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

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Pygmy Whitefish (*Prosopium coulterii*) are a small, glacial relict species with a disjunct distribution in northwestern North America and Siberia. 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 otoliths were collected, from a subsample of fish. We compared the precision of assessed ages between readers and between scales and otoliths, described growth for male and female Pygmy Whitefish, and published the first weight-length relationship for Pygmy Whitefish. Age assignments from scales and otoliths differed significantly (p<0.001), with otolith ages significantly greater at all ages. Much of this difference may be due to the first annulus missing on scales. Maximum otolith age was 9 for females and 7 for males, which equal the maximum age previously reported for Pygmy Whitefish but is older than what had been reported for Lake Superior. Growth was initially fast but slowed to only a few mm per year on average after age-3 for males and age-4 for females. Females were longer than males after age-3. Our results suggest that the size, age, and growth of Pygmy Whitefish in Lake Superior have not changed much since 1953.

**Keywords:** Lake Superior; otolith; weight-length; sexual dimorphism

**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 large fast-flowing rivers (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 areas to forage (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), although otoliths have been used more 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 estimated by multiple readers and a comparison of ages assessed from scales and otoliths has not been formally described 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; Heard and Hartman 1965), 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 growth from other studies. One key comparison will be with Eschmeyer and Bailey (1955) to determine if growth of Pygmy Whitefish in Lake Superior has changed since 1953.

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) published the only weight-length relationships (for each bi-monthly summer sampling period) for Pygmy Whitefish. FishBase (Froese and Pauly 2014) provided a weight-length relationship that was derived only from other species with a body shape similar to Pygmy Whitefish (Froese et al. 2013). 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 after 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, or 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 interval. 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. Annuli on otoliths 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 deemed 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 log10(W)-log10(TL) relationship among male, female, and immature Pygmy Whitefish were assessed with a dummy variable regression (Fox 1997) with lm() in R. Potential differences in length distributions between male and female Pygmy Whitefish were determined by comparing the cumulative length frequency distribution with a Kolmogorov-Smirnov test using ks.test() in R and the mean ranks of lengths with a Wilcoxon signed-rank test using wilcox.test() in R (Neumann and Allen 2007).

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 for sex (and its interaction with length) and then comparing these 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***

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. 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. The validity of assessed ages for fish less than 75 mm was poor as only 8.3% of scales and 36.4% of otoliths from these fish 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.

***Size***

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 150 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 log10(W)-log10(TL) relationship did not differ between female, male, and immature Pygmy Whitefish (F=1.60, p=0.175). The weight-length relationship fit to all sampled fish was log10(W) = -5.626 + 3.204log10(TL) (r2=0.983). The slope and back-transformed intercept from this model are both within the confidence intervals reported for those coefficients on FishBase (Froese and Pauly, 2014).

***Growth***

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 (Figure 4). 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 fish that appeared to be age-2 on the length frequency by one year, which suggests that a first annulus was missing or difficult to detect. Zemlak and McPhail (2004) also reported that the first annulus was not evident on scales. The first annulus may not form or be strongly evident because scales on Pygmy Whitefish appear to form at ca 27 mm TL (Heard and Hartman 1965) or longer (Zemlak and McPhail 2004) and observed (i.e., not back-calculated) lengths at the end of the first year are ca 45-55 mm TL (Heard and Hartman 1965; Zemlak and McPhail 2004). Future research on the lengths and the structure of scales from young-of-the-year Pygmy Whitefish may help resolve this issue.

Scales from larger fish were also difficult to assess as circuli were few and crowded at the scale margin. Minimal growth on the scale margin of sexually mature fish corresponds to the typical 1.0 to 4.0 mm per year increase in TL observed between sequential captures of tagged mature Pygmy Whitefish by Barnett and Paige (2014). Heard and Hartman (1965) expressed similar difficulties assessing age from scales of older fish.

We also had difficulties obtaining otolith thin sections that were clear in all areas of the section (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 a transect lateral from the sulcus, rather than around the entire otolith surface. We had particular difficulties with young fish where less than 40% of the otoliths from fish that appeared from the length frequency to be age-2 were correctly assessed as age-2. Zemlak and McPhail (2004) noted similar difficulties, especially with young fish where the otoliths were “small and fragile and it was not always possible to read them.”

Ages assessed from otoliths were generally higher than ages assessed from scales for all otolith ages with more than three fish. However, if one year is added to each scale age to adjust for the missing or non-detectable first annulus, then the mean scale age would not differ from the otolith age until after an otolith age of five. If future research can rectify the issue with the first annulus on scales, then scales and otoliths may be used interchangeably for Pygmy Whitefish as old as age-5. Unfortunately, given the high degree of variability in ages-at-length that we observed for Pygmy Whitefish, it will be difficult to define a maximum length for which scales could be used.

Our assessed ages for Pygmy Whitefish were highly variable with many length-classes in some ages and many ages within some length-classes. Similar levels of variability are evident in the assessed ages of Plumb (2006) (using otoliths) and Weisel et al. (1973) (using scales), though both metrics of variability were lower in Eschmeyer and Bailey (1955) and McCart (1963) (both using scales). This high level of variability may be a result of variability in assessing ages which is evident by the low percentage of perfect agreement between two readers and CVs of more than 9%, which are greater than the median CV of 7.6% that Campana (2001) reported from studies on a variety of species.

A high level of variability in observed lengths-at-age may also occur, however, for relatively long-lived species where growth is fast for only a few initial years and then very slow at older ages. Our results illustrate this type of growth for Pygmy Whitefish as half of the maximum size was attained by the second, for males, and third, for females, years of life and annual growth was only a few mm per year thereafter. Growth of older fish in Lake Superior appears to be slower than what is described for Pygmy Whitefish in other locations (Tables 3 and 4). However, this may be an artifact of the other studies having difficult ageing scales of olders fish, as our results are consistent with the direct observations of incremental growth from tagged fish made by Barnett and Paige (2014).

When compared to Lake Superior Pygmy Whitefish from 1953 (Eschmeyer and Bailey 1955), our fish had only a slightly longer maximum size and a similar pattern of more males at younger ages and females at older ages. Our mean lengths-at-age were very different from those reported by Eschmeyer and Bailey (1955), but would be similar if the first annulus was also missing on their scales. We observed an older maximum age for Lake Superior Pygmy Whitefish in 2013 than 1953, though 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. In summary, it does not appear that the size, age, and growth metrics that we measured have changed appreciably for Pygmy Whitefish in Lake Superior between 1953 and 2013.

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**References**

Aass P. 1972. Age determination and year-class fluctuation of cisco, *Coregonus albula* L., in the Mjøsa hydroelectric reservoir. Institute of Freshwater Research Drottningholm Report 52:5-22.

Barnes MA, Power G. 1984. A comparison of otolith and scale ages for western Labrador lake whitefish, *Coregonus clupeaformis*. Environmental Biology of Fishes 10:297-299.

Barnett HK, Paige DK. 2014. Characteristics of riverine broadcast spawning pygmy whitefish (*Prosopium coulterii*). Northwest Science. 88:155-168.

Baty F, Ritz C, Charles S, Brutsche M, Flandrois JP, Delignette-Muller ML. 2014. Nlstools: A toolbox for nonlinear regression in R. Available from: <http://cran.r-project.org/web/packages/nlstools/index.html>.

Beamish RJ, Fournier DA. 1981. A method for comparing the precision of a set of age determinations. Canadian Journal of Fisheries and Aquatic Sciences. 38:982-983.

Becker GC. 1983. Fishes of Wisconsin. University of Wisconsin Press, Madison, WI.

Benjamini Y, Hochberg Y. 1995. Controlling the false discovery rate: A practical and powerful approach to multiple testing. Journal of the Royal Statistical Society, Series B. 57:289-300.

Blanchfield PJ, Taylor EB, Watkinson DA. 2014. Morphological and genetic analyses identify a new record of a glacial relict: Pygmy Whitefish (*Prosopium coulterii*) from Northwestern Ontario. Canadian Journal of Zoology. 92:267–271

Campana SE. 2001. Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. Journal of Fish Biology. 59:197-242.

Campana SE, Annand MC, McMillan JI. 1995. Graphical and statistical methods for determining the consistency of age determinations. Transactions of the American Fisheries Society. 124:131-138.

Chang WYB. 1982. A statistical method for evaluating the reproducibility of age determination. Canadian Journal of Fisheries and Aquatic Sciences. 39:1208-1210.

Chereshnev IA, Skopets MB. 1992. A new record of pygmy whitefish, *Prosopium coulteri*, from amguem river basin (chukotski peninsula). Journal of Ichthyology. 32(4):46-55.

Eschmeyer PH, Bailey RM. 1955. The pygmy whitefish, *Coregonus coulteri*, in Lake Superior. Transaction of the American Fisheries Society. 84:161-199.

Evans GT, Hoenig JM. 1998. Testing and viewing symmetry in contingency tables, with application to readers of fish ages. Biometrics. 54:620-629.

Fox J. 1997. Applied regression analysis, linear models, and related methods. Sage Publications, Thousand Oaks, CA.

Francis RICC. 1988. Are growth parameters estimated from tagging and age-length data comparable? Canadian Journal of Fisheries and Aquatic Sciences. 45:936-942.

Froese R. 2006. Cube law, condition factor, and weight-length relationships: history, meta-analysis and recommendations. Journal of Applied Ichthyology. 22:241-253.

Froese R, Thorson JT, Reyes Jr RB. 2013. A Bayesian approach for estimating length-weight relationships in fishes. Journal of Applied Ichthyology. 30:78-85.

Froese R, Pauly D. 2014. FishBase, version 08/2014. [cited from 2014 Sep 23]. Available at: http://[www.fishbase.org](http://www.fishbase.org).

Gerritsen, HD, McGrath D, Lordan C. 2006. A simple method for comparing age-length keys reveals significant regional differences within a single stock of haddock (*Melanogrammus aeglefinus*). ICES Journal of Marine Science. 63:1096-1100.

Heard WR, Hartman WL. 1965. Pygmy whitefish, *Prosopium coulteri*, in the Naknek River system of southwest Alaska. Fishery Bulletin, U.S. Fish and Wildlife Service. 65:555-57.

Herbst SJ, Marsden, JE. 2011. Comparison of precision and bias of scale, fin ray, and otolith age estimates for lake whitefish (*Coregonus clupeaformis*) in Lake Champlain. Journal of Great Lakes Research.  37:386-389.

Jessop BM. 1972. Aging round whitefish (*Prosopium cylindraceum*) of the Leaf River, Ungava, Quebec, by otoliths. Journal of the Fisheries Research Board of Canada. 29:452-454.

Kimura DK, Lyons JJ. 1991. Between reader bias and variability in age-determination process. Fishery Bulletin, National Oceanic and Atmospheric Administration. 89:53-60.

Lindsey CC, Franzin WG. 1972. New complexities in zoogeography and taxonomy of the pygmy whitefish (*Prosopium coulteri*). Journal of the Fisheries Research Board of Canada. 29:1772–1775.

Maceina MJ, Boxrucker J, Bueckmeier DL, Gangl RS, Lucchesi DO, Isermann DA, Jackson JR, Martinez PJ. 2007. Current status and review of freshwater fish aging procedures used by state and provincial fisheries agencies with recommendations for future directions. Fisheries. 32:329-340.

Mackay WC. 2000. Status of the pygmy whitefish (*Prosopium coulteri*) in Alberta. Alberta Environment, Fisheries and Wildlife Management Division, and Alberta Conservation Association, Wildlife Status Report No. 27, Edmonton, AB.

McCart PJ. 1963. Growth and morphometry of the pygmy whitefish (*Prosopium coulteri*) in British Columbia. Dissertation, University of British Columbia.

McCart PJ. 1965. Growth and morphometry of four British Columbia populations of pygmy whitefish (*Prosopium coulteri*). Journal of the Fisheries Research Board of Canada. 22:1229-1259.

McPhail JD. 2007. The freshwater fishes of British Columbia. University of Alberta Press, Edmonton, AB.

McPhail JD, Lindsey CC. 1970. Freshwater fishes of northwestern Canada and Alaska. Fisheries Research Board of Canada, Bulletin 173. Ottawa, ONT.

McPhail JD, Zemlak RJ. 2001. Pygmy Whitefish studies on Dina Lake #1, 2000. Peace/Williston Fish and Wildlife Compensation Program Report No. 245.

Neumman RM, Allen MS. 2007. Size Structure. In: Guy CS, Brown ML, editors. Analysis and Interpretation of Freshwater Fisheries Data. American Fisheries Society: Bethesda, MD; p. 375-421

Ogle DH. 2013. fishR Vignette: Von Bertalanffy Growth Models. [cited from 2014 Aug 3]. Available from: <http://fishr.wordpress.com/vignettes/>.

Ogle DH. 2014. FSA: Fisheries stock analysis. Available from: <http://fishr.wordpress.com/fsa/>.

Ogle DH. 2014. NCStats: Helper functions for statistics at Northland College. Available from <http://www.rforge.net/NCStats/>.

Plumb MP. 2006. Ecological factors influencing fish distribution in a large subarctic lake system. M.Sc. Thesis, University of Alaska Fairbanks.

Quist MC, Pegg MA, DeVries DR. 2012. Age and growth. In: Zale AV, Parrish DL, Sutton TM, editor. Fisheries Techniques, third edition. American Fisheries Society: Bethesda, MD; p. 677-731

R Development Core Team. 2014. R: a language and environment for statistical computing. R Foundation for Statistical Computing. Available from: <http://R-project.org>.

Ritz C, Striebig JC. 2008. Nonlinear regression with R. Springer, NY.

Scott WB, Crossman EJ. 1973. Freshwater fishes of Canada. Fisheries Research Board of Canada, Bulletin 184. Ottawa, ONT.

Skurdal J, Vollestad LA, Qvenild T. 1985. Comparison of scales and otoliths for age determination of whitefish *Coregonus lavaretus*. Fisheries Research. 3:237-243.

Sullivan, M. 2011. Status of the pygmy whitefish (Prosopium coulterii) in Alberta: Update 2011. Alberta Wildlife Status Report, No. 27 (Update 2011). Edmonton, AB. 46 pp.

Taylor EB, Glow JL, Witt J, and Zemlak R. 2011. Connectivity among populations of pygmy whitefish (Prosopium coulterii) in northestern North America inferred from microsatellite DNA analyses. Canadian Journal of Zoology. 80:255-266.

Venables WN, Ripley BD. 2002. Modern applied statistics with S, fourth edition. Springer, New York.

Weisel GF, Dillon JB. 1954. Observations on the pygmy whitefish, *Prosopium coulteri*, from Bull Lake, Montana. Copeia 1954:124-127.

Wiedmer M, Montgomery DR, Gillespie AR, Greenberg, H. 2010. Late quaternary megafloods from Glacial Lake Atna, Southcentral Alaska, U.S.A. Quaternary Research. 73:413-424.

Weisel GF, Hanzel DA, Newell RL. 1973. The pygmy whitefish, *Prosopium coulteri*, in western Montana. Fishery Bulletin, U.S. Fish and Wildlife Service. 7:587-596.

Weisel GF, Dillon JB. 1954. Observations on the pygmy whitefish, *Prosopium coulteri*, from Bull Lake, Montana. Copeia. 2:124-127.

Witt JDS, Zemlak RJ, Taylor EB. 2011. Phylogeography and the origins of range disjunctions in a north temperate fish, the pygmy whitefish (*Prosopium coulterii*), inferred from mitochondrial and nuclear DNA sequence analysis. Journal of Biogeography. 38:1557–1569.

Yule DL, JD Stockwell, JA Black, KI Cullis, GA Cholwek, JT Myers. 2008. How systematic age underestimation can impede understanding of fish population dynamics: Lessons learned from a Lake Superior cisco stock. Transactions of the American Fisheries Society. 137:481-495.

Zemlak RJ, McPhail JD. 2004. Pygmy whitefish studies on Dina Lake #1, 2001. Peace/Williston Fish and Wildlife Compensation Program Report No. 270.

Zemlak RJ, McPhail JD. 2006. The biology of pygmy whitefish, *Prosopium coulterii*, in a closed sub-boreal lake: spatial distribution and diel movements. Environmental Biology of Fishes. 76:317-327.

**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.

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| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  |  | 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 (i.e., observed age-length keys). Ages are the consensus age from two readers of otoliths.

|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  |  | Female Age | | | | | | |  | | Male Age | | | | | | |
| TL (mm) |  | 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 observed total length-at-age (mm) and minimum and maximum total lengths for female Pygmy Whitefish from this study and from Keweenaw Bay (KB) and Isle Royale (IR) Lake Superior (Eschmeyer and Bailey 1955); Flathead Lake (FL; Weisel et al. 1973); Brooks Lake (BKL) and Naknek Lake (Heard and Hartman 1965); Cluculz Lake (CL), Tacheeda Lake (TL), MacLure Lake (ML), and McLeese Lake (MLL) (McCart 1963); and Dina Lake #1 (DL1; McPhail and Zemlak 2001). Lengths for populations marked with an asterisk were converted from fork to total length using the formula in Heard and Hartman (1965). The results from this study are predicted means from Von Bertalanffy growth models and values in parentheses are bootstrapped 95% confidence intervals.



|  |  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| Age |  | This Study | KB | IR | FL | BKL\* | NL\* | CL\* | TL\* | ML\* | MLL\* | DL1\* |
| 1+ |  | -- | 77 | 59 | 116 | 61 | 82 | 87 | 91 | -- | -- | 91 |
| 2+ |  | 64 (57-71) | 101 | 81 | 140 | 75 | 121 | 119 | 115 | 127 | 118 | 114 |
| 3+ |  | 88 (84-92) | 106 | 88 | 154 | 81 | 138 | 131 | 124 | 206 | 171 | 120 |
| 4+ |  | 105 (101-109) | 120 | 100 | 168 | -- | 150 | 138 | 130 | 238 | 210 | 128 |
| 5+ |  | 118 (113-121) | 126 | -- | -- | -- | 168 | 154 | 137 | 266 | 210 | 132 |
| 6+ |  | 127 (122-131) | 128 | -- | -- | -- | -- | 169 | 147 | 269 | -- | 133 |
| 7+ |  | 133 (127-139) | 136 | -- | -- | -- | -- | -- | -- | 279 | -- | 132 |
| 8+ |  | 138 (131-145) | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- |
| 9+ |  | 141 (132-151) | -- | -- | -- | -- | -- | -- | -- | 294 | -- | -- |
|  |  |  |  |  |  |  |  |  |  |  |  |  |
| min TL |  | 72 | 57 | -- | 89 | 52 | 55 | 89 | 84 | 114 | 114 | 29 |
| max TL |  | 150 | 138 | -- | 150 | 84 | 168 | 171 | 150 | 298 | 211 | 233 |

Table 4. Mean observed total length-at-age (mm) and minimum and maximum total lengths for male Pygmy Whitefish from this and other studies. Abbreviations and descriptions are the same as those for Table 3.

|  |  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| Age |  | This Study | KB | IR | FL | BKL\* | NL\* | CL\* | TL\* | ML\* | MLL\* | DL1\* |
| 1+ |  | -- | 76 | 63 | 117 | 61 | 83 | 99 | 88 | -- | -- | 79 |
| 2+ |  | 67 (63-71) | 94 | 78 | 128 | 69 | 118 | 123 | 97 | 131 | 120 | 101 |
| 3+ |  | 85 (82-89) | 102 | 85 | 140 | 77 | 128 | 126 | 117 | 208 | 166 | 110 |
| 4+ |  | 97 (93-100) | 106 | 92 | -- | -- | 144 | 126 | -- | 228 | 193 | 114 |
| 5+ |  | 103 (100-107) | 110 | -- | -- | -- | -- | 132 | -- | 201 | -- | -- |
| 6+ |  | 108 (103-113) | -- | -- | -- | -- | -- | -- | -- | 244 | -- | -- |
| 7+ |  | 110 (104-118) | -- | -- | -- | -- | -- | -- | -- | -- | -- | -- |
|  |  |  |  |  |  |  |  |  |  |  |  |  |
| min TL |  | 71 | 67 | -- | 84 | 48 | 55 | 95 | 84 | 114 | 114 | 67 |
| max TL |  | 124 | 118 | -- | 170 | 81 | 153 | 139 | 123 | 255 | 190 | 132 |

**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.