Age and Growth of the Pygmy Whitefish, *Prosopium coulterii*, in Lake Superior

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**Abstract**

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**

Pygmy Whitefish, Prosopium coulterii, Lake Superior, Growth, Age

**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.

**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; +1mm) 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 (W; +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.

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 (X-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 (XXX). 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***

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 the R statistical environment v3.1.1 (R Development Core Team 2014) which utilizes the false discover rate method (Benjamini and Hochberg 1995).

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 R. 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 and the coefficient of variation (Chang 1982, Campana et al. 2001) as computed with agePrecision() from the FSA package in R.

Assessed ages could not be validated because known-aged Pygmy Whitefish were not available to us. 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 some young ages of Pygmy Whitefish could be reasonably known and, thus, validated.

Age-length-keys were modeled using multinom() from the nnet package (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. 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 (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.

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All statistical tests used =0.05 to determine significance.

**Results**

The loge(W)-loge(TL) relationship did not differ between female, male, and immature Pygmy Whitefish (F=1.60, p=0.18). The relationship fit to all sampled fish is loge(W) = -12.955+3.204loge(TL) (r2=0.983).

No significant bias in assessed ages was detected between readers for scales (symmetry tests p>0.218) or otoliths (p>0.078). The two readers perfectly agreed on 68.8% of scale age and 57.6% of otolith age assessments and were within one year on 96.1% of scale and 94.6% of otolith assessments. Assessed ages differed between the two readers by as much as two years for scales and three years for otoliths. The coefficient of variation between readers was 9.2 for scale and 9.1 for otolith assessments. 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 assessed scale and otolith ages was detected (symmetry tests p<0.0005; Figure 2). Mean scale age was significantly lower than the assessed otolith age for all assessed otolith ages. The maximum assessed age was seven for males and nine for females.

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 2). This break was evident in samples from the previous seven years. However, the 2006 sample also exhibited a distinct break at 48-54 mm. Thus, we interpreted the fish shorter than 75 mm but longer than 50 mm captured in 2013 to be age-2, which allowed for a partial validation of assessed ages. For fish less than 75 mm, only 8.3% of scales and 36.4% of otoliths were assessed as age-2. Assessed otolith ages for these fish were fairly evenly distributed between age-1 and age-4; however, 91.7% of assessed scale ages were age-1.

Both structures had similar precision through age-2. Beyond that age, scale and otolith ages differed significantly (p<0.001), with otolith ages significantly greater after age-2 (**Fig 3**). Maximum otolith age was 9 for females and 8 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 (p<0.001; **Fig 4**).

Length frequency analysis was important in determining the length-at-age of Pygmy Whitefish. The length frequency distribution is based off of all Pygmy Whitefish collected in Lake Superior by the Lake Superior Biological Station from 1998-2013. The total length of 2013 Pygmy Whitefish in Lake Superior ranged from 55 to 150 mm. The age-2 year class stood out alone and very distinct with all fish being less than 75 mm (**Fig 5**). Based off of this result, all Pygmy Whitefish with a length less than 75-mm were assigned to the age-2 year class. The following year classes showed a tremendous amount of overlap, most likely due to slow growth rates and sexual dimorphism. Age-1 Pygmy Whitefish are not represented in the catch data.

Analysis of the sex ratio proved that females are the prominent sex in Lake Superior Pygmy Whitefish with 61.86% (120 females to 74 males) of the catch being female. When the sex ratio was analyzed by age class, it demonstrated the consistent trend of males being scarce and or missing entirely from older age classes (**Table 2**).

**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

**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.

**Table 1** Precision summary statistics between readers for each aging structure.

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| Structure | n | CV | APE | Percent of Absolute Difference in Ages | | | |
| 0 | 1 | 2 | 3 |
| Scale | 77 | 9.2 | 6.5 | 68.8 | 27.3 | 3.9 | N/A |
| Otolith | 90 | 8.7 | 6.2 | 58.9 | 35.6 | 3.3 | 2.2 |

**Table 2** Proportional table displaying the sex ratio of 2013 Lake Superior Pygmy Whitefish by age class.

|  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
| Age | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 |
| Female | 0.016 | 0.136 | 0.384 | 0.248 | 0.128 | 0.040 | 0.016 | 0.032 |
| Male | 0.128 | 0.167 | 0.397 | 0.141 | 0.115 | 0.051 | 0.000 | 0.000 |