Age and size characteristics of Coregonus kiyi from Lake Superior?

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**Abstract**

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**Keywords:** Coregonid, Population dynamics, Age validation, Length frequency analysis

**Introduction**

Kiyi are one of four deepwater cisco species (*Coregonus hoyi, C. kiyi, C. zenithicus, C. and C. nigripinnis*) that historically supported major fisheries and were the primary prey for Lake Trout in the Laurentian Great Lakes and (Zimmerman and Krueger, 2009). Kiyi were historically found in Lakes Huron, Michigan, Ontario, and Superior (Koelz, 1929), but presently occur only in Lake Superior. Kiyi were last collected in 1964 in Lake Ontario, 1973 in Lake Huron, and 1975 in Lake Michigan (COSEWIC, 2005). In Lake Superior, Kiyi are the most abundant deepwater pelagic species (Yule et al. 2013) and are listed as a species of special concern in Canada (Pratt and Chong 2012). The demise of Kiyi and other deepwater Ciscos in the other Great Lakes may have been due to interactions with invasive species (Becker, 1983) or increased exploitation in the 1920-1940s; though our lack of knowledge of Kiyi life history certainly curtails our understanding. Kiyi life history studies are limited to Koelz’s (1929) work in all the Great Lakes, Pritchard’s (1931) work in Lake Ontario, Deason and Hile’s (1947) work in Lake Michigan, and Pratt and Chong’s (2012) recent work in Lake Superior. The preservation and re-establishment of Laurentian Great Lakes deepwater pelagic ciscoes is a primary objective of Great Lake’s fish management agencies (Zimmerman and Krueger 2009).

Age, sex ratio, size, and recruitment dynamics are key life history attributes for understanding fish population dynamics (SINGLE CITE- A BOOK? Maceina et al., 2007; Quist et al., 2012). Our limited knowledge of these attributes for Kiyi are summarized in Table 1. Reported maximum ages of Kiyi based on scales were 6 years in Lake Ontario (Pritchard 1931), 10 years in Lake Michigan (Deason and Hile 1947), and 22 years based on otoliths in Lake Superior (Pratt and Chong 2012). Coregonid ages were traditionally estimated from scales, but Yule (2008) found scales to underestimate age of Cisco (*Coregonus artedi*). A direct comparison of paired estimates of scale- and otolith-derived ages for Kiyi has not been done. Maximum size ranged from 287 mm in Lake Michigan (Deason and Hile 1947) to 305 mm in Lake Superior (Pratt and Chong 2012). Sex ratios are skewed toward females and ranged from 77% in Lake Superior to 90% in Lake Michigan. Evidence of variable recruitment such as has been described for other Laurentian Great Lakes ciscoes (Myers et al., 2015) has not been presented for Kiyi.

The goals of this study were to describe the aforementioned life history attributes for Lake Superior Kiyi. Specifically we 1) compare scale and otolith estimated ages of Lake Superior Kiyi and describe the relative precision and bias between scales and otoliths and between readers for otoliths; 2) present data on size and weight-length relationship, and 3) describe recruitment dynamics over the past 10 years to assess if periodic strong year-classes are present for Kiyi and then use these data to provide a partial validation for Kiyi ages estimated from otoliths.

**Methods**

*Sampling and Data Collection*

Kiyi were collected during daylight at two stations on 5 June 2014 and at 21 stations from throughout Lake Superior between 7 July and 20 July 2014. Stations were categorized into five regions labeled as the Western Arm, Isle Royale, Northern Ontario, Southern Ontario, and Eastern Michigan (Figure 1). Fish were collected with the Research Vessel Kiyi (United States Geological Survey, Lake Superior Biological Station) using a Yankee bottom trawl with either a chain or rubber disk foot rope towed at approximately 3.5 km/h. Both nets had an 11.9 m head rope, 15.5 m foot rope, and a 2.2 m wing height with stretch mesh of 89 mm at the mouth, 64 mm for the trammel, and 13 mm at the cod-end. The June tows were cross-contour with a mean beginning depth of 26 m (range: 13-40), ending depth of 106 m (range: 68-144), and distance covered of 1.50 km (range: 1.47-1.53). The tows in July followed a depth contour, had a mean average depth of 186 m (range: 134-255), and a mean distance covered of 0.86 km (range: 0.76-0.91).

All Kiyi were immediately measured for total length (TL) to the nearest mm. A subsample of a maximum of five individuals per sex per 10 mm TL bin for fish between 160 and 279 mm and all Kiyi less than 159 mm and greater than 280 mm were immediately frozen. At a later date, the frozen fish were thawed at room temperature and TL, weight to the nearest gram, and sex (visually determined as female, male, or juvenile) were recorded and scales and sagittal otoliths were removed and placed in a paper envelope to air dry. Scales were removed from directly above the lateral line as close to the anterior margin of the dorsal fin as possible from either side of the fish.

In the laboratory, otoliths were embedded in clear epoxy (Buehler EpoKwick™ Epoxy, 5:1 ratio 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 1000 grit sandpaper before viewing in mineral oil on a black background with reflected light applied at approximately a 45 degree angle to the section. A digital image of each thin section, or images for some sections where all fields of the section were not clear on one image, was captured with a Nikon DS-Fi2™ camera attached to a Nikon SMZ745T™ stereo microscope. Digital images of scales pressed into 5 mm thick acetate slides were captured with the same camera and microscope from a subsample of fish captured in the Eastern Michigan region.

Two readers who were blind to any biological information related to the fish identified annuli on otoliths from the digital images. The combination of a translucent band representing fast growth and an opaque band representing slow growth on the sectioned otolith was interpreted as one year of growth. At the otolith margin, only completed opaque bands were counted as annuli, as partial growth from the capture year was present for some individuals. When the two readers disagreed on an age estimate, they further reviewed the otolith image in an attempt to achieve a consensus age estimate for analyses that required a single age estimate. One reader who was blind to biological information about the fish identified annuli on the scales from digital images. Annuli on scales were identified using “cutting-over” and “compaction” characteristics evident in the circuli (Quist et al., 2012).

Total lengths of all Kiyi collected in similar samplings (i.e., similar gear, from locations throughout Lake Superior, and restricted to June and July) were available from 2001-2013. Length frequency distributions from these years were examined for evidence of strong year-classes that could be used to partially validate ages estimated in 2014 and to estimate growth during the first few years of life.

*Statistical Analyses*

Differences in the length frequency distributions among regions were assessed with pairwise Kolmogorov-Smirnov tests (Neumann and Allen 2007; Ogle 2016a) that used the bootstrap procedure implemented in the ks.boot function from the Matching package v4.8-3.4 (Sekhon 2011) in the RTM statistical environment v3.2.2 (R Development Core Team, 2015) to minimize the effect of non-continuous length data on the test statistic (Abadie, 2002). P-values from these multiple tests were corrected with the Holm (1979) method implemented in the p.adjust function in R. Regional differences in mean lengths were assessed with a one-way ANOVA followed by Tukey’s HSD post-hoc method.

Bias in otolith ages between two readers (e.g., one reader consistently had lower age estimates than the other reader) and between scale and otolith ages from the same reader were estimated with age-bias plots (Campana et al., 1995) and the test of symmetry for the age-agreement table proposed by Evans and Hoenig (1998) and suggested for use by McBride (2015) as computed with the ageBias function from the FSA package v0.8.1 (Ogle, 2016b). If no significant bias between readers was detected, precision between readers was summarized as the percentage of fish for which the ages differed by zero or by one or fewer years and the average coefficient of variation (ACV; Chang, 1982; Kimura and Lyons, 1991) as computed with the agePrecision function from the FSA package.

Age-length keys (ALK; Fridriksson, 1934; Ketchen, 1949) derived from a multinomial distribution fit to the consensus otolith age estimates and 10 mm length categories were used to assess differences in ALKs. The multinomial models were fit using the multinom function from the nnet v7.3-11 package (Venables and Ripley 2002) as described in Gerritsen et al. (2006) and Ogle (2016a). Differences in ALKs between sexes within regions were assessed first. If no difference between sexes was found for all regions, then the sexes were pooled and differences in ALKs among regions were assessed. The p-values from these multiple comparison were adjusted with the Holm (1979) method.

Specific ages were assigned to all Kiyi captured in 2014 using region-specific (pooled sexes) ALKs and the method described by Isermann and Knight (2005) as implemented in the alkIndivAge function from the FSA package. Age-length keys based on observed consensus otolith ages rather than on the multinomial model fit were used so as not to average out any distinct year-classes that may have been present in the ALKs. Regional differences in the distribution of ages assigned with the ALKs were assessed with a chi-square test, whereas regional differences in mean age were assessed with a one-way ANOVA followed by Tukey’s HSD post-hoc method.

Weight-length relationships were modeled with log10(W) = log(a)+blog10(TL). Sex and regional differences in slopes and intercepts were assessed with a two-way dummy variable regression (). Because no slopes were found to differ, differences in intercepts between sexes within regions and between among all pairs of regions within each sex were assessed with specific model contrasts. The p-values from these contrasts were then adjusted with the Holm (1979) method.

Growth was assessed in two ways. First, the mix function from the mixdist package (MacDonald and Du 2012) was used to identify distinct modes that corresponded to two strong year-classes evident in the historical length frequencies. The algorithm was constrained to find only two or three modes in each sample year, use a constant coefficient of variation for each mode, and fit with a log-normal distribution. The mean, standard deviation, and standard error of total length for each well-fitted mode were then plotted to represent growth of Kiyi early in life. Second, the mean length at the three dominant ages present in 2014 were found. The mean length was compared among regions within each of the three dominant ages with a one-way ANOVA followed by a Tukey HSD post-hoc test.

All statistical tests used α=0.05 to determine significance.

**Results**

A total of 983 Kiyi were sampled in 2014. These fish were between 108 and 266 mm TL with a mean (SD) TL of 197 (19.3) mm. The length distribution of Kiyi from the Northern Ontario region differed significantly from the length distributions of Kiyi captured from all other regions (p < ), which did not differ (p > ). The Northern Ontario region had fewer longer fish, which resulted in a significantly shorter mean TL (p < ; Figure 2). In the subsample of 335 fish, four were juveniles and 60.1% of non-juvenile fish were female.

The examination of length frequencies from 2001 through 2014 revealed distinct modes near 80-100 mm in 2004, 2006, and 2010 (Figure 3). These modes corresponded to age-1 fish as Kiyi likely hatch at a size (10-12 mm) and time (early spring) similar to cisco (Oyadomari and Auer, 2007; Oyadomari and Auer, 2008). Thus, these cohorts corresponded to ages 11, 9, and 5, respectively, in 2014. There was little evidence for the 2005 cohort in 2007 which suggests few age-9 fish may exist in 2014.

Ages were estimated by two readers from 288 thin-sectioned otoliths. Of these otoliths, 22 (7.6%) were deemed unreadable (cracked or cloudy image) and were removed from further consideration. Ages estimated from the two readers perfectly agreed for 72.6% of the otoliths, agreed within one year for 97.0% of the otoliths, had a between-reader ACV of 2.8, and showed no significant systematic bias (; Figure 4). However, the mean estimated age for the second reader was slightly greater when the first reader estimated an age of 5 (95% CI: 5.1-5.4; ) and slightly lower when the first reader estimated an age of 12 (95% CI: 11.1-11.8; ). Mean scale age for each otolith age was less than the otolith age for all observed otolith ages with adequate sample sizes (p < ; Figure 5).

Kiyi for which a consensus otolith age estimate was obtained were used to generate ALKs. Four Kiyi less than 140 mm TL (all of the juvenile fish) were excluded from all ALK analyses because of sample size considerations. An additional seven fish that were estimated to be age-13 or older were also removed from the analysis that compared ALKs among regions because of sample size considerations. Age-length keys did not differ significantly between sexes within any region (p > ) or among regions when sexes were pooled (). Despite this finding, to minimize the loss of any regional differences in the relationship between age and length, region-specific observed age-length keys were generated and used to assign ages by region to the 979 sampled Kiyi that were longer than 140 mm.

The age distribution was bimodal in each region (Figure 6) with an upper mode centered at age-11 in all five regions and a lower mode that consisted of nearly equal numbers of age-5 and age-6 fish in all regions except for Eastern Michigan where there were nearly twice as many age-5 as age-6 fish. The age distribution, after age-4 and 5 fish were pooled and age-11 and older fish were pooled within each region for sample size reasons, differed significantly among regions (). Variability around the age-11 mode and the relative frequency of intermediate aged (ages 7-9) fish appeared to explain much of the difference in age distribution among regions.

The slopes of the weight-length relationships did not differ between sexes (), among regions (), or due to the interaction between sex and region (). The intercepts, however, differed between the sexes () and among the regions (), but not due to the interaction of sex and region (). Post hoc contrasts found that the intercept for females was greater than that for males for fish from Eastern Michigan (), but there were no differences between sexes for any other region (p > ). Post hoc contrasts showed that the intercepts did not significantly differ among regions for male Kiyi (), but that the intercept for females from Eastern Michigan and Southern Ontario did not signficantly differ (), but were significantly greater than for females from all other regions (p < ) except for when Southern Ontario was compared to the Western Arm (). The intercepts for females from the Western Arm, Northern Michigan, and Northern Ontario did not significantly differ ().

The mean lengths-at-ages 5, 6, and 11 differed signficantly among regions (Figure 7). Fish from East Michigan were significantly longer (p < ) at age-5 than age-5 fish from other regions which did not differ significantly (p > ). Fish from North Ontario were significantly shorter than fish from South Ontario and East Michigan at age 6 (p < ) and 11 (p < ) with no other significant differences at these ages (p > ). Kiyi from the 2003 and 2009 year-classes exhbited similar growth trajectories during at least the first five years of life (Figure 7).

**Discussion**

Examination of length frequencies from Kiyi captured in the 13 years prior to 2014 suggested that the age distribution of Lake Superior Kiyi in 2014 should be dominated by ages 5, 11, and, possibly, 9. The age distribution of Kiyi captured in 2014 did show a distinct upper mode at age 11 and a lower mode that was evenly distributed between ages 5 and 6. The next most predominant ages were on either side of the mode at age 11. If our interpretation of the historical length frequencies is correct, then these results suggest that ages estimated from otoliths are generally within one year of the true age of the fish, at least for fish that are age 5 and older.

Ages estimated from otoliths were consistently greater than ages estimated from scales for Lake Superior Kiyi captured in 2014. Given that otoliths appear to provide accurate estimates of the age of Kiyi, we recommend that scales not be used to estimate the age of Kiyi, at least for fish larger than 140 mm.

Precision between readers for thin-sectioned otoliths was very good as the ACV (2.8) was less than the 5 suggested by Campana (2001) to represent “high precision.” This result was somewhat surprising because both readers expressed difficulty interpreting the putative annuli near the center of otoliths when few annuli were present (i.e., relatively young fish) and at the margin on all otoliths. Due to the sporadic production of year-classes by Kiyi, our study suffered from having no young fish less than four years old. Without these fish, we could not develop a good understanding for the appearance of the first few annuli. Interpretation of the otolith margin is notoriously difficult (Campana, 2001). However, because our samples were restricted to two days in early June and a few days in the middle of July, we were not able to examine the otolith margin throughout the growing season to develop a better understanding of its appearance. We did examine length frequency distributions for three years when Kiyi were sampled in several months and these results suggested that substantial growth in length of Kiyi in Lake Superior was not evident until at least late July. This suggests that we should have seen little current season growth 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.

Our results suggest that accurate estimates of the age of Lake Superior Kiyi may be obtained by interpretation of thin-sectioned otoliths. However, a better understanding of the characteristics of the first few annuli and the appearance of the otolith margin will help reduce ageing error. This understanding will require sampling small young Kiyi in years when young Kiyi are present and sampling Kiyi throughout the open-water growing season. Until those samples are obtained, it appears that the age of Kiyi may be reliably estimated to within one year by careful examination of thin-sectioned otoliths.

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**Figure Captions**

Figure 1. Locations of 2014 Kiyi collections in Lake Superior with regions identified.

Figure 2. Relative frequency of total lengths (TL) for all Kiyi captured in Lake Superior in June-July 2014. Note that each plot has been scaled such that the mode has a height equal to 1.

Figure 3. Relative within-year frequency of total length for all Kiyi captured in Lake Superior from May-July 2001-2014. Note that each plot has been scaled such that the mode has a height equal to 1. The point with the horizontal lines represent the mean total length and approximate 95% confidence interval for fish from the 2003 (in 2004-2008) and 2009 (in 2010-2013) year-classes.

Figure 4. Difference in estimated otolith ages for Lake Superior Kiyi from two readers at estimated otolith ages for the first reader (i.e., a modified age-bias plot), with mean (short horizontal lines) and 95% confidence intervals (vertical lines). Darker points represent more individuals and gray confidence intervals represent estimated otolith ages for the first reader where the mean estimated otolith age for the second reader differed significantly. The horizontal dashed line represents ages that agreed. Sample sizes for each estimated otolith age of the first reader are shown above the x-axis.

Figure 5. Difference in estimated scale and otolith ages for Lake Superior Kiyi from one reader at estimated otolith ages for the reader (i.e., a modified age-bias plot), with mean (short horizontal lines) and 95% confidence intervals (vertical lines). Darker points represent more individuals and gray confidence intervals represent estimated otolith ages for the first reader where the mean estimated otolith age for the second reader differed significantly. The horizontal dashed line represents ages that agreed. Sample sizes for each estimated otolith age of the first reader are shown above the x-axis.

Figure 6. Frequency of ages assigned with regional age-length keys for all Kiyi captured in Lake Superior from June-July 2014. Note that each plot has a different scale for the y-axis.

Figure 7. Mean lengths-at-age for the 2003 and 2009 (dashed line) year-class of Lake Superior Kiyi as determined from modal length frequency analyses and for ages (after applying region-specific age-length keys derived from otoliths) 5, 6, and 11 by region for Kiyi captured in 2014. For ages 5, 6, and 11 the points from left-to-right are for the Western Arm, Northern Michigan, Northern Ontario, Southern Ontario, and Eastern Michigan. Vertical lines represent approximate 95% confidence intervals, many of which are so narrow as to be obscured by the mean point.

Table 1. Characteristics of total length (mm) and ages (after applying region-specific age-length keys derived from otoliths) by region for this study and for other studies. Note that Years=sample years, gear=sampling gear (BTR=bottom trawl, GN=gillnet), n=sample size, and SD=standard deviation, Structure=calcified structure examined to estimate age, and Age-5, Age-6, and Age-11 are the percentage of age-5, -6, and -11 fish. References for previous studies: 1Pratt and Chong (2012), 2Deason and Hile (1947), and 3Pritchard (1931). Different letters in the Mean columns represent means that are significantly different.

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| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  |  |  |  |  | Total Length (mm) | | |  | Age | | | | | | |
| Lake | Region | Years | Gear |  | n | Min-Max | Mean (±SD) |  | Structure | n | Min-Max | Mean (±SD) | Age-5 | Age-6 | Age-11 |
| *This study* | | | | | | | | | | | | | | | |
| Superior | Western Arm | 2014 | BTR |  | 153 | 142-232 | 196 (±18)b |  | Otoliths | 153 | 5-14 | 8.6 (±2.6)ab | 15% | 20% | 24% |
| Superior | N. Michigan | 2014 | BTR |  | 69 | 152-240 | 198 (±19)bc |  | Otoliths | 69 | 5-20 | 9.2 (±4.2)b | 22% | 17% | 13% |
| Superior | N. Ontario | 2014 | BTR |  | 355 | 126-239 | 190 (±17)a |  | Otoliths | 354 | 4-12 | 8.1 (±2.8)a | 25% | 22% | 37% |
| Superior | S. Ontario | 2014 | BTR |  | 65 | 126-253 | 202 (±22)bc |  | Otoliths | 64 | 4-16 | 8.7 (±2.9)ab | 17% | 19% | 38% |
| Superior | E. Michigan | 2014 | BTR |  | 341 | 108-266 | 203 (±20)c |  | Otoliths | 339 | 4-16 | 8.3 (±2.8)ab | 26% | 13% | 26% |
| *Previous studies* | | | | | | | | | | | | | | | |
| Superior1 | Ontario | 2007-09 | GN |  | 403 | 151-305 | 201 (±23) |  | Otoliths | 322 | 4-22 | 8.9 (±2.7) | -- | -- | -- |
| Michigan2 | -- | 1930-32 | GN |  | 6625 | 175-351 | 266 (--) |  | Scales | 1679 | 2-10 | 4.5 (--) | -- | -- | -- |
| Ontario3 | -- | 1926 | GN |  | 18 | -- | 238 (--) |  | Scales | -- | 1-6 | -- | -- | -- | -- |

Table 2. Characteristics of the weight-length relationships for Kiyi in each region of Lake Superior. Note that n=sample size, R2 = coefficient of determination, b=slope, log(a)=intercept from model assuming separate slopes (b) for each region and sex combination, log(a\*)=intercept from model that assumes a common slope (=3.064) for each region and sex combination, and =predicted weight from the model with a common slope at the median total length (=195 mm). Note that slopes did not differ among any sex and region combination, different letters represent intercepts that are significantly different among regions within each sex, and asterisks represent intercepts that are significantly different between sexes within a region.

|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  |  | Female Weight-Length | | | | | |  | Male Weight-Length | | | | | |
| Region |  | N | R2 | b | log(a) | log(a\*) |  |  | n | R2 | b | log(a) | log(a\*) |  |
| Western Arm |  | 40 | 0.945 | 2.935 | -5.035 | -5.329ab | 48.7 |  | 29 | 0.907 | 2.677 | -4.458 | -5.336z | 47.9 |
| N. Michigan |  | 31 | 0.915 | 3.058 | -5.326 | -5.339a | 47.5 |  | 17 | 0.926 | 3.432 | -6.197 | -5.361z | 45.1 |
| N. Ontario |  | 49 | 0.956 | 2.962 | -5.110 | -5.341a | 47.3 |  | 37 | 0.945 | 3.083 | -5.391 | -5.347z | 46.7 |
| S. Ontario |  | 26 | 0.924 | 3.233 | -5.700 | -5.298bc | 51.0 |  | 18 | 0.915 | 3.304 | -5.879 | -5.328z | 48.7 |
| E. Michigan |  | 53 | 0.958 | 3.151 | -5.501 | -5.336c\* | 52.2 |  | 31 | 0.929 | 3.154 | -5.543 | -5.336z\* | 47.9 |













