Aspects of the life history, including an assessment of ageing bias and precision, 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 total length, 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 from fish collected in 2013 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 did differ at age-3, 5.5 and 8 (all p<0.001). Female Pygmy Whitefish live longer, grow to a longer maximum length, and are 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 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 may have the greatest discontinuous range of any freshwater fish in North America (Eschmeyer and Bailey 1955). First discovered in British Columbia in 1892 (Kendall 1917), Pygmy Whitefish are principally distributed in North America along the Pacific and Rocky Mountains from the Columbia River north to Alaska. West of the continental divide, populations of Pygmy Whitefish have been widely distributed in the Columbia River system in Montana, Idaho, and Washington State, Skeena and Frasier River systems, in British Columbia, in the Bristol Bay and Alaska Peninsula region, and in the upper Yukon River system (Teslin River) (Scott and Crossman 1973). Since then, isolated populations of Pygmy Whitefish have been found east of the continental divide in northern Canadian lakes (Lake Athabasca, Great Bear Lake, Waterton Lake, and Elliot Lake), along with lakes in the Liard and Peace river systems (Scott and Crossman 1973; Witt et al. 2011; Lindsey 1972). A single population has been discovered in Ekityki Lake on the Chukotski Peninsula in northeastern Russia (Chereshnev and Skopets 1992). Most recently, populations have been discovered in Bluefish Lake on the Yellowknife River and Winnange Lake in northwestern Ontario (Vecsei and Panayi 2014; Blanchfield et al. 2014). Pygmy Whitefish were first documented in Lake Superior in 1952 and is the most easterly area of this disjunt North American distribution (Eschmeyer and Bailey 1955; Dryer 1966). The ultimate distributional range of Pygmy Whitefish may not be known because they are difficult to sample due to their small size and preference for deep, cold waters. Eschmeyer and Bailey (1955) did conclude that the disjunct populations known at that time were the same species and likely represented relicts of a continuously distributed species from the late Pleistocene that survived in deep lakes after the retreat of the Wisconsin glaciation.

Little is known about the life history and population dynamics of Pygmy Whitefish. However, Eschmeyer and Bailey (1955) conducted a comprehensive life history study of Pygmy Whitefish following their discovery in Lake Superior. According to Eschmeyer and Bailey (1955), Pygmy Whitefish adults are variable in length, have a sub-terminal mouth, are toothless, and have a broadly rounded snout. Gillrakers are short to moderate in length. Color is a pale tan, immaculate below and dusted lightly with melanophores on the lateral and dorsal surfaces of the head and body. The back is marked by an irregular series of about 12 to 14 dark spots (Eschmeyer and Bailey 1955). They are characterized by slow growth and small size at maturity (McCart 1963; Page 2011). The sizes attained by Pygmy Whitefish in different geographic areas varied, most likely because of differences in growth rates related to different environments.

No further studies of Pygmy Whitefish in Lake Superior have occurred since the initial work by Eschmeyer and Bailey (1955). Thus, we have two objectives for this study. First, we will describe the age and growth metrics for Pygmy Whitefish collected throughout Lake Superior from 2013 and 1953. Second, we will compare ages assessed from scales and otoliths.

**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 with either a #35 Yankee bottom trawl or a roller trawl. 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 distance covered of 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, the TL, weight to 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 even with the posterior edge of the dorsal fin and were placed in a coin envelope to air dry. Otoliths were scraped clean and placed into vials 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 scraped clean, and mounted between two glass slides. The scale was viewed with transmitted light with a Nikon SMZ745T™ stereo microscope (XX-XX magnification). Otolith thin sections were obtained by using a Buehler IsoMet™ low speed saw to remove a 24 micron thick section along the dorsoventral plane through the nucleus of the otolith embedded in a clear epoxy (BRAND AND RATIO HERE). Otolith thin sections were further lightly polished with 2000-grit sandpaper and were viewed in mineral oil on a black background with finely concentrated reflected light using the same stereo microscope (5x 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 (consistent with 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 (usually because only a few regenerated scales were found; XXX%) or otoliths (XXX%) were unreadable. Finally, 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 (0% lack of consensus for scales, XX% for 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 RTM statistical environment v3.1.1 (R Development Core Team 2014). If no significant bias was detected, the precision in scale ages and otolith ages between two readers were summarized with the percentage of fish for which the ages differed by different amounts, the coefficient of variation (CV; Chang 1982), and average percentage error (APE; ) 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 ages 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 with compSlopes() from the NCStats package v0.X.X (Ogle 2014) in R which utilizes the false discovery rate method (Benjamini and Hochberg 1995).

Age-length-keys were modeled using multinom() from the nnet package v7.3-8 (Venables and Ripley 2002) in R as described by Gerritsen et al. (2006). Modeled age-length-keys were compared between sexes (male and female) 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 will represent the mean length of age-3, age-5, and age-7 Pygmy Whitefish. Differences in VBGM parameters between sexes (male and female) were assessed by fitting models where all three parameters differed by sex, two parameters differed by sex, and one parameter differed by sex and 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 VBGMS 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 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 65 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 (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). This break was also evident in samples from the previous seven years. However, the sample from 2006 also exhibited a distinct break at 48-54 mm. From these observations, we concluded that fish captured in 2013 that were less than 75 mm (no fish were less than 54 mm) 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 could not be reliably determined for 11 (4.1%) of the subsampled fish due to damage from the trawl. 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 having a significantly (Wilcoxon test, W=8224, p<0.0005) longer median (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 is 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 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 sizes 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**

In many species of fish, sexual dimorphism in growth rates, size and longevity is evident, with females growing faster, attaining a larger size and having a longer lifespan than their male counterparts. This has been particularly proven in Pygmy Whitefish across North America (Eschmeyer and Bailey 1955; Heard and Hartman 1965; Mackay 2000; McCart 1963; Weisel and Dillon 1954; Zemlak and McPhail 2006). The difference between sexes is thought to be due to differences in the way males and females channel surplus energy into growth and reproduction. This appears to be prevalent in Lake Superior Pygmy Whitefish.

Otolith age determination proved to be difficult due to slow growth and seasonal bands causing significant noise and false annulus. Crowded annuli on older Pygmy Whitefish collected from Lake Superior were difficult to distinguish on scales, but more recognizable on otoliths. Similarly, annuli that were crowded near the edges of scales for slow-growing Pygmy Whitefish in Lake Superior were easier to recognize when otoliths were sectioned. Scale and otolith age comparisons proved that scales are a viable, non-lethal aging structure for the first 2 years of life; after which otolith ages are significantly greater. Because growth may be reduced as a result of sex differences and maturation, it is necessary to carry out age validation in the future over the entire range of ages. Error in aging may result in an accumulation of estimates in the aging structures at the age in which the aging technique fails. Such may have been the case in 1953, when scales were used as the only aging structure. Since Pygmy Whitefish show slow growth rates, finding areas of concentrated circuli proved to be challenging. Because of this, thin-sectioned otoliths should be used as the primary aging structure for this species. This present study is a first look at aging Pygmy Whitefish sagittal otoliths and age comparison between scales and otoliths. However, it is still possible to underage due to a slow growth rate, which can produce annuli that might be misinterpreted as checks or are not visible at all.

Lake Superior Pygmy Whitefish live longer than previously thought by Eschmeyer and Bailey (1955), but longevity probably has not significantly changed since 1953. Female Pygmy Whitefish live longer, grow to a longer maximum length, and are longer beginning at age-3 than males. The information gathered in this study helped close a 60 year gap in the biology and life history traits of Pygmy Whitefish in Lake Superior. Without age validation, it is difficult to place complete confidence in age assignments. Thus, we are hesitant to draw too many conclusions from this summary and further age structure analysis should be conducted.

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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 by consensus assessed otolith age within each 10-mm total length interval.

|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  |  | 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. Values in parentheses for this study 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 on Lake Superior where Pygmy Whitefish were collected in 2013 for this study.

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 at 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 1998-2013. The vertical 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.