Age, size, and recruitment of Coregonus kiyi from Lake Superior

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**Abstract**

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**Introduction**

Kiyi (*Coregonus kiyi*) are one of four deepwater cisco species (*C. hoyi, C. kiyi, C. nigripinnis*, and *C. zenithicus*) that historically supported major fisheries and were the primary prey for Lake Trout (*Salvelinus namaycush*) in the Laurentian Great Lakes (Zimmerman and Krueger, 2009). Kiyi were found in Lakes Huron, Michigan, Ontario, and Superior (Koelz, 1929), but presently occur only in Lake Superior (Scott and Crossman, 1973). Kiyi were last collected in 1964 in Lake Ontario, 1973 in Lake Huron, and 1974 in Lake Michigan (Todd, 1978 as cited in Parker, 1989). In Lake Superior, Kiyi are the most abundant deepwater pelagic species (Yule et al., 2013). The demise of Kiyi in the other Great Lakes may have been due to interactions with invasive species (Becker, 1983) or increased exploitation in the 1920-1940s (Scott and Crossman, 1973; Parker, 1989); though our lack of knowledge of Kiyi life history certainly curtails our understanding of these declines. Age, size, and recruitment dynamics are key life history attributes for understanding fish population dynamics (Maceina et al., 2007; Quist et al., 2012). Kiyi life history studies are limited to Koelz’s (1929) morphological descriptions of deepwater cisco and the works of Pritchard (1931) in Lake Ontario, Deason and Hile (1947) in Lake Michigan, and Pratt and Chong (2012) in the Canadian waters of Lake Superior.

A primary objective of the Laurentian Great Lake’s fisheries management community is to restore populations of deepwater cisco species. A step toward this goal is to increase our understanding of the life histories of deepwater cisco (Zimmerman and Krueger, 2009). In light of this goal and the lack of life history information on Kiyi, the purpose of this study was to describe the age, size, and recruitment dynamics for Lake Superior Kiyi. Specifically we 1) describe the size and weight-length relationships, 2) examine length frequencies from the last 10 years to assess if periodic strong year-classes are present, 3) compare ages estimated from the scales and otoliths, and 4) compare age distributions derived from otoliths to observed periodic strong year-classes to provide a partial validation for Kiyi ages estimated from otoliths.

**Methods**

*Sampling and Data Collection*

Kiyi were sampled at 102 locations during daylight between 19 May 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 done cross-contour with a mean beginning depth of 19.3 m (range: 11-40), ending depth of 60.9 m (range: 19-144), and a mean distance covered of 1.7 km (range: 0.5-3.8). The tows in July followed a depth contour, had a mean average depth of 190.6 m (range: 92-315), and a mean distance covered of 1.4 km (range: 1.2-1.5). Water temperature at depth of capture (i.e., lake bottom water temperatures) were measured with a SeaBird SBE19plus profiler (SeaBird Inc., Bellevue, WA).

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) and sexual maturity (mature, immature) were recorded and scales and sagittal otoliths were removed and placed in paper envelopes 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 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 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 (i.e., recruitment) which could be used to partially validate estimated ages for Kiyi captured 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 comparisons 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 as log10(W) = log10(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 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 during the first five years of life. Second, the mean length of 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 984 Kiyi were collected at 24 of the 102 locations sampled in 2014 (Figure 1). Kiyi were found at one station on 27 May 2014, at two stations on 5 June 2014, and at 21 stations between 7 July and 20 July 2014. Biomass and density ranged from 0-12 and 0-253 , respectively. Based on collections made at 22 on-contour sampling locations, the minimum and maximum depth of capture were 132 and 256 m. Maximum density (253 ) and biomass (12 ) were observed at 190 m. Bottom water temperatures at sites where Kiyi were collected ranged from 2.8-C with a mean of C.

The lengths of collected Kiyi 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 (sex- and length-stratified) subsample of 335 fish, four were juveniles and 60.1% of non-juvenile fish were female. Only 1 female and 9 males in the subsample were sexually immature. The smallest sexually mature fish in the subsample were a 142 mm female and a 152 mm male.

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) and reached a mean length of approximately 100 mm by the following spring in Lake Michigan (Tables 8 and 9 in Deason and Hile 1947). 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 that 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). The maximum observed age was 20 when otoliths were used, but only 8 when scales were used.

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 980 sampled Kiyi that were longer than 140 mm.

The age distribution (Figure 6; Table 1) was bimodal in each region 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 (Table 2) 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 > ). Thus, females were heavier than males at all lengths only for fish from Eastern Michigan. Post hoc contrasts showed that the intercept for females from Eastern Michigan and Southern Ontario did not significantly 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 (). Thus, females from Easter Michigan and Southern Ontario were generally heavier at the same length than females from the other regions. The intercepts did not significantly differ among regions for male Kiyi () which indicates that male Kiyi of the same length have statistical similar weights throughout Lake Superior.

The mean lengths-at-ages 5 and 11, but not age 6, differed significantly among regions (Figure 7). Fish from Eastern Michigan were significantly longer (p < ) at age-5 than age-5 fish from other regions, which did not differ significantly (p > ). Age 11 fish from Northern Ontario were significantly shorter than age-11 fish from all other regions except for Northern Michigan (p < ), with no other significant differences at this age (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**

Main findings of this study of Lake Superior Kiyi were that ages were more reliably determined using otoliths than scales, Kiyi are slow growing and long-lived, >20 years, and they appear to exhibit variable recruitment. These findings are consistent with previous findings for Kiyi and other deepwater ciscoes throughout the Laurentian Great Lakes (Prichard, 1931; Deason and Hile, 1947; Stockwell et al., 2009; Bunnell et al., 2010; Pratt and Chong, 2012, Myers et al., 2015). We found few differences in size, age, growth, and recruitment among regions. CAN WE ELIQUOENTLY SAY THAT WE FOUND FEW DIFFERENCES IN LIFE HISTORY ATTRIBUTES AMONG REGIONS and ADD A SUMMARY SENTENCE ON THE MAJOR DIFFERENCES BETWEEN MALES AND FEMALES?

Kiyi ages estimated from otoliths were consistently greater than ages estimated from scales (Fig. 5). This corroborates previous work on Lake Superior Cisco (Yule et al., 2008) and Pygmy Whitefish (*Prosopium coulteri*, Stewart et al., 2016), European Cisco, a.k.a., Vendace, *C. albula* (Aass, 1972), Canadian Lake Whitefish (*C. clupeaformis*, Mills and Beamish, 1980), and in general other long-lived slow-growing fish (GOT A CITE FOR THIS?). For example, Aass (1972) found scales ages to be up to 7 years younger than otolith ages for European Cisco. Our maximum Kiyi ages were 20 and XX years based on otoliths and XX and XX based on scales for females and males, respectively. Our maximum observed otolith age was similar to that observed by Pratt and Chong (2012) based on otoliths from Kiyi collected in Canadian waters of Lake Superior. Previous reported maximum Kiyi ages of 6 and 10 years based on scales from Lake Ontario (Pritchard, 1931) and Lake Michigan (Deason and Hile, 1947), respectively, should be considered inaccurate. Our maximum otolith age was similar to that observed for Lake Superior Cisco in 2005, maximum age of 21 for females and 17 for males (Yule et al., 2008). Stewart et al. (2016) reported maximum ages of Lake Superior Pygmy Whitefish were nine for females and seven for males. Otolith ages for Laurentian Great Lakes Bloater, the most common deepwater cisco remaining in the Laurentian Great Lakes, and Shortjaw Cisco, have not been published.

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 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) and 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. DO WE NEED TO DESCRIBE THAT WE DID THIS AND HOW WE DID THIS IN THE METHODS?

Examination of length frequencies from Kiyi captured in the 13 years prior to 2014 suggest that Kiyi experience highly variable recruitment. Age-1 fish were collected in only 3 of these 14 years (Fig. 3). 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.

Variable recruitment has been described for other Laurentian Great Lakes deepwater ciscoes including Cisco (Stockwell et al., 2009; Myers et al., 2015) and Bloater (Bunnell et al., 2010) as well as European Ciscoes (e.g., Aass, 1972; Nyberg et al., 2001; Marjomäki et al., 2004; Sandström et al., 2014). Our age 5, 9, and 11 year old Kiyi correspond to the 2009, 2005, and 2003 year classes. These years also had higher than average recruitment of Bloater and Cisco in Lake Superior (Vinson et al., 2014). Why Coregonid year class strength was high during these years and near zero in other years is unknown. Locally and globally, the factors underlying Coregonid recruitment; either density-independent physical environmental factors (e.g., annual weather patterns) that effect larval fishes directly or their food (Axenrot and Degerman, 2015) or density-dependent biotic factors (e.g., predation by or competition with Rainbow Smelt, *Osmerus mordax*, Myers et al., 2014) or a combination of the two, are not well understood. Though recent evidence of synchrony in Bloater (Bunnell et al., 2010) and Cisco populations (Myers et al., 2015) across the Laurentian Great Lakes and in Europe (Sandström et al., 2014) support the idea that environmental factors such as winter ice conditions, spring ice break-up date, and wind, play a major role in determining Coregonid year class strength.

When survival to age-1 does occur, growth is initially fast, as they grow to about 30% of their maximum length in their first year, but then slows precipitously particularly after age-5 (Figure 7). Prichard (1931) and Deason and Hile (1947) observed similar unhurried Kiyi growth in Lake Michigan and Lake Ontario. In Lake Michigan, fish grew 80-115 mm in their first year, about 20-30 mm per year between ages 2-4, and as little as 2 mm per year after age 5. Kiyi appear to grow to smaller maximum lengths in Lake Superior compared to that historically observed in Lakes Ontario and Michigan (Table 1). The mean (195 mm) and maximum (266 mm) [PLEASE CHECK THESE LENGTHS. THEY ARE FROM A DATA FILE I HAD] Kiyi we captured were smaller than that reported for Lakes Michigan (351 mm, Deason and Hile, 1947) and Ontario (~324 mm, Pritchard, 1931). The maximum length Kiyi collected by Pratt and Chong in Canadian waters of Lake Superior in 2007-9 was 305 mm and the mean was 201 mm. The maximum length (standard length) Kiyi collected by Koelz (1929) in 1917-25, was 204 mm in Lake Superior, and 245 mm in Lake Michig`an, 249 mm in Lake Huron, and 263 mm in Lake Ontario. An underlying factor for smaller Kiyi in Lake Superior is not apparent. Historical maximum lengths of other Coregonids in the Laurentian Great Lakes do not show this same pattern, i.e., individuals from other Lake Superior are not smaller for other deepwater Cisco species than that found in the other Laurentian Great Lakes using similar collection methods (e.g., Koelz, 1929, p. 316).

Kiyi appeared to be sexually mature at age-4, ca. 140-150 mm. This is similar to that reported for Lake Michigan populations based on scale ages (Prichard, 1931). Koelz (1929) smallest specimens (132-148 mm, standard length, 152-170 mm total length, based on conversion in Pratt and Chong, 2012) were mature. Like our collections, Deason and Hile (1947) collected few immature Kiyi. Their smallest mature female was 172 mm and mature male was 178 mm (THOUGH A LITTLE CONFUSING WHEN YOU READ THEIR SECOND MATURITY PARAGRAPH ON PAGE 133. OVERALL NEED TO CHECK TL v. SL v. FL, I MAY HAVE NOT ALWAYS SPECIFIED). More noteworthy may be Deason and Hile’s (1947) observation of immature individuals 241-312 mm in length which they interpreted as mature fish that may not spawn each year. The largest immature fish that we observed was a 207 mm male. The single immature female we observed was 125 mm. We collected too few immature individuals to speculate if Kiyi spawn each year. Skipped spawning was observed in anadromous spawning Cisco in James and Hudson Bay, Canada (Morin et al., 1982; Lambert and Dodson, 1990) and in Cisco and Lake Whitefish in Great Slave and Great Bear Lakes, Canada (Kennedy, 1949, 1953). We are not aware of it being reported in Laurentian Great Lake’s Coregonids. BIT OF A TANGENT SO PROBABLY SHOULDN”T SAY TOO MUCH. I COULD NOT FIND ANY PUBLISHED STATEMENT ON GREAT LAKES COREGONIDS SKIPPING SPAWNING. IF IT’S OUT THERE A REIVIEWER SHOULD POINT IT OUT.

Weight-length relationships did not differ between sexes or among regions. This was similar to that observed by Deason and Hile (1947) for Lake Michigan Kiyi who found greater differences among months and years than between sexes or locations. I DIDN’T GIVE THIS MUCH THOUGHT. COMPARATIVE DATA IS AVAILABLE IN DEASON AND HILE. NOT EASY FOR ME TO DECIPHER. I WOULD THINK IF WE DON”T ADD TO IT WE COULD DELETE THIS SECTION.

*Coregonid Ageing Recommendations*

Our results corroborate previous Coregonid scale-otolith aging studies Coregonids that found that scales significantly underestimated the age of Coregonids worldwide and that more accurate ages can be obtained by interpretation of thin-sectioned otoliths (Aass, 1972; Mills and Beamish, 1980; Yule et al., 2008; Stewart et al., 2016). We recommend that scales not be used to estimate Coregonid ages, at least for fish larger than about 120 mm, ca. age-1. To further improve age estimates, 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 Coregonids in years when they are present and sampling throughout the open-water growing season where feasible. Until those samples are obtained, it appears that the age of Kiyi and we suggest other Coregonids may be reliably estimated to within one year by careful examination of thin-sectioned otoliths. We also recommend additional comparative studies of scales and otoliths be conducted for other Laurentian Great Lakes Coregonids, e.g., Bloater and Shortjaw Cisco. WHAT ABOUT COLLECTING ANNUAL LENGTH FREQUENCY DATA?

*Conclusions*

In the past century, Kiyi has gone from a common Laurentian Great Lakes endemic species to mostly an extirpated one; and we don’t why. While not commercially or recreationally valuable, Kiyi are a key trophic link between zooplankton and Lake Trout (*Salvelinus namaycush*), the Great Lakes, top native predator (Gamble et al., 2011), which is a commercially and recreationally important species. Successful restoration of Lake Trout in the Laurentian Great Lakes may depend on restoration of native prey, which will depend on understanding their life histories (Zimmerman and Krueger, 2009). Lake Superior Kiyi appear to exhibit life history characteristics that have not drastically changed over the past century. This bodes well for using the contemporary Lake Superior fish community as a model for understanding historical Great Lakes ecosystem processes and we encourage more comprehensive study of Kiyi and other native species. Lake Superior is a refuge for many cold stenothermic species. Increased study of and long-term monitoring of these species, including age, growth, diet, and recruitment characteristics, may provide insight into how climate change may affect the deepwater fish fauna of Lake Superior and elsewhere.

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**Figure Captions**

Figure 1. Sampling locations in Lake Superior in 2014 with regions identified. Solid symbols denote locations where Kiyi were collected.

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. Plots are labeled as the year sampled. 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.

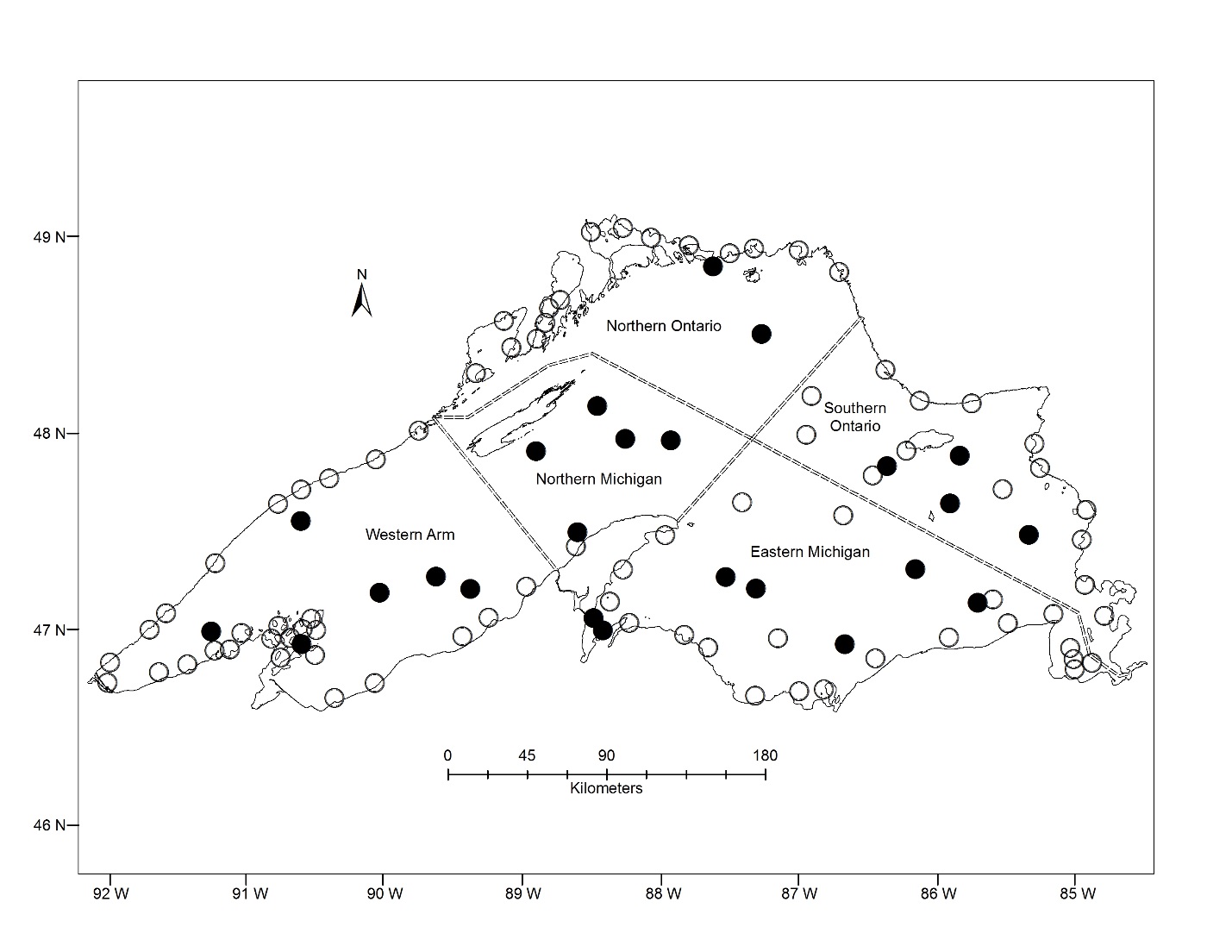
Figure 7. Mean lengths-at-age for the 2003 and 2009 (dashed line) year-class of Lake Superior Kiyi as determined from modal length frequency analyses and for ages (after applying region-specific age-length keys derived from otoliths) 5, 6, and 11 by region for Kiyi captured in 2014. For ages 5, 6, and 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 Kiyi 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 were significantly different. Maximum length of Kiyi in Lake Ontario were based on average fork length data in Prichard (1931 Table 19) and a total length (TL) to fork length (FL) conversion of FL = 0.9146 TL in Pratt and Chong (2012).

|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  |  |  |  |  | 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 | ?->324 | 238 (--) |  | Scales | -- | 1-6 | -- | -- | -- | -- |

Table 2. Characteristics of the weight-length relationships for Kiyi in each region and for all 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 at the median total length (=195 mm) from the model with a common slope. 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 |
| All Regions |  | 199 | 0.945 | 3.145 | -5.509 | -- | 49.3 |  | 132 | 0.927 | 3.138 | -5.511 | -- | 47.4 |



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