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The fin-ray method of aging lake whitefish

Kenneth H. Mills & Sandra M. Chalanchuk

Department of Fisheries and Oceans, Freshwater Institute, 501 University Crescent, Winnipeg, Mb., Canada R3T 2N6 (e-mails: MillsK@dfo-mpo.gc.ca, ChalanchukS@dfo-mpo.gc.ca)

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We report the results of a long-term age validation of the fin-ray method of aging lake whitefish (*Coregonus clupeaformis*). We further compare fin-ray ages with otolith ages and describe a technique to back-calculate lengths of lake whitefish. Using ages determined from individuals when tagged, we correctly predicted the ages determined from fish when they were recaptured one to 28 years later for 1092 (73%) of the 1492 individuals that we examined. When differences occurred between predicted and actual ages at recapture, there was no tendency for the actual ages to be greater or less than the predicted age. We found no significant difference between fin-ray and otolith ages for individual lake whitefish from two other lakes, although the ages agreed for only 49% of the age pairs. We used the upper section of the first pelvic fin ray to back-calculate fork lengths of lake whitefish from one population using the direct proportionality method, and compared these predicted lengths with actual lengths recorded one to three years earlier when fish were tagged to validate the method.

Introduction

Scales are the traditional structure used in the routine aging of lake whitefish (*Coregonus clupeaformis*). The method was described in detail by Van Oosten (1929) and has been used for more than 75 years for lake whitefish. The justification for this lake whitefish aging method was published by Van Oosten (1923) using scales from lake whitefish held in the New York Aquarium for a known period of time. More recently, Hoagman (1968) held lake whitefish in large hatchery ponds where fish grew at much faster rates than those used by Van Oosten from the New York Aquarium. He identified annular marks on the scales as well as two ancillary marks. Power (1978) was the first to question the validity of scale ages for lake whitefish in northern Canada, where populations are frequently unexploited and growth is slow. He found that the otolith ages for a sample of 37 fish were much older than corresponding scale ages. This was followed by the study of Mills and Beamish (1980) who compared scale and fin-ray ages for 15 populations of lake whitefish. They found that fin-ray ages were frequently greater than scale ages for southern as well as northern unexploited populations. They validated their fin-ray ages in a two-year mark-recapture experiment. Other researchers (Aass 1972, Skurdal *et al*. 1985) have reported that otolith ages are greater than scale ages for other coregonids and scale ages have frequently been reported less than otolith ages for other species (Campana 2001).

The purposes of this study are to present long-term results of a mark-recapture validation for fin-ray ages for one population of lake whitefish, and to present a comparison of fin-ray and otolith ages for two other populations. Back-calculation of lengths using scales is frequently used to study the growth history of lake whitefish. We developed a technique to back-calculate lengths of lake whitefish and have used this extensively in our study of lake whitefish growth. A third purpose of this study is to describe this technique and present a validation of the back-calculated lengths.

Methods

Study area

We conducted all studies at the Experimental Lakes Area (ELA), northwestern Ontario, Canada. The lakes are located in boreal forest underlain by Precambrian granites and gneisses. There are many small, un-named lakes in this area. Lakes were assigned numbers during the initial survey of the area and we will use the numbers listed in Cleugh and Hauser (1971) to identify the study lakes in this report. Lake whitefish occur in many ELA lakes and all populations are unexploited.

Mark-recapture age validation

We conducted the mark-recapture validation of fin-ray ages of lake whitefish in Lake 226 at the ELA. Lake whitefish were captured in the fall of each year from 1973 to 2001 using small-mesh trap nets and short-sets of experimental gill nets. Lake whitefish were quickly removed from gill nets and held overnight in pens before sampling the following day. We anesthetized (using tricaine®, better known as MS-222), weighed (g), and measured (fork length mm) each fish. Then we removed two to three of the leading pelvic fin rays from one fin close to the body. We tagged each fish with an individually numbered t-bar tag or modified Carlin tag (White & Beamish 1972) in 1973, and used only the Carlin tags until 1995. Then, after one year of tagging with both Carlin and numbered Visible Implant (V.I.) tags (Haw *et al.* 1990), we used only V.I. tags through 2001. When we recaptured tagged lake whitefish one or more years later, we removed two to three of the leading fin rays from the opposite pelvic fin. If rays had already been removed from both pelvic fins, we removed two to three rays from a pectoral fin.

We dried the clipped fin rays in scale envelopes, mounted the fin rays in epoxy, and cut cross sections (approximately one mm thickness) using either a jeweler's saw with a very fine blade (1973–1984) or an Isomet® thin-sectioning machine with a diamond cutting wheel (1985–2001). The angle and thickness of sections cut using the machine were more consistent than those cut using the jeweler's saw. We then viewed the sections using a compound microscope at 16–320 power using transmitted light. We selected the section cut closest to the base of the ray to use for aging, but found no difference in ages among the first 4 sections cut at the base of the fin. Although annuli were clear on sections of all rays on pectoral and pelvic fins, the first ray was wider in cross-section than other rays and there was greater separation between annuli than on cross-sections of other rays.

Annuli appeared as clear rings in the fin-ray sections (Fig. 1). We determined that these were formed during winter months by capturing lake whitefish, removing fin rays, and examining the peripheries of the rays during each month of the ice free seasons in 1974 and 1975 (Mills 1981). Darker matrix material was formed during the summer growth season and first appeared on the edges of the rays when fish started growing in length. An accessory mark was formed on the fin rays during the first summer of fish life (Fig. 1A and B). We have observed this in sections of lake whitefish from all the populations we have sampled during the past 30 years regardless of whether lake whitefish have come from a southern or northern population. As fish became older, the amount of dark material between annuli lessened. For lake whitefish with ages greater than 10–15 years, there was little dark matrix between the clear bands, and frequently the bands were directly adjacent to each other in very old fish (Fig. 1D).

We calculated a predicted age for each recaptured lake whitefish by adding the appropriate number of years between marking and recapture to the age determined when the fish was marked.

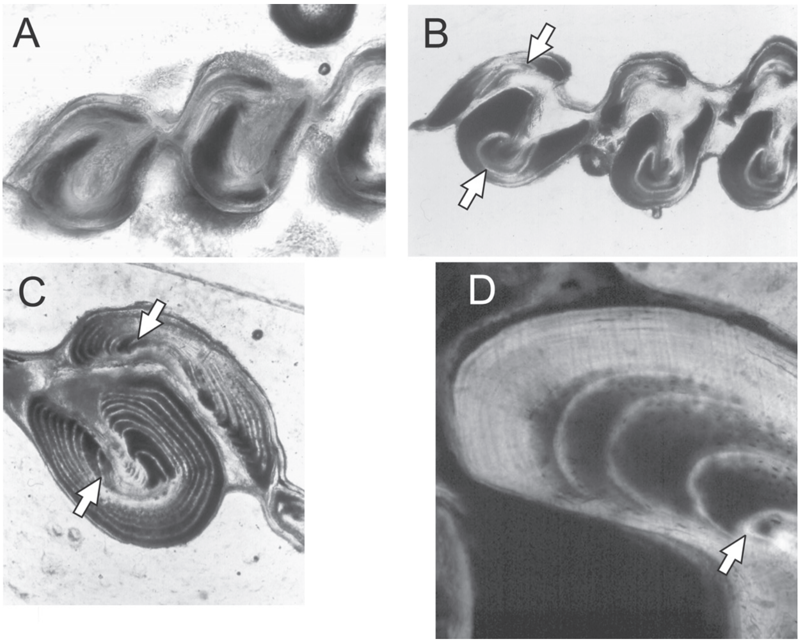

Fig. 1. Fin ray sections from pelvic fins of lake whitefish. — **A**: The first 3 rays from an age 0 (10 cm fork length, 12 g) fish captured in fall 1976 (160×). Each ray is composed of an upper and lower section. The anterior ray of the fin is on the left. — **B**: The first three rays from an age 1 lake whitefish (24×). — **C**: The first ray from an age 8 lake whitefish (24×). — **D**: The upper portion of the first ray from an age 24 lake whitefish (annuli on edge of fin hard to distinguish)(160×). The first annulus is indicated by arrows on the upper and lower portions of the first fin ray in **B** and **C**, and on the upper section in **D**.

We then compared this predicted age with the actual age determined from the fin rays removed from the fish when it was recaptured, and calculated percent agreement (PA, Campana 2001) between the pairs of ages using all age pairs. We used a paired *t*-test to determine if there were significant differences between the predicted and actual ages at recapture, and the χ^2 test of symmetry (Hoenig *et al*. 1995) to analyse differences in the distribution of differences between age sets.

The lake whitefish in Lake 226 grew more quickly during the years of nutrient additions to this lake, 1973–1980, and the first two years after these additions were terminated (Mills *et al*. 1998), than subsequent years. Therefore, we calculated percent agreement between all predicted and actual age pairs, and separate calculations for the periods of fast growth and slow growth. We used the *G*-test of independence (Sokal & Rohlf 1995) to determine if the percentage agreement was different between the two growth periods.

Fin ray–otolith comparisons

We captured lake whitefish from ELA Lakes 259 and 468 in September 2001 using overnight sets of experimental gill nets (11-, 25-, 30-, 33-, 38- and 45-mm bar mesh). We removed two to three pelvic fin rays and the sagittal otoliths from each fish. We processed and aged the pelvic fin rays as described above. Otoliths were dried, mounted, and sectioned in the same fashion as fin rays. We sectioned entire otoliths and obtained four to six cross sections, depending on the size of the whole otolith. We aged the otoliths using a compound microscope, viewing the sections at 64 to 320 power using transmitted light. Otolith annuli were similar to fin-ray annuli (clear bands) with dark matrix between the bands (Fig. 2). We used the criteria of Beamish (1979) to identify annuli on otoliths. We selected the center section of each otolith to obtain the fish age, but found identical ages using the sections immediately adjacent to the middle section.

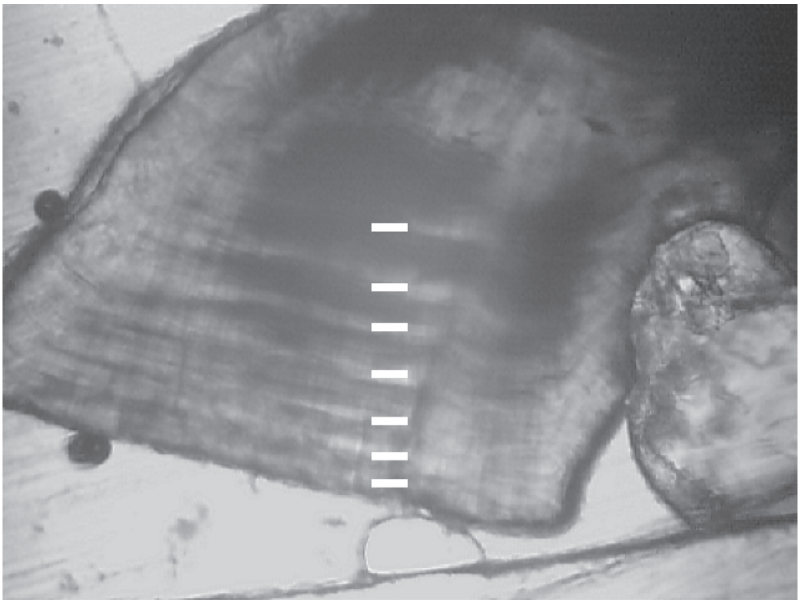

Fig. 2. The ventral portion of a transverse otolith section from a Lake 468 age 7 lake whitefish (160×). Annuli are indicated by white bars.

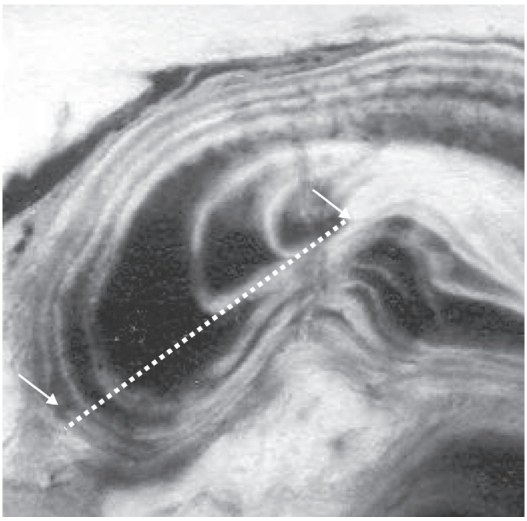

Fig. 3. The upper portion of the first pelvic fin ray showing the plane used to measure back-calculations (160×). The first annulus and periphery of the ray are indicated by arrows.

We compared pairs of otolith and fin-ray ages using the percent agreement (PA) method, and used a paired *t*-test to determine if significant differences occurred between the sets of ages. We used the χ^2 test of symmetry (Hoenig *et al.* 1995) to analyse the distribution of differences between age pairs.

Back-calculations

We used the posterior portion of the upper first fin ray (Fig. 3) to back-calculate fork lengths of Lake 226 lake whitefish. An individual fin ray is made up of two components, a smaller dorsal portion and a larger ventral portion. Annuli are formed on each of the components. We found that the shape of the first annulus sometimes changed as fish became larger and older in the lower, larger portion of the first fin ray, while there was little change in the shape of the first annulus on the smaller upper component of the first ray. Therefore, we used the upper portion to develop the back-calculation method. Because neither portion of a fin ray is symmetrical, and there is not an exact area that could be identified as a "focus" to initiate the measurments, as is possible on scales and otoliths, we measured the distance from the edge of the first annulus to the farthest point on the posterior edge of this ray at 160× as our back-calculation plane (Fig. 3).

We compared the total length of the fin-ray measurement with actual fork lengths of Lake 226 lake whitefish ($N = 1292$) and found a strong linear relationship ($R^2 = 0.87$; Fig. 4). When we examined the absolute value of residuals from the regression, we found the average difference between the actual fork length and predicted fork length was 6 mm and there was no tendency to over- or underestimate fork lengths (sign test, $P > 0.6$). During the early years of study in Lake 226, we removed pelvic fin rays from fish captured during each month of the ice-free season (Mills 1981). When we examined the sections and compared growth on the periphery of the rays with fork-length growth, we saw no evidence of uncoupling of fin-ray growth from fork-length growth as is well known for otolith growth (Campana 1990, Morita & Matsuishi 2001). Therefore, we used the modified direct proportionality (Fraser-Lee) method (Bagenal & Tesch 1978, DeVries & Frie 1996) to back-calculate lengths of Lake 226 lake whitefish as:

$$l_i = c + \frac{f_i}{f}(l - c) \quad (1)$$

where l_i is length of fish when annulus i was formed, l is length of fish at the time the fin-ray was removed, f_i is length to annulus i on the fin ray, f is total fin-ray cross-section length, and c is the correction factor needed because the relationship between fish length and fin-ray length is not directly proportional. We used $c = 128.7$, the y-intercept from the regression of fork length on fin-ray length. This corresponded closely to the fork length when growth was first detected on fin-ray sections of age 1 fish after over-wintering from age zero.

To test the method, we back-calculated lengths of Lake 226 lake whitefish from fin rays taken when 171 tagged fish were recaptured. We compared the back-calculated fork lengths from these fish with the corresponding fork lengths recorded when individuals were marked one ($N = 67$), two ($N = 71$), and three ($N = 33$) years earlier using paired t-tests.

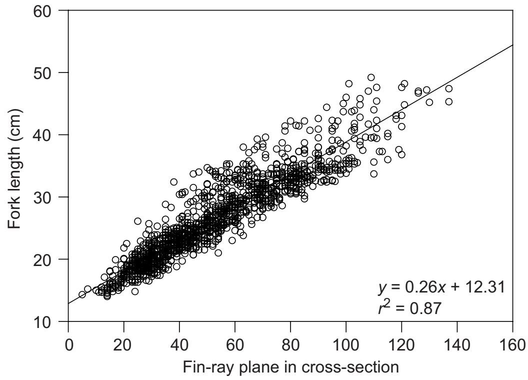

Fig. 4. The relationship between total length of the fin-ray plane used for back-calculations and lake whitefish fork length. The regression line of fork length on fin-ray length is also shown.

Results

Fin-ray age validation

We found good agreement between the predicted ages for recaptured Lake 226 lake whitefish, based on ages at marking, and the actual ages determined at recapture one to 14 years later (Fig. 5). The percentage agreement (PA) between predicted recapture ages and actual ages for the entire data set was 73% (1092 of 1492 age pairs) and most of the differences between age pairs were only one year (64%, 254 of 400). There was no significant difference between the ages predicted at recapture and the actual ages (t-test: $P = 0.3$), and there was also no significant difference in symmetry of the distribution of differences in age pairs ($\chi^2 = 90.1$, 91 d.f., $P = 0.50$) between the proportions of fish whose ages at recapture were greater or less than predicted. When we stratified the results into pairs of ages for the period of fast growth in Lake 226 and pairs during the later slow growth period, there was no significant difference ($P = 0.10$) in the percentage agreement (74% and 72%, respectively) between the two time periods. Most (89%) of the age pairs were for fish where the recapture fins had been removed one to four years after the original fin rays had been removed when fish were marked, but we also had 165 age pair comparisons where the number of years between marking and recapture was greater than five years.

Fin ray–otolith comparisons

We found no significant differences between pairs of fin-ray and otolith ages for lake whitefish from Lake 259 (t-test: $P = 0.5$) or Lake 468 (t-test: $P = 0.7$). Although the percent agreement between sets of ages was 49% for Lake 259 fish and 48% for Lake 468 fish (Fig. 6), most of the differences between ages were only one year.

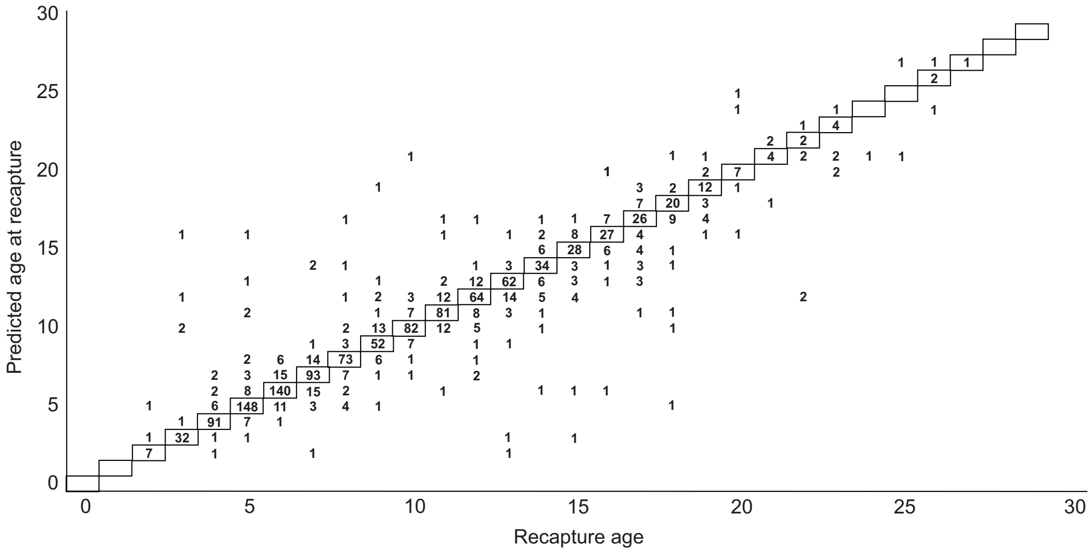

Fig. 5. Agreement between predicted ages of individual Lake 226 lake whitefish and actual ages when recaptured (N = 1492). Numbers in boxes are cases where the predicted age at recapture equaled the actual age of fish determined from fin rays removed at recapture.

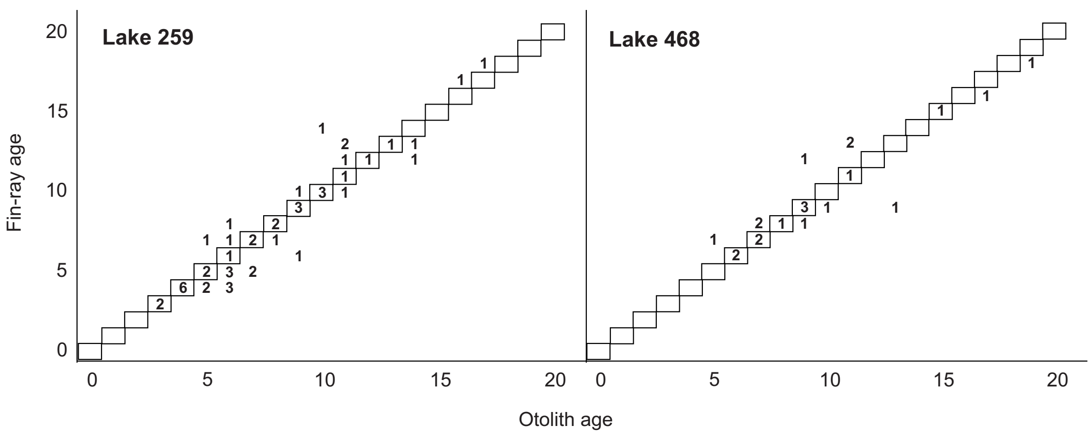

Fig. 6. Agreement between fin ray and otolith ages for Lakes 259 and 468 lake whitefish. Numbers in boxes are cases where the otolith age equaled the fin-ray age.

When there were differences between ages for the same fish, there was also no significant difference in the symmetry of the distribution of differences (Lake 259: χ^2 = 90.1, 17 d.f., P = 0.24; Lake 468: χ^2 = 10, 10 d.f., P = 0.35).

Back-calculations

We found no significant difference between the fork lengths measured when lake whitefish were tagged and the corresponding back-calculated lengths based on the fin rays removed when individuals were recaptured (t = 1.65, 172 d.f., P = 0.19). We recaptured individuals one to three years after initial marking, so were able to compare back-calculated lengths with measured lengths for each of these time periods. There were no significant differences in individual tests of measured and back-calculated lengths for the 1 (t = 1.29, 66 d.f., P = 0.20), 2 (t = –0.08, 71 d.f., P = 0.93), or 3 (t = 1.46, 33 d.f., P = 0.15) year time periods. The mean difference between back-calculated and actual fork lengths was

1.02 mm when pairs of measurements from all 3 years were combined. The absolute difference (ignoring whether the predicted length was greater or less than actual length) was 7.6 mm. There was no significant tendency for back-calculated lengths to be either greater or smaller than actual lengths (Z-test: $P > 0.1$).

Discussion

The ability to easily age fishes is often viewed as a great advantage of fish biologists over researchers studying other animal groups (Campana 2001). This has allowed us to develop special techniques to use these data, such as growth back-calculations, catch-curve, and cohort analyses. Management decisions for fish populations are frequently based on parameters like catch-at-age, first age of maturity, age distribution, and mean age in the commercial catch. All these parameters depend on accurate, or nearly accurate aging. Our expectation is that we can accurately predict the age of an individual fish from one year to the next year. We also assume that there should also be agreement between ages derived from different aging structures — fin rays, otoliths, or scales — from the same fish. The reality is frequently different. Ages determined from different aging structures taken from a fish often do not agree (Campana 2001). The reasons that are often given to explain the differences are: difficulty in determining the first annulus, annuli clustered on the edge of the structure, or that the structure was poorly prepared for aging. There are many other explanations. While it is extremely encouraging to us that there is good predictability of fin-ray ages of lake whitefish based on our mark-recapture results, it is probably just as important that there was no bias in the distribution of differences between actual and predicted ages. Similarly, even though the percent agreement was not particularly good between ages determined from the fin-ray and otolith sections, there was no tendency for ages determined from one structure to be greater or less than those determined using the other structure. This, coupled with the high predictability of the fin-ray ages for marked individuals, confirms the earlier conclusions of Mills and Beamish (1980) for the accuracy of the fin-ray method of aging lake whitefish.

When Mills and Beamish (1980) published their initial results of fin-ray aging of lake whitefish, they had only two years of recapture data (1974 and 1975) to base their results. In addition, we know that at that time, some lake whitefish were growing faster in one basin of Lake 226, due to nutrient additions, than in the other basin (Mills & Chalanchuk 1987). Lake whitefish growth quickly slowed after nutrient additions were terminated in 1980 (Mills *et al.* 1998). Mark-recapture age pairs during these slow periods of lake whitefish growth made up approximately 40% of the data set. When we further examined data for differences in predictability of recapture ages between the fast and slow growth periods in Lake 226, we found no difference in agreement of ages or tendency for recapture ages to be greater or less than predicted. While Mills and Beamish (1980) reported differences in predictability of ages between lake whitefish in different basins of Lake 226 based on fish growth, this difference was not evident in data collected after the nutrient additions were terminated, even though lake whitefish were growing slower. We suspect this may be due to the shift from hand-cutting fin-ray sections to using the mechanical section cutter that yielded more consistent and better quality sections. We did find some large differences between recapture ages and predicted ages, sometimes greater than 10 years, and we had cases where there was a 5-year or more difference between fin-ray and otolith ages (Fig. 6). When there was a large disagreement between predicted and actual mark-recapture ages or between fin-ray and otolith ages, it could usually be traced to either incorrectly recording a tag number during field sampling, or a mistake made during the storage, mounting and cutting of fin rays or otoliths. These types of errors are almost inevitable, and are likely the explanation when we observed great differences in ages between predicted ages at recapture and the actual ages or when large differences between ages from the two aging structures occurred.

Two of the greatest problems in aging almost any fish are identifying the first annulus (Fig. 1B) and identifying the terminal annulus on the edge of rays of very old fish (Fig. 1D).

In fin-ray aging of lake whitefish, an ancillary mark is formed during the first summer of life. The distance between this mark and the actual first annulus in cross-sections is sometimes less in sections of the first fin ray from old (≥ age 15) than very young fish on the lower portion of fin-ray section. Therefore, it is not surprising that a one-year difference can occur in mark-recapture age validation studies or in comparisons of ages between structures. Incorrect identification of the first annulus is a persistent problem in aging many species, particularly when few age zero or age one fish are captured to set a baseline for aging older, larger individuals. We did not have this problem for Lake 226 lake whitefish. We frequently captured age zero and age one individuals in large trap nets (Mills 1981, 1985, Mills & Chalanchuk 1987).

Back-calculating lengths of fish is an accepted technique to increase the amount of growth information that we obtain from one aging structure. Back-calculations have frequently been used in conjunction with scale and otolith aging (Bagenal & Tesch 1978, DeVries & Frie 1996, Morita & Matsuishi 2001, Campana 2001). Therefore, it is not surprising that a similar technique is possible using fin-ray sections. Because there was no tendency for predicted lengths to be greater or less than actual lengths, we believe our method can be used to give unbiased lengths of fish at earlier ages. There were minor differences between predicted and actual lengths and these could have many explanations. Growth of lake whitefish might have continued after we removed fin rays when fish were initially marked; some individuals were captured early in the fall while others were captured late in the fall. This could result in a back-calculated fork length greater than the actual length we recorded when the fish was marked. Based on our mark-recapture data obtained in the fall and subsequent spring of many of the years of study in Lake 226 and other ELA lakes, we know that lake whitefish lose length and weight over winter at the ELA. Erosion of scales through the winter is well known. We do not know whether this occurs in fin rays when fish shrink during winter months, but this could be an explanation for predicted lengths less than actual lengths of individuals. One should expect these types of errors and this should be a caution when interpreting change in growth based on any back-calculations.

We have used the fin-ray method of aging lake whitefish for more than 28 years at the ELA and we have applied this method to other species: lake trout (*Salvelinus namaycush*), white sucker (*Catostomus commersoni*) (Chalanchuk 1984), northern pike (*Esox lucius*), lake herring (*Coregonus artedi*), yellow perch (*Perca flavescens*), and pearl dace (*Margariscus margarita*). We usually process 50 or more fins at the same time, mount a large number of fins in epoxy, cut them in quick succession and fix the sections on microscope slides, and then age the sections in batches. By mass-processing the fins, we reduce the time spent on an individual fin to about 12 minutes, much less than the one hour per fish reported for fin-ray aging by Ihde and Chittenden (2002). The fin-ray method is probably most valuable when researchers wish to sample fish and return them live to a lake. This is the reason we started using this technique more than 30 years ago. In recent years, it is also a valuable technique for aging fish from areas of the Canadian Arctic, where cultural values of local residents dictate that even a dead fish should not be unduly mutilated, which occurs when collecting otoliths.

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