Age, growth and size of Lake Superior Pygmy Whitefish (*Prosopium coulterii*) in 2013

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In 1952, Pygmy Whitefish (*Prosopium coulterii*) were discovered in Lake Superior, which was at least 1770 km from all previous records of occurrence. A comprehensive life history study was published in 1953, but no further life-history studies of Lake Superior Pygmy Whitefish have occurred since. In 2013, we collected Pygmy Whitefish at 28 stations from throughout Lake Superior. The total length of all fish and the weight, sex, and maturity were recorded, and scales and sagittal otoliths were collected for a subsample of fish. Age assignments from scales and otolith thin-sections differed significantly (p<0.001), with otolith ages significantly greater after age-2. Maximum otolith age was 9 for females and 7 for males in 2013, compared to scale ages of 7 for females and 5 for males in 1953. Mean lengths of males and females in 2013 differed at age-3, 5.5 and 8 (all p<0.001). Female Pygmy Whitefish live longer, grow to a longer maximum length, and were longer beginning at age-3 than males. Our results suggest that the growth dynamics of Pygmy Whitefish have not changed much in 60 years, and support the conclusion that Pygmy Whitefish live longer than previously thought, though overall longevity probably has not changed since 1953.

**Keywords:** Lake Superior; sexual dimorphism; age; growth; weight-length;

**Introduction**

The Pygmy Whitefish (*Prosopium coulterii*), is a small coregonine fish that is best known for its remarkably disjunct distribution. In North America, Pygmy Whitefish are widely distributed west of the Continental Divide but are patchily distributed east of the Divide (Scott and Crossman 1973; McPhail 2007; Wiedmer et al. 2010; Witt et al. 2011; Barnett and Paige 2014; Blanchfield et al. 2014), including the eastern-most population in Lake Superior (Eschmeyer and Bailey 1955). Pygmy Whitefish, however, are not endemic to North America as they have been collected on the Chukotsk Peninsula, Siberia (Chereshnev and Skopets 1992).

Pygmy Whitefish is a glacial relict species (Taylor et al. 2011; Blanchfield et al. 2014) that was originally thought to inhabit only large, cold, deep, oligotrophic lakes (Scott and Crossman 1973; Weisel et al. 1973; Zemlak and McPhail 2006). However, populations of Pygmy Whitefish have been described from small lakes (Taylor et al. 2011), from strictly riverine populations (McPhail and Lindsey 1970; Mackay 2000), and from lakes where Pygmy Whitefish migrate into tributary rivers for spawning (Heard and Hartman 1966; Wiesel et al. 1973; Barnett and Paige 2014). In lakes, Pygmy Whitefish are generally associated with the bottom in the deepest areas (Becker 1983), though they may make diel migrations to shallower water (Zemlak and McPhail 2004; Zemlak and McPhail 2006).

Age data is a key component for understanding the ecology and population dynamics of fish populations (Maceina et al. 2007; Quist et al. 2012). Typically, scales have been used to assess age of Pygmy Whitefish (Weisel and Dillon 1954; Eschmeyer and Bailey 1955; Heard and Hartman 1965; McCart 1965; Weisel et al. 1973; Barnett and Paige 2014), but otoliths have been used recently (McPhail and Zemlak 2001; Zemlak and McPhail 2004; Plumb 2006; Sullivan 2011). Scales underestimate age for many fish (Maceina et al. 2007), including several coregonids that are closely related to Pygmy Whitefish (Aass 1972; Jessop 1972; Barnes and Power 1984; Skurdal et al. 1985; Yule et al. 2008; Herbst and Marsden 2011). The precision of ages determined from multiple readers and a comparison of ages assessed from scales and otoliths has not been formally examined for Pygmy Whitefish. Our first objective is to examine between-reader precision for scales and otoliths and to compare ages assessed from scales and otoliths of Pygmy Whitefish.

Pygmy Whitefish are small, with a maximum total length (TL) for most populations between approximately 150 and 275 mm (e.g., Eschmeyer and Bailey 1955; McCart 1965). Growth of Pygmy Whitefish appears to be fast prior to sexual maturity, which may occur between the second and fourth years of life (Weisel et al. 1973; XXX), and considerably slower following sexual maturity (McCart 1965). Growth of males and females is similar during the initial fast-growth period, but females are larger at older ages and have a longer lifespan (Eschmeyer and Bailey 1955; McPhail and Zemlak 2001; Zemlak and McPhail 2004). Our second objective is to describe the growth of Lake Superior Pygmy Whitefish and to make comparisons with other descriptions of growth. One key comparison will be with Eschmeyer and Bailey (1955) to determine if growth of Pygmy Whitefish in Lake Superior has changed since 1952.

Finally, Froese (2006) made a strong argument for the utility and continued publication of weight-length relationships for fish from a variety of populations. Zemlak and McPhail (2004) contain the only published weight-length relationships (for each bi-monthly summer sampling period) for Pygmy Whitefish. Thus, our third objective is to report the weight-length relationships for male and female Pygmy Whitefish in Lake Superior.

**Materials and Methods**

***Sampling and Data Collection***

Pygmy Whitefish were collected at 28 stations throughout Lake Superior (Figure 1) between 21-May and 20-July 2013. Fish were collected with the United States Geological Survey Lake Superior Biological Station R/V Kiyi using a Yankee bottom trawl with either a chain or rubber disk foot rope. 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 trawl was towed cross-contour beginning in shallower water at approximately 3.5 km/h. The tows had a mean beginning depth of 41.8 (range: 10.6-140.0) m, ending depth of 91.5 (range: 37.6-156.0) m, and the mean distance covered was 1.77 (range: 0.64-3.25) km.

All, or a subsample if the catch was large, captured Pygmy Whitefish were immediately measured for total length (TL) to the nearest mm and placed on ice to be further processed once the vessel was moored. If a subsample of fish was measured, then the TL for individual unmeasured fish was computed in proportion to the lengths of measured fish. Once the vessel was moored, TL, weight to the nearest 0.1 g, and sex (visually determined as female, male, immature) were recorded for as many fish as time allowed. Saggital otoliths and scales were initially removed from as many as six fish of each sex per 10 mm TL category. However, this scheme resulted in few males and few overall fish longer than 120 mm. Thus, scales and otoliths were extracted from more males and more females longer than 120 mm. Scales were removed from directly above the lateral line below the posterior edge of the dorsal fin and were placed in a coin envelope to air dry. Excess tissue was removed from otoliths before being placed into a vial to air dry. No frozen or preserved Pygmy Whitefish were used in this study.

In the laboratory, scales were removed from the envelopes, soaked in water, gently cleaned (between fingers and with a scalpel), and mounted between two glass slides. Scales were viewed using transmitted light with a Nikon SMZ745T™ stereo microscope (20-75x magnification). Otoliths were embedded in clear epoxy (Buehler EpoKwick**®** Epoxy, 5:1 ratio Resin to Hardener) before a 24 micron 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 2000-grit sandpaper before viewing in mineral oil on a black background with finely concentrated reflected light using the same stereo microscope (50x magnification). Digital images of scales and otoliths were obtained with a Nikon DS-Fi2™ camera attached to the stereo microscope.

Two readers, who were blind to any biological information related to the fish, identified annuli on the scales and otoliths from the digital images. Annuli on scales were identified using “cutting-over” and “compaction” characteristics evident in the circuli (Quist et al. 2012). The scale edge was considered to be an annulus as no new growth was observed (McCart (1963). Annuli on scales were identified by discontinuities in the otolith structure that were usually most obvious on the otolith margin lateral from the sulcus. The edge of the otolith was considered an annulus on most specimens, though some specimens showed some evidence of new growth. Some fish were excluded from further study because the scales (1.9%) or otoliths (0.4%) were unreadable. For fish where the ages from the two readers disagreed, the two readers met and attempted to develop a consensus age. If the readers could not agree on an age then that fish was removed from the comparison of ages assessed from scales and otoliths.

***Statistical Analyses***

Bias in scale ages and otolith ages between two readers and between consensus scale and otolith ages were assessed with age-bias plots (Campana 1995) and three measures of symmetry for the age-agreement table (Evans and Hoenig 1998) as computed with ageBias() from the FSA package v0.X.X (Ogle 2014) in the RTM statistical environment v3.1.1 (R Development Core Team 2014). 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 to three or more years, the coefficient of variation (CV; Chang 1982; Kimura and Lyons 1991), and average percentage error (APE; Beamish and Fournier 1981) as computed with agePrecision() from the FSA package.

Assessed ages could not be validated because known-aged Pygmy Whitefish were not available and were not collected from throughout the year (Campana 2001). However, we examined the length frequency distribution of all fish captured in 2013 and all fish captured in similar sample collections from 2006-2012 to determine if the age of some fish (likely young and small) could be ascertained and compared to ages assessed from scales and otoliths.

Potential differences in the loge(W)-loge(TL) relationship among male, female, and immature Pygmy Whitefish were assessed with a dummy variable regression (Fox 1997). When a difference in slopes was detected, pairwise comparisons among slopes were conducted by controlling the false discovery rate (Benjamini and Hochberg 1995) as implemented in compSlopes() from the NCStats package v0.X.X (Ogle 2014) in R.

Age-length-keys were modeled as described by Gerritsen et al. (2006) using multinom() from the nnet package v7.3-8 (Venables and Ripley 2002) in R. Modeled age-length-keys were compared between male and female Pygmy Whitefish by fitting a model with and without a dummy variable (and its interaction with length) for sex and then comparing models with a likelihood ratio test (Gerritsen et al. 2006).

Growth was summarized with the Francis (1988) parameterization of the von Bertalanffy growth model (VBGM) with the minimum (three) and maximum (seven) age in common between the two sexes defining the parameters. Thus, the model parameters represent the mean length of age-3, age-5, and age-7. Differences in VBGM parameters between males and females were assessed by fitting models where all three parameters differed by sex, two parameters differed by sex, and one parameter differed by sex, and then comparing the fit of nested subsets of these models with an extra sum-of-squares test as described generally by Ritz and Streibig (2008) and specifically for VBGM by Ogle (2014). Models were fit using the “port” algorithm of nls() in R. Parameters and lengths predicted from the VBGM for both sexes were summarized with boot-strapped confidence intervals constructed with nlsBoot() from the nlstools package v1.0-0 (Baty et al. 2014) of R as described in Ogle (2014). To help anchor the left sides of the VBGM for model fitting, all unknown sex fish less than 75 mm were assigned an age of 2 and randomly allocated to the male or female group.

All statistical tests used =0.05 to determine significance.

**Results**

***Age Assessment***

No significant bias in assessed ages was detected between readers for scales or otoliths (symmetry tests in Table 1). The two readers perfectly agreed on 68.8% of scale and 57.6% of otolith assessments and were within one year on 96.1% of scale and 94.6% of otolith assessments (Table 1). Assessed ages differed between the two readers by as much as two years for scales and three years for otoliths (Table 1). The coefficient of variation between readers was 9.2 for scale and 9.1 for otolith assessments (Table 1). The two readers reached a consensus age on all 77 assessed scales and on all but 2 of the 92 assessed otoliths.

A significant bias between ages assessed from paired scales and otoliths was detected (symmetry tests in Table 1; Figure 2). Mean assessed age was significantly lower for scales than for otoliths for all otolith ages with a sample size > 3 (Figure 2).

The distribution of TL for Pygmy Whitefish captured in 2013 indicated a distinct break between fish less than 75 mm and those greater than 79 mm (Figure 3). A break at approximately the same length was also evident in samples from the previous seven years. However, the sample from 2008 also exhibited a distinct break at 48-54 mm. Zemlak and McPhail (2004) observed age-0+ fish in 2001 with scale pockets, absent of scale development, present in fish with a length of 27 mm fork length (FL) and parr marks discernable at 36 mm (FL). From these observations, we concluded that fish that were less than 75 mm (no fish were less than 54 mm) in 2013 were two years old, which allowed for a test of ages assessed from scales and otoliths for fish less than 75 mm. Only 8.3% of scales and 36.4% of otoliths from fish less than 75 mm were assessed as age-2. Ages assessed from otoliths were fairly evenly distributed between age-1 and age-4 for these fish; however, all other ages assessed from scales were age-1 (91.7%).

***Life History Summaries***

The TL of all 3091 Pygmy Whitefish collected in 2013 ranged from 54 to 151 mm with a mean (+SD) of 95.2 (+17.7) mm. Of the 269 subsampled Pygmy Whitefish, TL ranged from 55 to 151 mm with a mean of 97.1 (+22.5) mm and W ranged from 0.8 to 32.0 g with a mean of 6.6 (+4.5) g. Sex was not determined for 11 (4.1%) of the subsampled fish. Of the remaining 258 fish, 48.5% were female, 30.2% were male, and 21.3% were immature. The length distribution of 125 subsampled females differed from that of 78 males (Kolmogorov-Smirnov test, D=0.59, p<0.0005) with females significantly (Wilcoxon test, W=8224, p<0.0005) longer (median TL of 114.0 mm) than males (94.5 mm). The maximum consensus assessed age from otoliths was nine for females and seven for males.

The loge(W)-loge(TL) relationship did not differ between female, male, and immature Pygmy Whitefish (F=1.60, p=0.175). The relationship fit to all sampled fish was loge(W) = -12.955+3.204loge(TL) (r2=0.983).

The observed age-length keys for Pygmy Whitefish were quite variable (Table 2). As many as five (of seven) ages were represented in one 10-mm TL interval and as many as five (of nine) TL intervals were represented in one age-class for females. Similarly, for males, as many as three (of six) ages were found in one 10-mm TL interval and as many as three (of six) TL intervals appeared in one age-class. No significant difference was found between age-length keys for male and female Pygmy Whitefish (2=14.8, p=0.391).

Comparisons of VBGM indicated that the length-at-age-3 parameter did not differ (F=0.65, p=0.423) but the lengths-at-age-5 (F=22.8, p<0.0005) and at age-7 (F=15.6, p<0.0005) parameters were significantly less for male than female Pygmy Whitefish. Growth was initially fast with half of the maximum size attained by the second year of life for male and by the third year of life for female Pygmy Whitefish (Table 3). After the initial fast growth, both male and female Pygmy Whitefish grew only a few mm per year on average (Table 3).

**Discussion**

We found age assessment of Pygmy Whitefish from both scales and otoliths to be difficult. Scales from small fish appeared straightforward, but we consistently under-estimated age-2 fish by one year suggesting that a first annulus was missing or difficult to detect. Scales from larger fish were also difficult to assess as circuli were few and crowded at the scale margin. We also had a difficult time obtaining otolith thin sections that were clear in all fields of view (i.e., putative annuli were evident near the otolith margin but not the center, or vice versa). In addition, most of the putative annuli could only be reliably detected along the otolith margin lateral from the sulcus, rather than around the entire otolith surface. Less than 40% of the otoliths from fish that appeared from the length frequency to be age-2 were assessed as age-2.

Difficulties in assessing ages was evident in variable assessed ages. Moderate variability in age assessments among readers was evident by perfect agreements of less than 70% (though, agreement to within one year was more than 94%) and CVs of over 9% which are greater than the median of 7.6% that Campana (2001) reported from studies on a variety of species. Our observations of number of ages within a single length-class or number of length-classes within a single age (for otoliths) were similar to those found by Weisel et al. (1973) for length-classes within an age, but higher than that of Eschmeyer and Bailey (1955) and McCart (1963) for both measures (for scales).

Ages assessed from otoliths were generally higher than ages assessed from scales. In 2000, Zemlak and McPhail (2004), reported that the first year’s annulus did not show on many scales, and using both scales and otoliths for aging structures, concluded that scales generally underestimated age in juveniles and adults. However, if one year was added to the scale ages to account for apparent missing or non-detectable fist annulus then the mean scale age was not different from the otolith until after an otolith age of five. Thus, if future research can rectify the issue related to the first annulus on scales, then scales and otoliths could be used interchangeably for Pygmy Whitefish as old as age-5. Furthermore, given the lack of old fish and the great variability in ages from otoliths, using scales for all fish, assuming that the first annulus issue is resolved, would likely result in very minor differences in metrics derived from ages for Pygmy Whitefish.

The life history metrics we examined in this paper appear to have changed little from Eschmeyer and Bailey (1955) descriptionsin 1952-53. Our fish had a slightly longer maximum size, a similar pattern with males more prevalent at younger ages and females at older ages, and similar growth rates (Table 3). In addition, we documented a difference in mean length-at-age for Pygmy Whitefish after age-4, which is consistent with observations made for other populations across North America (Eschmeyer and Bailey 1955; Heard and Hartman 1965; Mackay 2000; McCart 1963; Weisel and Dillon 1954; Zemlak and McPhail 2006). Our results suggest, however, that Pygmy Whitefish in Lake Superior live to an older age than previously thought. This observation is likely a result of our use of otoliths to assess age and should be treated as a provisional conclusion until otolith ages can be validated.

NEED SOMETHING TO FINISH WITH HERE.

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**Tables**

Table 1. Sample size (n), p-values from three tests of symmetry for the age-agreement table (McNemar’s, Evans-Hoenig (E-H), and Bowker’s test), coefficient of variation (CV), average percent error (APE), and percentage of fish by differences in ages for comparisons between two readers for scales, between two readers for otoliths, and between consensus ages of scales and otoliths for Lake Superior Pygmy Whitefish. The CV and APE were not computed for the scale to otolith comparison because a significant bias in age was detected.

|  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  |  | Symmetry Test p-values | | |  |  | % by Difference in Age | | | |
| Comparison | n | McNemar | E-H | Bowker | CV | APE | 0 | 1 | 2 | >3 |
| Scales | 77 | 0.414 | 0.218 | 0.593 | 9.2 | 6.5 | 68.8 | 27.3 | 3.9 | -- |
| Otoliths | 92 | 0.078 | 0.351 | 0.427 | 9.1 | 6.4 | 57.6 | 37.0 | 3.3 | 2.2 |
| Scales/Otoliths | 65 | <0.0005 | <0.0005 | <0.0005 | -- | -- | 13.8 | 36.9 | 26.2 | 23.1 |

Table 2. Percentage of female and male Lake Superior Pygmy Whitefish within each 10-mm total length (TL) interval. Ages were determined by consensus between two readers.

|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  |  | Female Otolith Age | | | | | | |  | | Male Otolith Age | | | | | | |
| TL |  | 3 | 4 | 5 | 6 | 7 | 8 | 9 |  | 2 | | 3 | 4 | 5 | 6 | 7 |
| 70-79 |  | 100 | -- | -- | -- | -- | -- | -- |  | 83 | | 17 | -- | -- | -- | -- |
| 80-89 |  | 67 | 33 | -- | -- | -- | -- | -- |  | -- | | 57 | 29 | -- | 14 | -- |
| 90-99 |  | 33 | 50 | 17 | -- | -- | -- | -- |  | -- | | 11 | 67 | 22 | -- | -- |
| 100-109 |  | 17 | 50 | 33 | -- | -- | -- | -- |  | -- | | -- | 75 | -- | -- | 25 |
| 110-119 |  | -- | 40 | 40 | 20 | -- | -- | -- |  | -- | | -- | -- | 40 | 40 | 20 |
| 120-129 |  | 14 | 43 | 14 | 14 | 14 | -- | -- |  | -- | | -- | -- | 100 | -- | -- |
| 130-139 |  | -- | -- | 29 | 29 | 14 | 14 | 14 |  | -- | | -- | -- | -- | -- | -- |
| 140-149 |  | -- | -- | -- | 33 | -- | -- | -- |  | -- | | -- | -- | -- | -- | -- |
| 150-159 |  | -- | -- | -- | -- | -- | -- | 100 |  | -- | | -- | -- | -- | -- | -- |

Table 3. Mean total length-at-age (mm) for female and male Lake Superior Pygmy Whitefish from this study and from Keweenaw Bay (KB), Isle Royale (IR), Apostle Islands (AI), and Laughing Fish Point (LFP) as summarized in Eschmeyer and Bailey (1955). Age was assessed from scales in all but this study. The results from this study are predicted means from Von Bertalanffy growth models and values in parentheses are bootstrapped 95% confidence intervals.

|  |  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  |  | Female | | | | |  | Male | | | | |
| Age |  | This Study | KB | IR | AI | LFP |  | This Study | KB | IR | AI | LFP |
| 1 |  | -- | 46 | 37 | 46 | 46 |  | -- | 49 | 40 | 50 | 48 |
| 2 |  | 64 (57-71) | 69 | 64 | 71 | 68 |  | 67 (63-71) | 71 | 68 | 75 | 79 |
| 3 |  | 88 (84-92) | 88 | 82 | 94 | 90 |  | 85 (82-89) | 87 | 81 | 95 | 92 |
| 4 |  | 105 (101-109) | 107 | 96 | 112 | 106 |  | 97 (93-100) | 98 | 88 | 108 | 102 |
| 5 |  | 118 (113-121) | 117 | -- | 122 | 118 |  | 103 (100-107) | 106 | -- | -- | 106 |
| 6 |  | 127 (122-131) | 123 | -- | 126 | 123 |  | 108 (103-113) | -- | -- | -- | -- |
| 7 |  | 133 (127-139) | 130 | -- | 136 | -- |  | 110 (104-118) | -- | -- | -- | -- |
| 8 |  | 138 (131-145) | -- | -- | -- | -- |  | -- | -- | -- | -- | -- |
| 9 |  | 141 (132-151) | -- | -- | -- | -- |  | -- | -- | -- | -- | -- |

**Figure Captions**

Figure 1. Locations of Lake Superior Pygmy Whitefish collections in 2013.

Figure 2. Mean (and 95% confidence intervals) consensus scale age at paired consensus otolith ages (i.e., an age-bias plot) for Lake Superior Pygmy Whitefish. The diagonal dashed line is the age-agreement line. Sample size for each assessed otolith age is shown above the x-axis.

Figure 3. Length frequency histograms (2 mm wide bins) for Lake Superior Pygmy Whitefish by year from 2006-2013. The vertical dashed line is at 75 mm.

Figure 4. The fit (solid lines) and 95% confidence bands (dashed lines) from Von Bertalanffy Growth Models (VBGM) fit to male and female Lake Superior Pygmy Whitefish. Solid symbols represent observed ages for known sex fish and open symbols are immature fish less than 75 mm total length that were randomly assigned to male or female to assist in fitting the VBGM.