estimate for that individual. For example, consider an individual for which four replicate image interpretations were conducted. If a potential annulus was identified on one image but not on the other three replicates, the data set that included the potential annulus would be less precise; therefore, the data set that did not include the potential annulus would be used to calculate an age estimate, provided that the overall D-value was less than 6%. Alternatively, if a potential annulus was identified as an annulus on the other three replicates for that individual, then the data set that included the potential annulus would be more precise and would be selected to calculate an age estimate. Once the most precise data set was identified, mean age was calculated and truncated to the nearest integer.

Truncating the mean age to the nearest integer was a further measure to eliminate false or potential annuli because that helped to ensure correspondence between the age estimate and the number of annuli present on all images from a given individual. The truncated mean age estimate was then corrected for edge growth and month of capture. This posthoc correction was based on reconciling observed growth on the edge of the structures and the conventional 1 January fish birthday rule (Hile 1936; Jearld 1983). If an individual was captured between 1 January and 30 May and no growth was evident on the edge of the structures (i.e., an annulus had not yet formed), 1 year was automatically added to the age of that fish. In contrast, if new growth was present on the edge of the structure (i.e., an annulus had formed), the age was accepted without correction. In most cases replicate interpretations from a given individual fish had been characterized by the analysts as having the same edge condition. In nearly all cases where edge conditions differed, one analyst had identified an annulus on or directly adjacent to the margin of the structure, whereas the other analyst had not, resulting in a difference of 1 year in the interpretation. If this situation arose, images were re-examined by both analysts and edge conditions were adjusted by consensus.

Analyses.—Paired t-tests were used to compare the mean scale ages of lake whitefish with the mean otolith ages among years (2002–2004) for Georgian Bay and the main basin of Lake Huron. Coefficient of variation and D (Chang 1982) were used as precision metrics. To examine relative precision among structures, the number of replicate scale and otolith interpretations (pooled across years and basins) required to achieve a D-value less than 6% was compared using a paired t-test. In cases where the precision indices and the level of agreement between methodologies were poor, a Bowker's chi-square test of symmetry was used to look for evidence of systematic disagreement between the scale and otolith methods (Hoenig et al. 1995). Mean otolith age minus mean scale age was plotted against otolith age to determine the range of nominal ages over which the two methods resulted in comparable age estimates.

To examine methodological differences in growth, mean total length was plotted against scale and otolith age for each year and basin combination. We applied a two-factor analysis of variance (ANOVA) including the interaction term with aging method (i.e., scale and otolith) and estimated age as the main effects to length-at-age data for age groups 5–10. Data were pooled across years and because growth of lake whitefish in Georgian Bay appeared to be faster than in the main basin of Lake Huron, one ANOVA was conducted for each basin. Because the interaction terms of the ANOVAs did not reach statistical significance in either basin, multiple comparison procedures were not

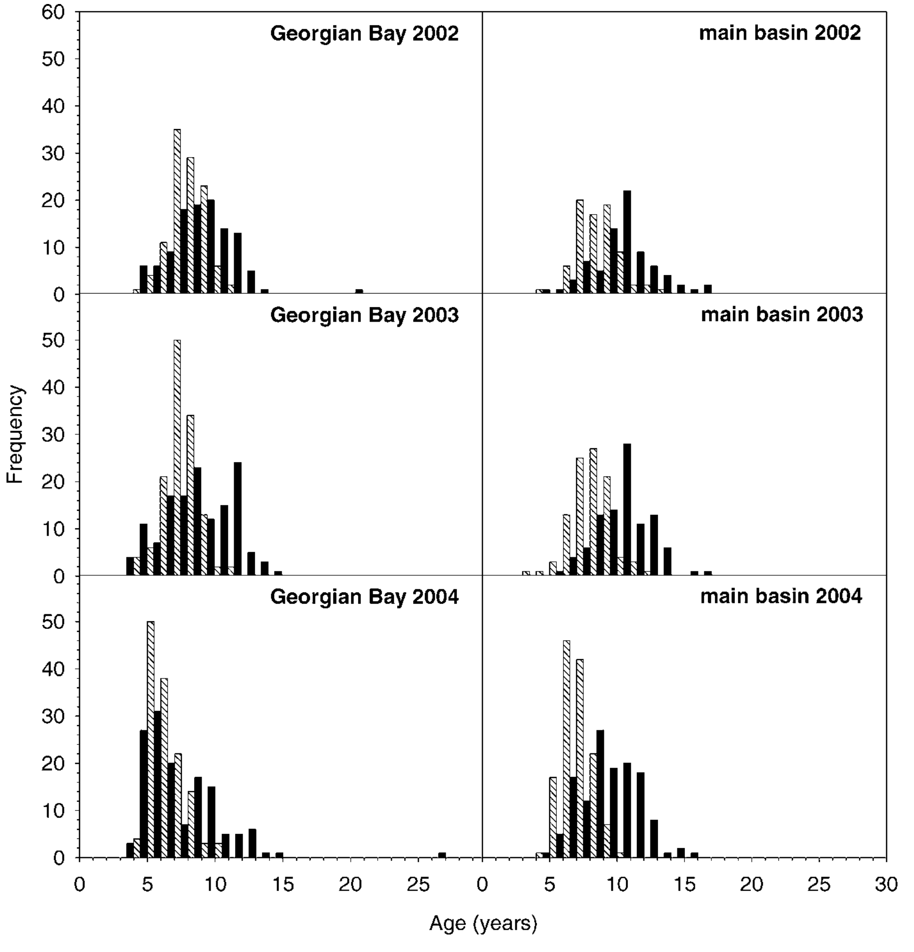

FIGURE 2.—Otolith-based (solid bars) and scale-based (crosshatched bars) age-frequency distributions of lake whitefish captured in the main basin and Georgian Bay areas of Lake Huron surrounding the Bruce Peninsula during 2002–2004.

conducted. Instantaneous total mortality (*Z*) was estimated for each basin (pooled across years) using the slope of a linear regression through the descending limb of otolith- and scale-based catch curves (Ricker 1975). An *F*-test for the equality of regression slopes was used to detect differences in *Z* between aging methodologies for each basin. Statistical methodologies were conducted using SPSS 14.0 (SPSS, Inc., Chicago, Illinois) or SigmaStat 3.5 (Systat Software, Inc., San Jose, California) at the $\alpha = 0.05$ significance level.

Results

We found systematic differences between otolith- and scale-based age estimates for lake whitefish in Georgian Bay (GB) and the main basin (MB) of Lake Huron. Mean otolith age was significantly greater than mean scale age in both basins each year (2002–2004; all $P < 0.001$; Table 1; Figure 2). There were more age-groups represented when basing age estimates on otoliths (12 $\pm$ 1 year-classes) rather than scales (8 $\pm$ 1 year-classes; Table 1). Otolith-based age distributions were broad, and a much greater proportion of the population was age 10 and older. In contrast, scale-based age distributions were truncated and grouped tightly around the modal age (Figure 2). Forty-nine percent of the fish aged by otoliths were greater than 10 years of age, whereas only 5% of those aged by scales were. Between 2002 and 2004, the mean age of the catch decreased in both basins regardless of age estimation methodology.

The otolith and scale methods agreed 16% ($n = 60$) of the time for GB fish and only 9% ($n = 27$) of the time for MB fish. The overall CV for the otolith and scale age estimation methodologies pooled across years and basins was 5.52% and 2.68%, respectively.

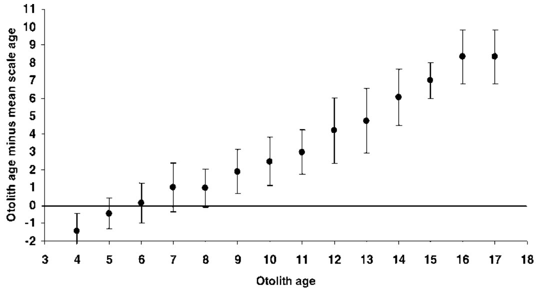

FIGURE 3.—Differences between estimates of otolith and mean scale age (y-axis) versus otolith age (x-axis) for lake whitefish pooled across spatial areas of Lake Huron and years (2002–2004). The zero line indicates 100% agreement between scale and otolith age estimates.

Similarly, D was higher for otoliths (1.91) than for scales (1.72). Despite the fact that scales had lower overall precision values, the mean number of replicates required to achieve a desirable level of precision ($D <$ 6.0) did not differ significantly between otoliths ($\bar{x} =$ 2.34 $\pm$ 0.32) and scales ($\bar{x} = 3.18 \pm 1.46$; $t = -1.14$, $P = 0.29$). Chi-square tests of symmetry provided further support that there was poor agreement between the otolith and scale methods for both GB ($\chi^2 =$ 197.38, df $= 38$, $P < 0.0001$) and MB lake whitefish ($\chi^2 = 252.22$, df $= 50$, $P < 0.0001$). Based on the chi-square analysis, systematic differences between the otolith and scale methodologies were first detected at age 6 (Figure 3). For fish older than age 6, otolith interpretations typically exceeded scale interpretations. In contrast, for fish less than age 6, scale-based estimates frequently exceeded otolith estimates, particularly in GB (Figure 3).

Mean length at age was consistently lower for lake whitefish 5–10 years of age when otolith ages were used rather than scale ages. In GB, both aging method (i.e., scale versus otolith; $F = 21.90$, $P < 0.001$) and age ($F = 44.23$, $P < 0.001$) contributed significantly to the variation in length at age. Similarly, aging method ($F = 15.96$, $P < 0.001$) and age ($F = 9.91$, $P < 0.001$) significantly explained the variation in length at age of MB lake whitefish. The interaction between these factors was not significant for GB fish ($F = 2.02$, $P =$ 0.074) or for the MB fish ($F = 1.13$, $P = 0.343$) (Figure 4). Growth rates were faster in GB than in the MB and growth of young lake whitefish (ages 4–6) appeared to be faster than for older fish in each basin (ages 7–18).

Age at recruitment to the gill-net fishery was age 11 based on otoliths and age 7 based on scales (Figure 5). Otolith- and scale-based Z estimates for GB were 1.26 and 0.98, respectively (Table 2). In comparison, main-basin estimates of Z were 0.57 based on otoliths and 0.85 based on scales. Although the slopes of the two methodologies differed in magnitude for GB, the slopes of the regressions through the descending limbs of the catch curve did not differ significantly ($F = 2.38$, $P = 0.263$). In contrast, the slopes for the otolith and scale catch-curves did differ significantly for the MB ($F = 7.73$, $P = 0.0498$).

Discussion

Despite the obvious caveat that our age estimates were not validated, the implications of our research are twofold: (1) scales and otoliths can produce different estimates of age for commercially exploited stocks of lake whitefish in Lake Huron and (2) estimates of lake whitefish growth and mortality can be affected by aging methodology. Thus, studies to validate the accuracy of lake whitefish age estimation in the Lake Huron are required to improve our understanding of the dynamics of this commercially and culturally valuable species.

Understanding the variability in age estimates associated with a suite of calcified structures can lend corroboratory evidence for the validity of the method (Campana 2001). Large differences in age estimates among calcified structures can be indicative of inaccurate aging methodologies, aging structures, or issues associated with interpretation. Quantifying the direction and magnitude of bias associated with an aging structure can also be a useful means to set bounds of uncertainty for age-based population models. Precision data associated with replicate interpretations are also useful for establishing the ease of interpretation and the reliability of the structure to provide consistent age and growth data. However, Hoenig et al. (1995) pointed out that precision metrics can over-summarize data and are difficult to interpret, particularly when there are systematic differences between methodologies. Our age estimation methodology imposed such constraints. While we found that scales provided more precise age estimates than did otoliths, that result was an artifact of our methodology. In particular, as age increases, CV inherently decreases; therefore, because our methodology required a threshold level of precision (i.e., $D = 6\%$) for which an age estimate was deemed acceptable, scale interpretations were forced to be precise due to the absence of older fish when using this method. To overcome this problem, and simplify the interpretation of our precision metrics, we could have limited the number of replicate interpretations to three for each individual fish. If we were to make such modifications to our analytic design, we predict that otolith-based age estimates would be more precise than scale-based estimates. Despite the challenges imposed by our

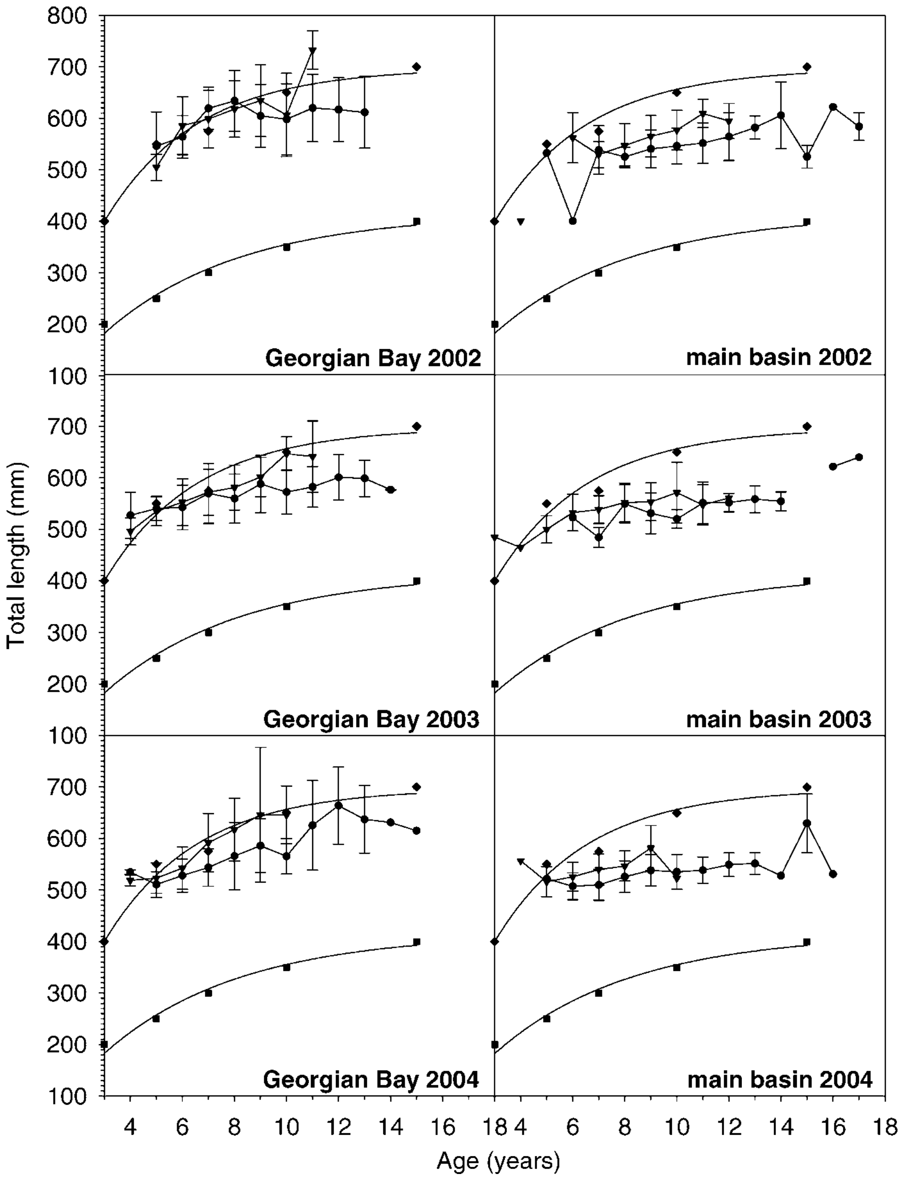

FIGURE 4.—Mean ± SE total length versus age for otoliths (circles) and scales (triangles) for each year and basin. The solid curves represent the approximate minimum (squares) and maximum (diamonds) bounds of the growth rates for lake whitefish reported in the literature (Healey 1975).

methodology, precision estimates for both scales (CV = 2.68%) and otoliths (5.52%) fell within acceptable limits (Campana 2001).

Our results are in accord with a mounting body of evidence that the scale method of age estimation for lake whitefish may be unreliable under certain growth conditions. Neth (1955) reported that some tagged lake whitefish in Little Moose Lake, New York, failed to form a scale annulus between marking and recapture. In a comprehensive study comparing scale ages of lake whitefish from Lake Michigan with age estimates obtained from several other bony structures, Ovchynnyk (1962) found scales to be "very good" for age estimation in fish less than age 6, but were unreliable beyond the age of maturation. Power (1978) reported that otolith ages could be more than double those based on scales for unexploited lake whitefish from lakes in northern Quebec. In a study of 15 Canadian lakes,

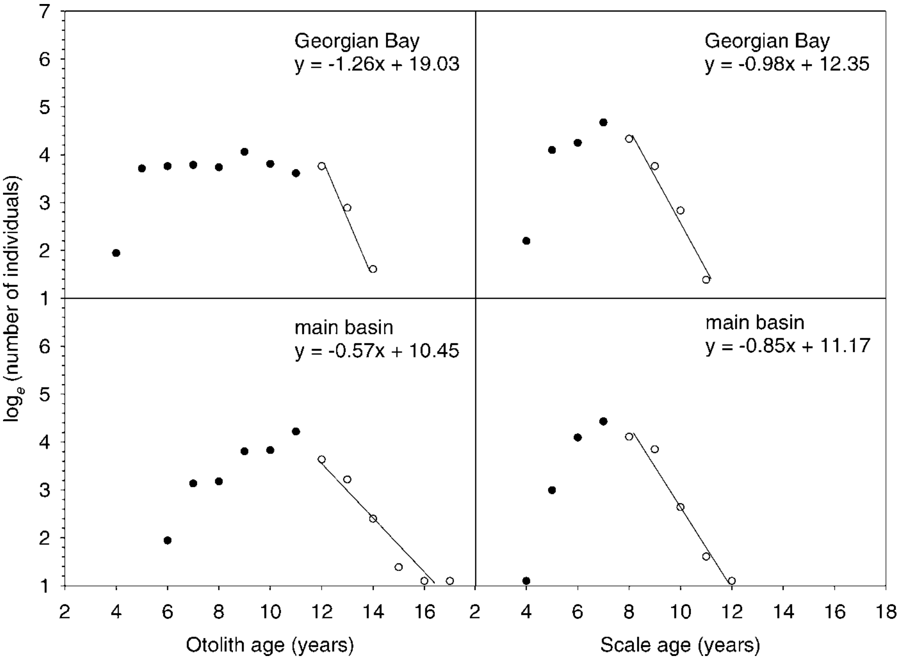

FIGURE 5.—Catch curves for lake whitefish based on estimates of otolith age (left panel) and scale age (right panel) for Georgian Bay (top row) and main basin (bottom row) Lake Huron between 2002 and 2004. Age at recruitment for otoliths and scales was 11 and 7 years, respectively. Linear regressions were fit to age at recruitment + 1 year (white circles).

Mills and Beamish (1980) reported that there was good agreement between scale and fin ray aging methods for young, fast-growing populations of lake whitefish, but that fin ray ages were generally greater than scale ages for slow-growing populations. Similarly, Barnes and Power (1984) demonstrated that otolith ages were greater than scale ages for 71% of fish sampled from Churchill Falls, Labrador. More recently, Muir (2004) reported that some lake whitefish from Georgian Bay failed to form a scale annulus between marking and recapture. Mills and Chalanchuk (2004) and Mills et al. (2004) demonstrated that otoliths and fin rays from lake whitefish tagged and subsequently recaptured provided more accurate age estimates than did scales for slow-growing, unexploited stocks. Taken together, these studies support the hypothesis that beyond the

TABLE 2.—Estimates of instantaneous total mortality per year for lake whitefish as determined from either scale ages or mark–recapture in the main basin of Lake Huron and Georgian Bay from this study and others. Methods of estimating mortality are as follows: mark–recapture (M–R), scale age catch curve (SCC), fin ray age catch curve (FCC), otolith age catch curve (OCC), tag returns (TR), and scale age statistical catch-at-age analysis (SCAA). The SCAA estimates were obtained from the Chippewa Ottawa Resource Authority (CORA) in northern Michigan waters of Lake Huron during 2002–2004.

				Mortality	
Basin	Source	Method	Ages	Mean	Range
Georgian Bay	Budd (1957)	TR		0.77	
	Cucin and Regier (1965)	SCC	2–9	0.62	0.48–0.95
	This study	OCC	11–15	1.26	
	This study	SCC	8–11	0.98	
Main basin	Budd (1957)	M–R		0.56	0.53–0.59
	Budd and Cucin (1962)	SCC	2–7	0.93	
	Spangler (1970)	M–R	2–4	0.89	0.76–0.99
	Mills and Beamish (1980)	SCC	1–6		0.72–0.94
	Mills and Beamish (1980)	FCC	1–6		0.69–0.93
	This study	OCC	12–17	0.57	
	This study	SCC	8–13	0.85	
	CORA	SCAA	4–12	0.45	0.39–0.52

age of maturation, scales may provide less reliable estimates of age than otoliths or fin rays for some lake whitefish stocks.

Given the magnitude of the variability associated with scale and otolith ages, we investigated the potential effects on estimates of growth and mortality of lake whitefish. Because declines in lake whitefish growth have been more dramatic in the southern MB of Lake Huron than in GB, we expected differences in age, growth, and mortality between otoliths and scales to be more pronounced in the MB. In general, our results were consistent with that prediction; however, both scale- and otolith-based growth estimates for GB lake whitefish were higher than expected. The differences in growth between the basins may have been driven by density-dependent factors. In the MB, lake whitefish population abundance peaked in the mid-1990s and had begun declining by 2000, yet remained 4–5 times higher than in the previous decade (Mohr and Ebener 2005). In contrast, lake whitefish abundance continued to increase in GB through 2000 (Mohr et al. 2003; Mohr and Ebener 2005). Based on scale estimates, abundant year-classes produced in the early 1990s should have been senescing and exiting the fisheries by 2000. In contrast, based on otolith age estimates, these year-classes still comprised the bulk of the commercial harvest in both GB and the MB. Healey's (1980) compensatory growth hypothesis predicts that lake whitefish growth in the MB should have been increasing in compensatory fashion in response to increased mortality and declining abundance, while it should have been declining in GB. Regardless of the structure used to interpret age, we found that mean age in the catch declined in both basins. Based on otoliths, it appeared that growth declined slightly between 2002 and 2004 in Lake Huron, but that trend was not evident based on scales and both otolith- and scale-based growth rates appeared to be stable in Georgian Bay.

Both the otolith- and scale-based Z estimates for GB were higher than those previously reported for lake whitefish in this bay (Table 2). In contrast, the Z estimates for the MB were within the range previously reported; otolith-based estimates were near the lower end of the range, whereas scale-based estimates were near the upper end (Table 2). In comparison, Mohr et al. (2003) reported that in 2002 estimates of Z from statistical catch-at-age models and cohort analysis ranged from 0.39 to 0.44 for GB lake whitefish and from 0.38 to 0.65 for MB lake whitefish. These estimates were from the same stocks that we sampled, but are only consistent with our otolith-based estimates for the MB. Potential explanations for the inconsistency between our results and those of Mohr et al. (2003) include (1) error associated with our sampling design, (2) inadequate sample size, (3) inaccurate age estimation, and (4) the over- or underrepresentation of one or more cohorts in our samples. Regardless of these inconsistencies, our study has shown that aging method can affect the magnitude of lake whitefish mortality estimates.

Management Implications

Reliable age estimates are critical to estimating population parameters such as growth and mortality and ultimately abundance. Systematic underaging can result in body weights of older fish being averaged in with those of younger fish resulting in an increase in mean weight at age or length at age (Tyler et al. 1989). Although we were unable to conclude that systematic underaging of lake whitefish in Lake Huron has occurred, the slower otolith-based growth schedules observed in this study are consistent with the declines in growth and condition of lake whitefish observed in the MB in the late 1990s through 2004 (Kratzer 2007). The potential overestimation of lake whitefish growth based on scale aging may have acted to dampen density-dependent signals throughout the late 1990s and early 2000s. If growth has indeed been overestimated, then target exploitation rate and mortality (Mohr et al. 2003; Ebener et al. 2005) used to project harvest limits may have been held artificially low, thereby exacerbating density-dependent competition among lake whitefish life stages or among stocks. Healey (1980) demonstrated that the major response of lake whitefish to exploitation rates of 20–30% was an increase in growth rate that resulted in earlier maturation and shorter generation times. Kratzer (2007) recently reported evidence of density-dependent effects on lake whitefish growth and condition in Lake Michigan and recommended that harvest regulations be implemented to reduce densities with the predicted response of increased growth and condition of fish that are more marketable.

Over the spatial and temporal range of this study, the lake whitefish harvest limits that were implemented in Ontario waters of Lake Huron were not reflective of lake whitefish growth and abundance. For example, in the main-basin management area 4–4 (Mohr et al. 2003), harvest limits were decreased by an average of 21% between 1995 and 2004. In contrast, total allowable catches for our study region in Georgian Bay were increased by 100% over the same period. These changes in harvest limits were based on several factors, including declining growth, condition, and mortality, but if scale underaging had indeed occurred harvest limits in the main basin should have increased, as they did in Georgian Bay.

While it is premature to recommend increased harvest limits to reduce lake whitefish population abundance in the southern main basin of Lake Huron, lake whitefish density-dependence should be reexamined using validated age estimates.

Despite the fact that previous studies have found otoliths or fin rays to be superior to scales for aging slow-growing fishes, Casselman (1987) pointed out that otoliths also overestimate age. As such, ongoing field validation is required to conclusively determine the accuracy of lake whitefish age estimation methodologies in response to changing food web dynamics in the Laurentian Great Lakes. Campana (2001) provided a comprehensive review of age validation methodologies. Of these methodologies, planting fish of known age is the most rigorous and widely applicable means of validating lake whitefish age estimates in the Laurentian Great Lakes. However, mark–recapture studies offer a proven, more economical, and feasible alternative (Mills and Chalanchuk 2004; Mills et al. 2004). By comparing scales and pectoral fin rays from the time of marking and recapture, the periodicity of annulus formation can be validated over the duration of the study. Age interpretations from sagittal otoliths collected from recaptures can also be compared with the other methodologies as a means of corroborating interpretations. For example, Mills and Beamish (1980) used mark–recapture to examine the validity of the scale and fin ray methods of age estimation for lake whitefish in two experimental lakes in northwestern Ontario. Of 984 marked fish, 224 (23%) were recaptured at least 1 year later and annuli were clearly identifiable on both the scales and fin rays of fish from one of the lakes but were unclear or absent from the scales of fish from the second lake. In exploitation experiments in four lakes in the Northwest Territories, Healey (1980) observed that mark–recapture lake whitefish ($n = 8$) between the ages of 7 and 12 laid down approximately one annulus each year; however, these annuli were difficult to distinguish on the scales. More recently, Mills and Chalanchuk (2004) and Mills et al. (2004) validated the otolith and fin ray methods as accurate estimators of age for unexploited lake whitefish stocks. Another advantage of mark–recapture studies is that natural and instantaneous mortality estimates can be validated, as is currently being done in the southern main basin of Lake Huron (M. P. Ebener and coworkers, proposal for a study of the distribution of lake whitefish in Lake Huron submitted to the U.S. Fish and Wildlife Service, 2003).

In summary, we recommend that mark–recapture studies be undertaken to validate lake whitefish age estimation methodologies and mortality estimates in the Laurentian Great Lakes. These studies should be conducted on an individual stock basis and should be designed to assess the spatial and temporal variation in annulus formation and mortality schedules based on scales, pectoral fin rays and sagittal otoliths. Without validating the accuracy of lake whitefish age estimates, managers will be faced with the possibility that age, growth, and mortality estimates for this commercially important species are flawed.

Acknowledgments

We thank the Chippewas of Nawash Unceded First Nation commercial fishers for providing us access to their harvests and the Nawash Chief and Council for supporting this research. We especially thank Mary Stanish and Dorene Keeshig (Nawash fisheries assessment technicians) and the rest of the fisheries assessment staff for all of their efforts in collecting, processing, and analyzing samples.

References

Allen, R. J. 1985. Analysis of scale age and growth for lake whitefish (*Coregonus clupeaformis*) from Lake Simcoe. Ontario Ministry of Natural Resources, Peterborough, Ontario, Canada.

Bagenal, T. B. 1978. Methods for assessment of fish production in fresh water, 3rd edition. Blackwell Scientific Publications, Edinburgh.

Barnes, M. A., and G. Power. 1984. A comparison of otolith and scale ages for western Labrador lake whitefish (*Coregonus clupeaformis*). Environmental Biology of Fishes 10:297–299.

Beamish, R. J., and G. A. McFarlane. 1983. The forgotten requirement for age validation in fisheries biology. Transactions of the American Fisheries Society 112:735–743.

Budd, J. 1957. Movements of tagged whitefish in northern Lake Huron and Georgian Bay. Transactions of the American Fisheries Society 86:128–134.

Budd, J. C., and D. Cucin. 1962. Exploitation of Canadian Lake Huron whitefish. Transactions of the American Fisheries Society 91:223–224.

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.

Casselman, J. M., editor. 1983. Age and growth assessment of fish from their calcified structures: techniques and tools, volume 8. National Oceanic and Atmospheric Administration, Washington, D.C.

Casselman, J. M. 1987. Determination of age and growth. Pages 209–242 *in* A. H. Weatherley and H. S. Gill, editors. The biology of fish growth. Academic Press, New York.

Casselman, J. M., and K. A. Scott. 2000. A general procedures manual for CSAGES-calcified structure age–growth data extraction software, version 5.2. Ontario Ministry of Natural Resources, Picton, Ontario, Canada.

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

Chilton, D. E., and R. J. Beamish. 1982. Age determination methods for fishes studied by the groundfish program at the Pacific Biological Station. Canadian Special Publication of Fisheries and Aquatic Sciences 60.

Cucin, D., and H. A. Regier. 1965. Dynamics and exploitation of lake whitefish in southern Georgian Bay. Journal of the Fisheries Research Board of Canada 23:221–274.

Ebener, M. P., J. R. Bence, K. R. Newman, and P. J. Schneeberger. 2005. Application of statistical catch-at-age models to assess lake whitefish stocks in the 1836 treaty-ceded waters of the upper Great Lakes. Pages 271–309 *in* L. C. Mohr and T. F. Nalepa, editors. Proceedings of a workshop on the dynamics of lake whitefish (*Coregonus clupeaformis*) and the amphipod *Diporeia* spp. in the Great Lakes. Great Lakes Fishery Commission Technical Report 66.

Healey, M. C. 1975. Dynamics of exploited whitefish populations and their management with special reference to the Northwest Territories. Canadian Journal of Fisheries and Aquatic Sciences 32:427–428.

Healey, M. C. 1980. Growth and recruitment in experimentally exploited lake whitefish (*Coregonus clupeaformis*) populations. Canadian Journal of Fisheries and Aquatic Sciences 37:255–267.

Hile, R. 1936. Age and growth of the cisco, *Leucichthys artedii* (LeSueur) in the northeastern highlands of Wisconsin. U.S. Bureau of Fisheries Bulletin 48:427–444.

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 52:364–367.

Jearld, A. J., editor. 1983. Age determination. American Fisheries Society, Bethesda, Maryland.

Johnson, G. E. 1986. Techniques and criteria used to age Lake Superior lake whitefish (*Coregonus clupeaformis*). Ontario Ministry of Natural Resources, Thunder Bay, Ontario, Canada.

Kratzer, J. F., W. W. Taylor, and M. Turner. 2007. Changes in fecundity and egg lipid content of lake whitefish (*Coregonus clupeaformis*) in the upper Laurentian Great Lakes between 1986–87 and 2003–05. Journal of Great Lakes Research 33:922–929.

Mills, K. H., and R. J. Beamish. 1980. Comparison of fin ray and scale age determinations for lake whitefish (*Coregonus clupeaformis*) and their implications for estimates of growth and annual survival. Canadian Journal of Fisheries and Aquatic Sciences 37:534–544.

Mills, K. H., and S. M. Chalanchuk. 2004. The fin ray method of aging lake whitefish. Annales Zoologici Fennici 41:215–223.

Mills, K. H., E. C. Gyselman, S. M. Chalanchuk, and D. J. Allan. 2004. Growth, annual survival, age, and length frequencies for unexploited lake whitefish populations. Annales Zoologici Fennici 41:263–270.

Mohr, L. C., A. Cottrill, and S. Milne. 2003. Review of status of lake whitefish populations in the waters surrounding the Bruce Peninsula, 2003. Ontario Ministry of Natural Resources, Owen Sound, Ontario, Canada.

Mohr, L. C., and M. P. Ebener. 2005. Status of lake whitefish (*Coregonus clupeaformis*) in Lake Huron. Pages 105–125 *in* L. C. Mohr and T. F. Nalepa, editors. Proceedings of a workshop on the dynamics of lake whitefish (*Coregonus clupeaformis*) and the amphipod *Diporeia* spp. in the Great Lakes. Great Lakes Fishery Commission Technical Report 66.

Mohr, L. C., and T. F. Nalepa, editors. 2005. Proceedings of a workshop on the dynamics of lake whitefish (*Coregonus clupeaformis*) and the amphipod *Diporeia* spp. in the Great Lakes. Great Lakes Fishery Commission Technical Report 66.

Muir, A. M. 2004. Age estimation of lake whitefish (*Coregonus clupeaformis*) in Lake Huron: reducing the uncertainty. Master's thesis. University of Guelph, Guelph, Ontario, Canada.

Neth, P. C. 1955. Assessment of a control program for common whitefish *Coregonus clupeaformis* and round whitefish *Prosopium quadrilaterale* in little Moose Lake, New York. Master's thesis. Cornell University, Ithaca, New York.

Ovchynnyk, M. M. 1962. The use of scales and bones for age determination of the Great Lakes whitefish *Coregonus clupeaformis* (Mitchill). Zoologischer Anzeiger 175:198–217.

Power, G. 1978. Fish population structure in Arctic lakes. Canadian Journal of Fisheries and Aquatic Sciences 35:53–59.

Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Fisheries Research Board of Canada Bulletin 191.

Spangler, G. R. 1970. Factors of mortality in an exploited population of whitefish, *Coregonus clupeaformis*, in northern Lake Huron. Pages 515–529 *in* C. C. Lindsey and C. S. Wood, editors. Biology of coregonid fishes. University of Manitoba Press, Winnipeg, Canada.

Tesch, F. W. 1971. Age and growth. Pages 93–123 *in* W. E. Ricker, editor. Methods for assessment of fish production in fresh waters. Blackwell Scientific Publications, London.

Tyler, A. V., R. J. Beamish, and G. A. McFarlane. 1989. Implications of age determination errors to yield estimates. Canadian Special Publication of Fisheries and Aquatic Sciences 108:27–35.

Van Oosten, J. 1923. The whitefishes (*Coregonus clupeaformis*): a study of the scales of whitefishes of known ages. Zoologica 2:381–412.

Van Oosten, J. 1939. The age, growth, sexual maturity, and sex ratio of the common whitefish *Coregonus clupeaformis* Mitchill of Lake Huron. Papers of the Michigan Academy of Science, Arts and Letters 24:195–221.