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MANAGEMENT BRIEF

Age, Year-Class Strength Variability, and Partial Age Validation of Kiyis from Lake Superior

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Abstract
Age estimates of Lake Superior Kiyis *Coregonus kiyi* from scales and otoliths were compared and 12 years (2003–2014) of length frequency data were examined to assess year-class strength and validate age estimates. Ages estimated from otoliths were precise and were consistently older than ages estimated from scales. Maximum otolith-derived ages were 20 years for females and 12 years for males. Age estimates showed high numbers of fish of ages 5, 6, and 11 in 2014, corresponding to the 2009, 2008, and 2003 year-classes, respectively. Strong 2003 and 2009 year-classes, along with the 2005 year-class, were also evident based on distinct modes of age-1 fish (<110 mm) in the length frequency distributions from 2004, 2010, and 2006, respectively. Modes from these year-classes were present as progressively larger fish in subsequent years. Few to no age-1 fish (<110 mm) were present in all other years. Ages estimated from otoliths were generally within 1 year of the ages corresponding to strong year-classes, at least for age-5 and older fish, suggesting that Kiyi age may be reliably estimated to within 1 year by careful examination of thin-sectioned otoliths.

The Kiyi *Coregonus kiyi* is one of eight cisco species (Longjaw Cisco *C. alpenae*, Cisco *C. artedi*, Bloater *C. hoyi*, Deepwater Cisco *C. johannae*, Blackfin Cisco *C. nigripinnis*, Shortnose Cisco *C. reighardi*, and Shortjaw Cisco *C. zenithicus*) that historically existed in the Laurentian Great Lakes (Koelz 1929). Kiyis were found in Lakes Huron, Michigan, Ontario, and Superior (Koelz 1929) but presently occur only in Lake Superior (Eshenroder et al. 2016). The demise of Kiyis in the other Great Lakes is not well understood but may have been due to increased abundances of the Alewife *Alosa pseudoharengus* and Rainbow Smelt *Osmerus mordax* (Christie 1974), overfishing (Moffett 1957; Smith 1964; Parker 1989), or introgression into a generic deepwater cisco swarm by interbreeding with other deepwater cisco species (Eshenroder et al. 2016). In contrast to Lakes Michigan and Huron, Kiyis in Lake Superior appear to have retained their morphological characters and have not introgressed to a species swarm (Eshenroder et al. 2016). The Kiyi is presently the most abundant deepwater (>100 m) pelagic species in Lake Superior (Yule et al. 2013).

Accurate age estimates are fundamental to understanding the life history and population dynamics of fish (Beamish and McFarlane 1983). However, estimation of age for long-lived fishes can be difficult because of crowded annuli on the margins of calcified structures due to slow growth (Campana 2001). Systematic underestimation of fish age can lead to overestimates of growth and mortality rates (Mills and Beamish 1980) and can compromise the understanding of year-class strength (Yule et al. 2008). Maximum reported ages of Kiyis in earlier studies based on examination of scales were 6 years from Lake Ontario (Pritchard 1931) and 10 years from Lake Michigan (Deason and Hile 1947). More recent otolith-based maximum age estimates for Lake Superior Kiyis were over 20 years (Gorman 2012; Pratt and Chong 2012). These results agree with other studies' findings that age estimates derived from otoliths and fin spines or rays typically exceed the age estimates derived from scales (Maceina et al. 2007; Quist et al. 2012). A comparison of scale- and otolith-derived ages of Kiyis has not been conducted, and the ages of

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deepwater ciscoes have not yet been validated (sensu Beamish and McFarlane 1983).

High interannual variation in year-class strength was not historically described for cisco species in the Laurentian Great Lakes (Koelz 1929). Dryer and Beil (1964) observed a minor twofold to threefold fluctuation in year-class strength of Ciscoes in Lake Superior based on commercial fishery landings from 1950 to 1959 and scale-derived age estimates. Later work evaluating Cisco populations in Lake Superior (Hoff 2004; Stockwell et al. 2009; Rook et al. 2012; Myers et al. 2015) and Bloater populations within Lakes Huron, Michigan, and Superior (Bunnell et al. 2010) showed large tenfold to 2,795-fold differences in year-class strength as measured by densities of age-0 or age-1 fish. Yule et al. (2008) demonstrated how age underestimation associated with scale-derived ages for Lake Superior Ciscoes could lead to an inaccurate understanding of the regular production of strong year-classes. Interannual variability in Kiyi year-class strength has not been evaluated.

The purpose of this study was to (1) compare Lake Superior Kiyi ages estimated from scales and otoliths, (2) evaluate variability in year-class strength of Kiyis, and (3) assess the validity of otolith-derived Kiyi ages by comparing the distribution of age estimates to strong year-classes identified from annual length frequency distributions.

METHODS

Age analyses.—Fish collections were made at 102 locations throughout Lake Superior (Figure 1) during daylight between May 19 and July 20, 2014. Collections were made with the U.S. Geological Survey's R/V *Kiyi* using a Yankee bottom trawl with either a chain or rubber disk footrope towed at approximately 3.5 km/h. Both nets had an 11.9-m headrope, a 15.5-m footrope, and a 2.2-m wing height, with stretch meshes of 89 mm at the mouth, 64 mm for the trammel, and 13 mm at the cod end. Nearshore trawling in May and June

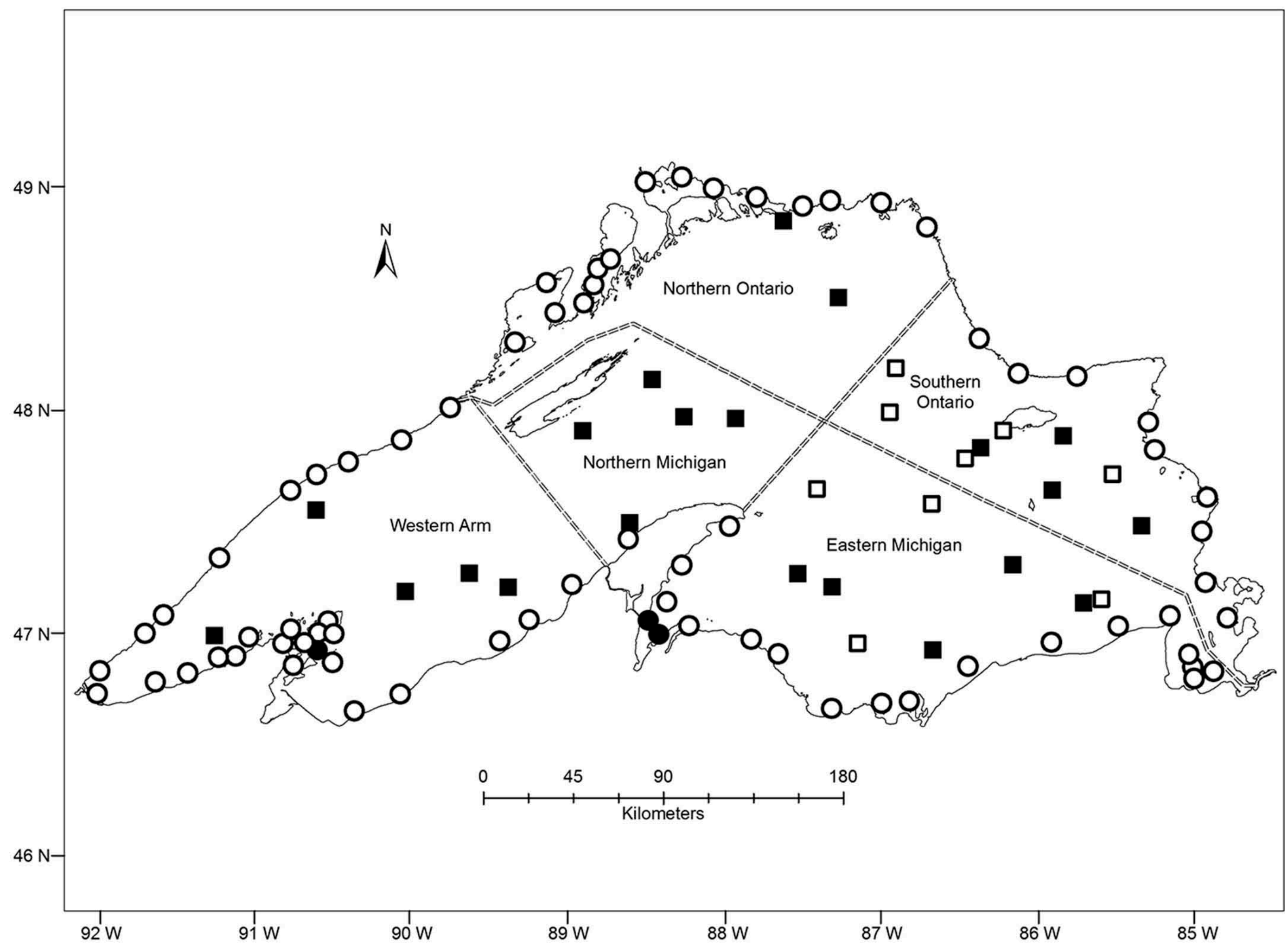

FIGURE 1. Sampling locations in Lake Superior and the five regions used for subsampling Kiyis for age estimation in 2014. Squares denote offshore sites; circles denote nearshore sites. Solid symbols denote locations where Kiyis were collected.

was cross-contour, with a mean beginning depth of 19 m (range = 11–40 m), mean ending depth of 61 m (range = 19–144 m), and mean distance covered of 1.7 km (range = 0.5–3.8 km). Offshore trawling in July followed a constant depth contour with a mean average depth of 191 m (range = 92–315 m) and mean distance covered of 1.4 km (range = 1.2–1.5 km). Trawl distance was determined from the ship's geographic positioning system. Kiyis were identified based on morphological characteristics, such as fin length and eye diameter, as described by Koelz (1929) and Eshenroder et al. (2016). Individuals for which identification was ambiguous were not included in this study. All Kiyis collected were counted, weighed in aggregate, and frozen for later processing. Relative density (fish/ha) and biomass (kg/ha) were estimated by dividing collection counts and aggregate weights by the area swept during each trawl tow.

Frozen fish were thawed at room temperature before TL (nearest 1 mm), weight (nearest 1 g), and sex (visually determined as female, male, or juvenile) were recorded. A lakewide representative sample for estimating age was obtained by selecting 10 individuals per 10-mm length bin from 160-mm and larger Kiyis collected in each of five regions (Figure 1). All fish smaller than 160 mm were used for estimating age because fish of this size were rare. Otoliths were removed via the "up through the gills method" described by Secor et al. (1992). Scales were removed from either side of the fish, directly above the lateral line and as close to the anterior margin of the dorsal fin as possible (Hogman 1968). Scales and sagittal otoliths were placed in paper envelopes to air dry.

Otolith preparation followed the commonly used (Quist et al. 2012) "embed and polish" method described by Secor et al. (1992). Otoliths were embedded in clear epoxy (Buehler EpoKwick, 5:1 ratio of resin to hardener) before a 0.5-mm-thick section through the nucleus along the dorsoventral plane was obtained with a Buehler IsoMet low-speed saw. Otolith thin sections were lightly polished with 1,000-grit sandpaper before viewing in mineral oil on a black background with reflected light applied at approximately a 45° angle to the section. A digital image of each thin section (Figure 2) was captured with a Nikon DS-Fi2 camera attached to a Nikon SMZ745T stereomicroscope. Multiple images were used for some otolith sections when a single image that was clear and focused in all areas could not be obtained. Age estimates were also generated by analysis of scales from Kiyis collected from the eastern Michigan region. Age was estimated from scales for a limited number of fish because we expected a clear difference in age estimates between scales and otoliths, as has been shown for numerous other fishes, including other coregonines (e.g., Maceina et al. 2007; Yule et al. 2008; Quist et al. 2012; Stewart et al. 2016). Digital images were captured from scales pressed into 5-mm-thick acetate slides with the same camera and microscope used for examining the otoliths.

Two readers, both of whom were blind to any biological information related to the fish, identified annuli on scales and otoliths from the digital images. One reader had approximately 25 years of experience in estimating age from scales and otolith thin sections, and the other reader had approximately 2 years of previous experience in age estimation. However, the inexperienced reader was trained to estimate age on Kiyi scales and otolith thin sections that were not included in this analysis. The combination of a translucent band (representing fast growth) and an opaque band (representing slow growth) on the sectioned otolith was interpreted as 1 year of growth (Figure 2). Only a completed opaque band at the otolith margin was counted as an annulus, as partial growth from the capture year was present for some individuals. Annuli on scales were identified based on the "cutting-over" and "compaction" characteristics evident in the circuli (Quist et al. 2012). After initial analyses that compared age estimates between readers (see below), the two readers further reviewed the scale or otolith image to achieve a consensus age estimate for analyses that required a single estimate of age.

Bias in scale-derived and otolith-derived age estimates between two readers (e.g., one reader consistently estimated lower ages than the other reader) and between consensus

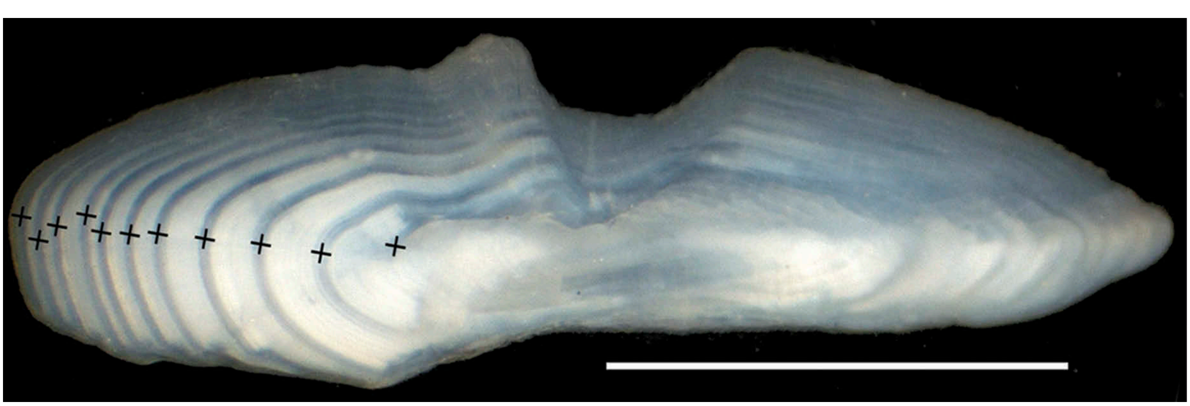

FIGURE 2. Thin-sectioned otolith from a 206-mm male Kiyi captured at an offshore site in the northern Ontario region on July 20, 2014. This individual was estimated to be 11 years old (scale bar = 1 mm).

scale-derived and otolith-derived age estimates was assessed with the Evans and Hoenig (1995) test of symmetry for the age-agreement table (as suggested for use by McBride 2015), a modified age–bias plot (Campana et al. 1995; Muir et al. 2008a), and a one-sample *t*-test that evaluated whether the mean difference in ages at each reference age differed from zero (Ogle 2016). Reference ages for age–bias plots and one-sample *t*-tests were the ages estimated by the more experienced reader or the ages obtained from otoliths. The method of Holm (1979) was used to adjust for multiple comparisons in the one-sample *t*-tests. One-sample *t*-tests were not computed when the sample size was less than 3. Precision between readers was summarized as (1) the percentage of fish for which the ages were in exact agreement or differed by 1 year or less and (2) the average coefficient of variation (Chang 1982; Kimura and Lyons 1991). Age bias and precision metrics were computed with the "ageBias" and "agePrecision" functions, respectively, from the Fisheries Stock Assessment (FSA) package version 0.8.13 (Ogle 2017) in R version 3.4.0 (R Development Core Team 2017). All tests used an α value of 0.05 to determine statistical significance.

An age–length key (Fridriksson 1934; Ketchen 1949) was constructed from consensus otolith-derived age estimates. For all Kiyis captured in 2014, the age–length key was used to assign specific ages via the method described by Isermann and Knight (2005) as implemented in the "alkIndivAge" function from the FSA package.

Length frequency year-class identification.—Annual Kiyi length frequency data from the same locations and months and that were collected using the same methods were available from nearshore sites for the period 2003–2014 and from offshore sites for 2011–2014 (Vinson et al. 2016). Length frequency distributions from these years were visually examined for evidence of strong year-classes (i.e., recruitment), which could be used to assess the validity of the estimated ages for Kiyis captured in 2014. Kiyis likely hatch at a size (10–12 mm) and time (spring) similar to Ciscoes (Oyadomari and Auer 2007, 2008) and were likely not present as age-0 fish in these annual trawl samples. In Lake Michigan, Kiyis reached a mean SL of approximately 100 mm the following spring at age 1 (i.e., the spring after hatch; Deason and Hile 1947). Thus, clusters of fish in our annual spring and summer collections with distinct modes less than 110 mm TL were identified as age-1 fish. The relative number of age-1 fish in these samples was used as an index for the strength of the previous year's year-class of Kiyis.

RESULTS

In total, 984 Kiyis were collected at 24 of the 102 locations sampled in 2014 (Figure 1). Kiyis were found at three nearshore locations between May 27 and June 5, 2014, and at 21 offshore locations between July 7 and July 20, 2014. Biomass and density estimates from individual trawl tows ranged from 0 to 12 kg/ha and from 0 to 253 fish/ha, respectively. The minimum and maximum depths of capture at 21 on-contour sampling locations were 132 and 256 m. Maximum biomass (12 kg/ha) and density (253 fish/ha) were observed at 190 m. Total lengths of Kiyis ranged from 108 to 266 mm, with a mean of 197 mm (SD = 19.3).

Age Analyses

Ages of Kiyis in 2014 were estimated from 62 pressed scales. A consensus age was reached for all scales. Scale-derived age estimates from the two readers agreed for 46.8% of the fish, agreed within 1 year for 87.1% of the fish, and had an average coefficient of variation of 8.7%. A statistically significant bias in scale-derived age estimates between readers was evident (P = 0.009; Figure 3). The inexperienced reader generally estimated age from scales as being 1 year younger when the experienced reader's estimate was 6 years or older, although this was only statistically significant at age 6 (95% CI = 4.65–5.49 years; P = 0.002).

Ages of Kiyis in 2014 were also estimated from 288 thin-sectioned otoliths. Of these, 22 (7.6%) otoliths were deemed unreadable (cracked or cloudy image) and were removed from further consideration. There was no statistically significant

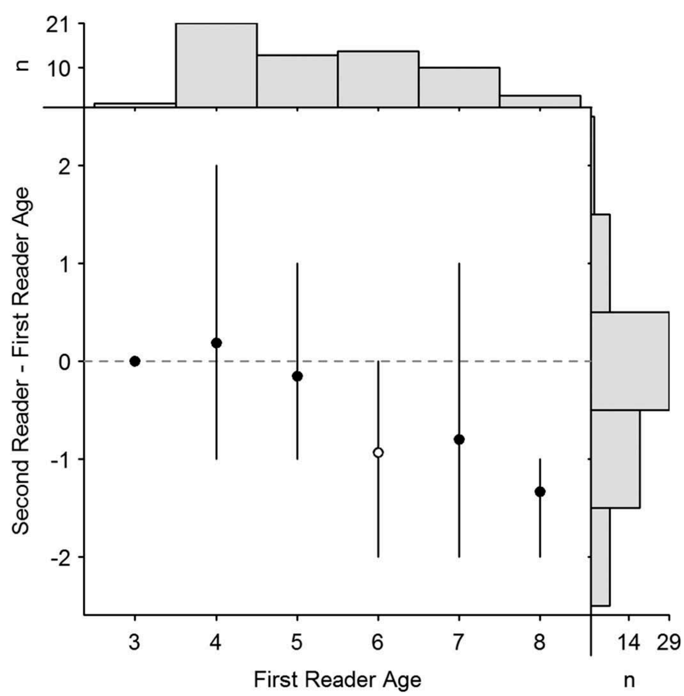

FIGURE 3. Mean (points) and range (vertical intervals) of differences in scale-derived age estimates for Lake Superior Kiyis between two readers, plotted in relation to the age estimates generated by the first (more experienced) reader. All fish were collected from the eastern Michigan region (Figure 1). Black shaded points indicate either that the age estimates were not significantly different between readers or that the sample size was too small (<3 fish) to test for a difference. The top histogram is the sample size for scale-derived age estimates produced by the first reader; the right histogram is the distribution of differences in scale-derived age estimates between readers.

systematic bias in otolith-derived age estimates between the two readers (P = 0.445; Figure 4). However, the mean age estimated by the inexperienced reader was slightly greater when the experienced reader estimated an age of 5 (95% CI = 5.1–5.4 years; P < 0.001) and was slightly lower when the experienced reader estimated an age of 12 (95% CI = 11.1–11.8 years; P = 0.031). Otolith-derived age estimates from the two readers agreed perfectly for 72.6% of the fish, agreed within 1 year for 97.0% of the fish, and had an average coefficient of variation of 2.8%.

A statistically significant bias between consensus scale- and otolith-derived age estimates was detected (P < 0.001; Figure 5). Mean consensus scale-derived age estimates were less than the consensus otolith-derived age estimate for the same fish for all five ages with a sample size of at least 3 fish (P < 0.008).

The maximum estimated age was 20 years for female Kiyis and 12 years for males based on examination of otoliths and was 8 years for both females and males based on analysis of scales. The minimum estimated age was 4 years from otoliths and 3 years from scales for both females and males. The distribution of otolith-derived age estimates for Kiyis captured in 2014 showed distinct modes at age 11 and at age 5 or 6 (Figure 6), corresponding to the 2003, 2008, and 2009 year-classes.

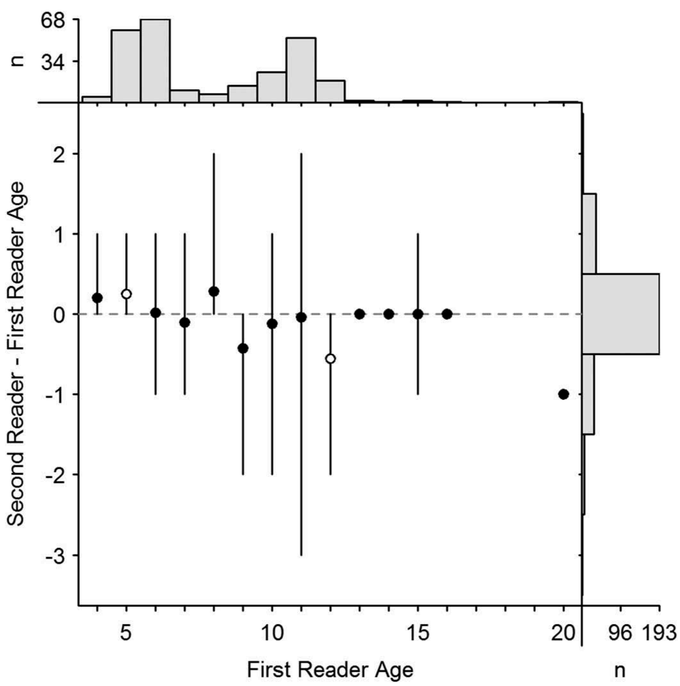

FIGURE 4. Mean (points) and range (vertical intervals) of differences in otolith-derived age estimates for Lake Superior Kiyis between two readers, plotted in relation to the age estimates generated by the first (more experienced) reader. Black shaded points indicate either that the age estimates were not significantly different between readers or that the sample size was too small (<3 fish) to test for a difference. The top histogram is the sample size for otolith-derived age estimates produced by the first reader; the right histogram is the distribution of differences in otolith-derived age estimates between readers.

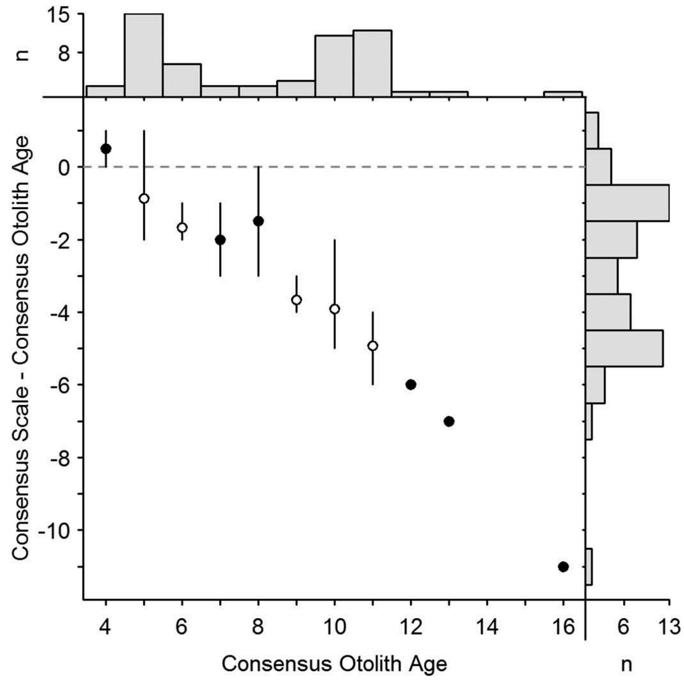

FIGURE 5. Mean (points) and range (vertical intervals) of differences between scale- and otolith-derived age estimates for Lake Superior Kiyis, plotted in relation to otolith-derived age estimates (consensus ages from the two readers). Black shaded points indicate either that the age estimates were not significantly different between structures or that the sample size was too small (<3 fish) to test for a difference. The top histogram is the sample size for otolith-derived age estimates; the right histogram is the distribution of differences between scale- and otolith-derived age estimates.

Length Frequency Year-Class Identification

Examination of length frequency distributions from Kiyis captured in 2003–2014 showed that clusters of fish with a mode less than 110 mm were present in high numbers during 2004, 2006, and 2010 and either were not detected or were detected at very low numbers in all other years (Figure 7). The fish in these clusters corresponded to the 2003, 2005, and 2009 year-classes, respectively. The cluster of Kiyis from the 2003 year-class was distinct in subsequent years until at least 2006. In 2007, the cluster of Kiyis from the 2005 year-class either was not evident or the fish had grown enough to be indistinguishable from Kiyis of the 2003 year-class. Kiyis from the 2009 year-class were still distinct in 2010, but by 2013 they were either not evident or had grown enough to be indistinguishable from older fish. Only one distinct mode was evident in the length frequency distribution from 2014.

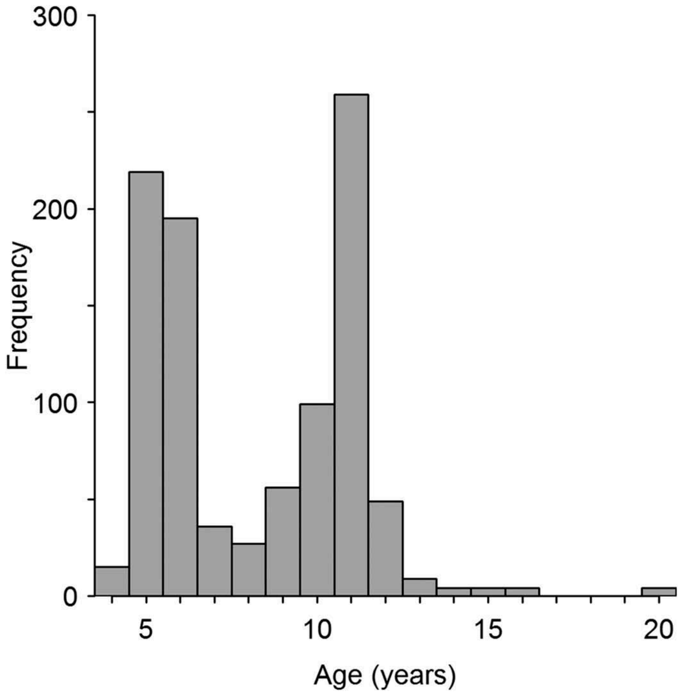

FIGURE 6. Frequency of otolith-derived age estimates for all Lake Superior Kiyis captured during May–July 2014. Ages were expanded from an age–length key based on consensus otolith-derived age estimates generated by two readers.

DISCUSSION

Precision between readers for thin-sectioned otoliths was very good, as the average coefficient of variation (2.8%) was less than 5%, which Campana (2001) suggested as representative of "high precision." This result is somewhat surprising because both readers expressed difficulty interpreting putative annuli near the center of otoliths when few annuli were present (i.e., relatively young fish) and at the margin on all otoliths (Figure 2). Due to the sporadic production of year-classes, no fish with an otolith-derived age less than 4 years was collected in 2014. Without these young fish, an understanding of the appearance of the first few annuli could not be developed. Interpretation of the otolith margin is notoriously difficult (Campana 2001), and a better understanding of the otolith margin also could not be developed because our samples were restricted to 2 d in early June and a few days in mid-July rather than throughout the May–September growing season. However, length frequency distributions for three other years when Lake Superior Kiyis were sampled in several months suggested that substantial growth in length was not evident until at least late July; thus, little of the current season's growth should have been observed on the otolith thin sections in our sample. However, 21% and 36% of the otoliths were categorized by reader 1 and reader 2, respectively, as having evidence for growth in the current season.

Kiyi ages estimated from otoliths were consistently greater than ages estimated from scales. This is consistent with previous results for Ciscoes in Lake Superior (Yule et al. 2008); Pygmy Whitefish *Prosopium coulterii* in Lake Superior (Stewart et al. 2016); Round Whitefish *Prosopium cylindraceum* in Canada (Jessop 1972); Lake Whitefish *Coregonus clupeaformis* in Canada (Mills and Beamish 1980; Barnes and Power 1984), Lake Michigan (Muir et al. 2008b), and Lake Huron (Muir et al. 2008a); European Vendace *Coregonus albula* (Aass 1972); and many other fishes (Maceina et al. 2007; Quist et al. 2012). Our maximum otolith-derived age estimates of 20 years for females and 12 years for males are similar to the findings of (1) Pratt and Chong (2012), who observed maximum otolith-derived age estimates of 22 years for female Kiyis and 16 years for males collected in Canadian waters of Lake Superior; and (2) Gorman (2012), who reported Kiyi life spans exceeding 20 years in Lake Superior. These ages are similar to the maximum otolith-derived age estimates for Ciscoes in Lake Superior (21 years for females and 17 years for males; Yule et al. 2008).

Distinct modes in length frequency distributions for 2003–2014 provided evidence of strong year-classes and partially validated our otolith-derived age estimates. The mode of age-11 fish in 2014 corresponds well with the 2003 year-class, and the mode of age-5 and age-6 fish in 2014 corresponds—with some aging error (see below)—to the 2009 year-class present in the length frequency distributions. However, a mode of age-9 fish, which would correspond to the 2005 year-class present in the length frequency distributions, was not observed in 2014. This lack of age-9 fish in our 2014 age analysis could be attributed to the apparent smaller size of that year-class as compared to the 2003 and 2009 year-classes. Thus, with the exception of age-9 fish, our otolith-derived age estimates from 2014 were generally within 1 year of ages corresponding to strong year-classes of Kiyis.

Our determination of strong year-classes from the trawl-based length frequencies is dependent on the mode of the smallest fish being near 100 mm TL. This primarily occurred only in 2004 and 2010. Kiyis likely hatch at a size (10–12 mm) and time (spring) similar to those of Ciscoes (Oyadomari and Auer 2007, 2008). In Lake Michigan, Kiyis reached a mean SL of approximately 100 mm at age 1 during the spring after hatch (Deason and Hile 1947). Additionally, modal progression analysis (Du 2002) showed that the mean of the cluster of smallest Kiyis in 2004 was 86 mm (SD = 11) and had grown to 112 mm (SD = 11) in 2005 and to 137 mm (SD = 11) in 2006. Similarly, the mean of the cluster of smallest fish in 2010 was 83 mm (SD = 7) and had grown to 120 mm (SD = 10) in 2011. Given that the annual change in means of these clusters of fish is more than two times the SD, it is unlikely that growth would be poor enough that multiple year-classes would form one cluster at small sizes and then grow substantially together in subsequent years. Thus, these

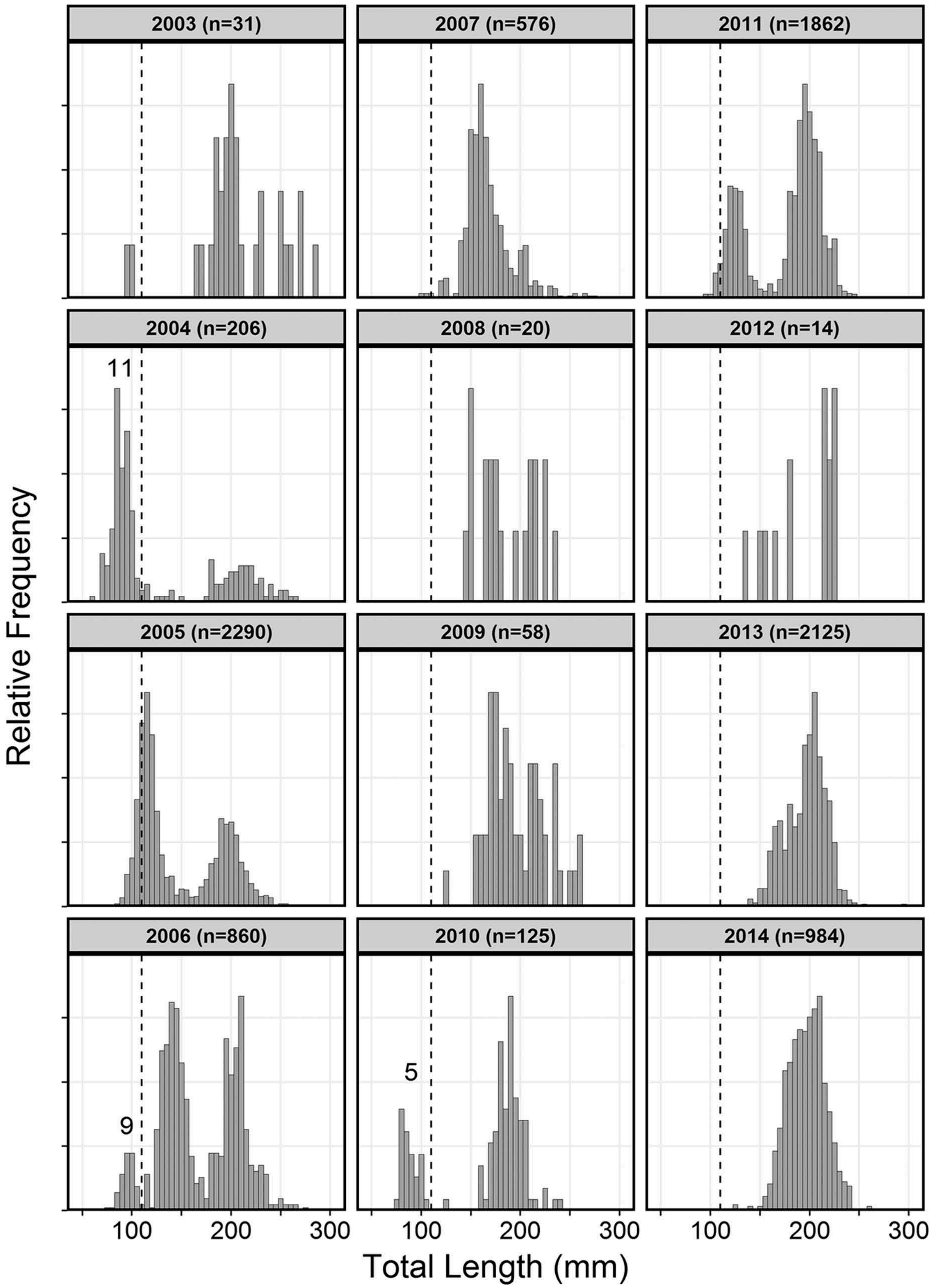

FIGURE 7. Relative within-year frequency of TLs for all Lake Superior Kiyis captured during May–July from nearshore locations in 2003–2010 and from both nearshore and offshore locations in 2011–2014. Plots are labeled with the year sampled and with the total sample size. Each plot is scaled such that the mode has a height equal to 1. Numeric labels shown on the panels for 2004, 2006, and 2010 represent the 2014 age (years) of the fish in those modes. The dashed vertical line in each plot at 110 mm was used to identify the TL mode for age-1 fish.

clusters of small Kiyi in 2004 and 2010 most likely comprise only age-1 fish.

From these findings, it appears that Kiyi age may be reliably estimated to within 1 year by examination of thin-sectioned otoliths. Aging error may be reduced with a better understanding of the characteristics of the first few annuli and the appearance of the otolith margin. We recommend that otoliths be collected from small (young) Kiyis in years when they are present and from Kiyis collected throughout the open-water growing season when feasible. Continued annual collections of length frequency data, along with otoliths from these fish, will allow for further validation of Kiyi age estimates from otoliths. Because otoliths appear to provide an accurate estimate of age and because age estimates from scales were less than those for all otolith age estimates, scales should no longer be used to estimate the age of Kiyis.

The annual length frequency distributions suggested that Kiyis experience high interannual variability in year-class strength. During 2003–2014, only three strong year-classes were observed at age 1. Variable recruitment has been observed in other *Coregonus* spp. (e.g., Vendace: Axenrot and Degerman 2015; Cisco: Hoff 2004, Stockwell et al. 2009, and Myers et al. 2015; Arctic Cisco *C. autumnalis*: Fechhelm and Fissel 1988 and Fechhelm and Griffiths 1990; Bloater: Bunnell et al. 2006, 2010, Gorman 2012, and Collingsworth et al. 2014; Shortjaw Cisco: Gorman 2012). Strong Kiyi year-classes in 2003, 2005, and 2009 correspond to the higher-than-average year-class strengths observed for Bloaters and Ciscoes in Lake Superior (Stockwell et al. 2009; Yule et al. 2008; more recent data in Vinson et al. 2016). Recruitment synchrony has also been observed within Bloater populations (Bunnell et al. 2006, 2010) and Cisco populations (Myers et al. 2015) across the Great Lakes and in Europe (Sandström et al. 2014). Hypothesized factors underlying year-class strength variation in *Coregonus* spp. include density-independent physical environmental factors, such as annual weather patterns that affect larval fishes directly or their food (Axenrot and Degerman 2015), density-dependent biotic factors (e.g., predation by or competition with Rainbow Smelt; Myers et al. 2015), spawner sex ratios (Bunnell et al. 2006), or a combination of these factors. Synchrony among disjunct populations and between species in the same region supports the idea that environmental factors (e.g., winter ice conditions, the date of spring ice break-up, and wind) play a major role in determining the year-class strength of *Coregonus* spp.

Our results indicate that Lake Superior Kiyis are long-lived and exhibit high interannual variability in year-class strength that may be synchronous with recruitment patterns exhibited by other *Coregonus* spp. The critical period for survival (sensu Hjort 1914; Houde 2008) appears to be prior to age 1, as distinct year-classes observed at age 1 appeared to survive to older ages. Although Kiyis currently are not commercially or recreationally valuable like some *Coregonus* spp., Kiyis represent a key trophic link between zooplankton and Lake Trout *Salvelinus namaycush*, the top native predator in the Great Lakes (Gamble et al. 2011), which is a commercially and recreationally important species. Successful restoration of deepwater ciscoes in the other Great Lakes may depend on understanding their life histories (Zimmerman and Krueger 2009). Additionally, Lake Superior is a refuge for many cold stenothermic species like the Kiyi, which is currently classified as "vulnerable" on Canada's list of endangered species (Turgeon and Bernatchez 2003). Increased study of and long-term monitoring of Kiyis and other cisco species, including their age, growth, diet, and recruitment characteristics, may provide insights into how climate change could affect the deepwater fish fauna of Lake Superior and elsewhere.

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