

Rainbow Smelt (*Osmerus mordax*) age and
growth in Whitefish Bay, Lake Superior,
with an analysis of age estimation effort.

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Abstract

In the Laurentian Great Lakes, nonnative Rainbow Smelt (*Osmerus mordax*) provide forage for Lake Trout (*Salvelinus namaycush*) and other predatory fish and are potential competitors with and predators of young *Coregonus* species. In recent years, Rainbow Smelt populations have declined across the Laurentian Great Lakes. This study is centered on Whitefish Bay, located at the Eastern end of Lake Superior, which is warmer and has a lower abundance of Lake Trout than other parts of Lake Superior. I compared age, after identifying an appropriate ageing structure, and growth metrics between Rainbow Smelt collected from Whitefish Bay in 2015 to collections made from other times and locations. I found no significant bias in estimated ages between readers for thin sectioned and whole cleared otoliths, but a significant bias between readers was detected for whole uncleared otoliths. Average coefficient of variation between readers was lowest for thin sectioned otoliths. For the same reader, the only significant bias detected was where whole uncleared otoliths underestimated the age for fish with an estimated otolith thin section age of 3. Results indicate that thin sectioned otoliths appear to be the superior structure for estimating the age of Rainbow Smelt. Maximum ages and growth rates differed between Rainbow Smelt from Whitefish Bay in 2015 and those from many of the other times and locations examined. The oldest fish in 2015 was 3 years old, whereas 5 and 6 year old fish were found in all of the other studies. Mean lengths-at-age for age-1 and age-2 Rainbow Smelt from Whitefish Bay in 2015 were intermediate compared to all other studies. However, age-3 Rainbow Smelt from the 2015 sample were noticeably smaller than from all other studies. The maximum age and growth differences for Rainbow Smelt among these periods and locations may be related to the observed population declines. Additional studies will be required to determine if this pattern is evident in other years and locations in Lake Superior.

Introduction

Rainbow Smelt (*Osmerus mordax*) are native to the northern drainages of the Western Atlantic, Pacific, and Arctic oceans (Figure 1; Scott and Crossman 1973; McClane 1974). They invaded the Laurentian Great Lakes in the early 20th century and found their way into Lake Superior in the early 1930s (Van Oosten 1937). Since their invasion, Rainbow Smelt have played an important ecological role in all of the Laurentian Great Lakes (Feiner *et al.* 2015), particularly as forage for Lake Trout (*Salvelinus namayacush*; Dryer *et al.* 1965; Ray *et al.* 2007) and as potential competitors with and predators of young *Coregonus* species (Selgeby *et al.* 1978; Myers *et al.* 2009). As reported by commercial harvest, which is often biased due to concentrated effort, populations in Lake Superior peaked in 1950-1960 (Baldwin *et al.* 1979). Since the mid to late 1980s, populations have fluctuated, but the overall trend has been downward, particularly since 2001 (Gorman 2007; Pratt *et al.* 2016).



Figure 1. Rainbow Smelt native range (shaded areas; USGS 2016).

Rainbow Smelt are a short-lived species that can reach a maximum age of seven in their native range (Bailey 1964). In Lake Superior, Rainbow Smelt age and growth were described for Western Lake Superior in the early 1960s (Bailey 1964),

during 1976 and 1977 (Schaefer *et al.* 1981), and between 1977-1980 (Luey and Adelman 1984). Similar studies have not been conducted in Eastern Lake Superior. Whitefish Bay, located on the Eastern side of Lake Superior (Figure 2), was chosen for this study to address this lack of data. Furthermore, Whitefish Bay was chosen for this study based on the unique dynamics of the ecosystem. Whitefish Bay is relatively warmer than most of Lake Superior (NOAA Great Lakes Surface Environmental Analysis 2015; USGS unpublished data), there is a low abundance of Lake Trout relative to much of the lake (Sitar *et al.* 2000; Wilberg and Hansen 2003; USGS unpublished data), and there is also low interspecific competition between Rainbow Smelt and *Coregonus* species due to recent population declines in Cisco (*Coregonus artedi*), Bloater (*Coregonus hoyi*), and Lake Whitefish (*Coregonus clupeiformis*; Pratt *et al.* 2016; USGS unpublished data).

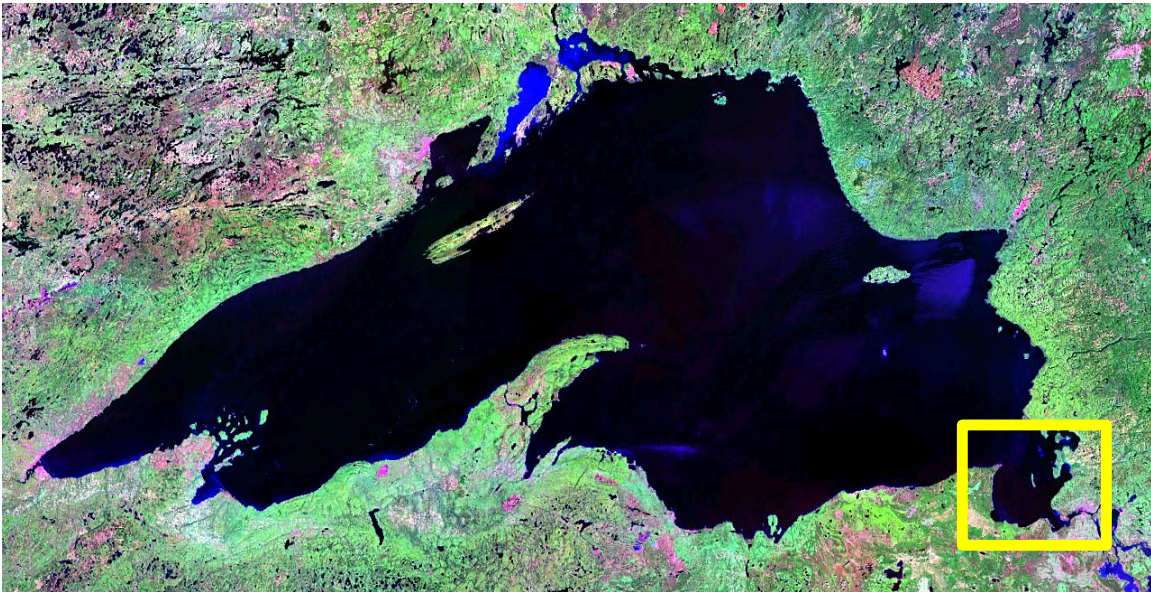


Figure 2. Lake Superior with Whitefish Bay highlighted by the yellow box (Landsat 2007).

Knowing the age of a fish (or having a precise estimate) allows fisheries scientists to create models that provide a better understanding of the dynamics of the stock and how the population changes in response to environmental and anthropogenic changes. The age of Rainbow Smelt has been estimated using scales

(McKenzie 1958, Bailey 1964, Jilek *et al.* 1979, Schaefer *et al.* 1981, Luey and Adelman 1984, Henderson and Nepszy 1989, Elzey *et al.* 2010), fin rays (Walsh *et al.* 2008), and whole otoliths (Sirois *et al.* 1998, Walsh *et al.* 2008). Walsh *et al.* (2008) found that ages estimated from sectioned fin rays were most precise among three readers, followed by whole cleared otoliths and then whole uncleared otoliths. Walsh *et al.* (2008) did not evaluate thin sectioned otoliths for assigning age estimates to Rainbow Smelt.

The primary objective of this study is to compare precision in ages among whole cleared otoliths, whole uncleared otoliths, and thin sectioned otoliths. Then, using the most precise ageing structure, describe the age distribution, growth (length-at-age), and weight-length relationship for Rainbow Smelt from Whitefish Bay in 2015. I then describe potential temporal changes in the age distribution and growth metrics by comparing my results to results from previous studies on Rainbow Smelt in Lake Superior. I hypothesize that Rainbow Smelt from Whitefish Bay will be older and larger than Rainbow Smelt from other areas of the lake due to the lack of predators such as Lake Trout, low competition via reduced *Coregonus* species density, and warmer water than compared to the other parts of Lake Superior.

The secondary objective of this study is to compare the time (effort) required to process each ageing structure for all three methods. Additionally, I will summarize the age distributions and growth using the ages from each structure to determine if these metrics differ among structures. These results will guide managers and supervisors to make the most cost-effective and scientifically sound decisions for their respective agencies with respect to estimating the age of Rainbow Smelt.

Methods

Rainbow Smelt were collected from Whitefish Bay, Lake Superior during June 2015. A Yankee bottom trawl (11.9-m headrope and 6.4-mm mesh cod end) was towed cross-contour with the United States Geological Survey (USGS) R/V Kiyi. Starting depths ranged from 10.1m to 37.0m with an average of 22.6m. Ending

depths ranged from 65.8m to 100.0m with an average of 76.5m. Once on deck, a total of 20 fish per 10mm length bin and all fish > 160mm were frozen in water to be processed in the laboratory two to three months later.

In the laboratory, fish were thawed by placing the plastic bag in a sink with room temperature water. Once thawed, individual fish were measured (total length; TL) to the nearest millimeter, weighed to the nearest 0.1 gram, and sagittal otoliths were removed and stored in micro-centrifuge tubes with a unique identification label. The sagittal otoliths were immersed in dilute (10%) bleach (NaOCl) to clean and then rinsed with distilled water so that bleach crystals did not form on the surface (Secor *et al.* 1991). Water was removed from the otolith surface with a paper towel and then covered with 95% ethanol for 5 minutes to remove water from within the otolith (Secor *et al.* 1991). After cleaning, otoliths were allowed to air dry before being stored in a micro-centrifuge tube. One otolith from each fish was cleared by immersing it in a 70:30 ethanol:glycerin solution for 30 days (Walsh *et al.* 2008). After viewing the other otolith whole, it was mounted in EpoKwick™ fast cure epoxy resin with the sulcus facing downward. A 0.3mm-0.5mm thick thin section of the transverse plane from the dorsal to the ventral side (Secor *et al.* 1991) was cut with a Buehler™ low-speed isomet saw (Buehler, Isomet Model 11-1180, Lake Bluff, Illinois). Sections were mounted on a clear glass microscope slide with EpoKwick™ fast cure epoxy resin. A drop of mineral oil was applied to all otoliths for viewing with a Nikon Eclipse E200 compound microscope using reflected light at 40-100x magnification.

Ages were estimated by two readers (one more experienced than the other) from whole cleared, whole uncles, and thin sectioned otoliths. The readers did not have any knowledge of fish size, sex, or maturity, which may bias the reader's interpretation of age (Morison *et al.* 1998). Scales were not used to estimate age as the majority of fish in the trawl collections retained few if any scales. Furthermore, sectioned fin rays were not used as the handmade chuck and three-blade set up used by Walsh *et al.* (2008) could not be replicated.

Bias in age estimates between readers with the same structure and between different structures with the same reader were estimated with age-bias plots

(Campana *et al.* 1995) and by testing for symmetry in an age-agreement table (Evans and Hoenig 1998) with `ageBias()` from the FSA package v0.7.9 (Ogle 2015) in the R™ statistical environment v3.2.2 (R Development Core Team, 2015). If no significant bias between readers or between structures was detected, precision between readers and between structures was described with the average coefficient of variation (ACV; Chang 1982; Kimura and Lyons 1991) as computed with `agePrecision()` from the FSA package, and as the percentage of fish for which the ages differed by zero years (full agreement).

An age-length key (ALK; Fridriksson 1934; Ketchen 1949) was derived for Rainbow Smelt from Whitefish Bay in 2015 from the more experienced reader's thin sectioned otolith age estimates and using 10mm length bins. The subsample of fish for which ages were estimated from the otoliths did not cover the full range of lengths in the original sample; therefore, I assumed that fish with lengths not represented in the ALK had the same distribution of ages as fish in the closest length bin. Specific ages were assigned to all Rainbow Smelt captured in Whitefish Bay in 2015 using the ALK and the method described by Isermann and Knight (2005) as implemented in the `alkIndivAge()` function from the FSA package. From this, mean length-at-age and the age distribution were computed.

To determine the effort required to process each otolith with each methodology, the times required for each step (removal, preparation, and reading; excluding epoxy cure time and clearing time) in the preparation were recorded to the nearest 0.25 minute (15 seconds). A one-way ANOVA followed by a Tukey HSD comparison were used to determine statistical differences in the mean total preparation time among the three methodologies.

The weight-length relationship was described by fitting a linear regression to common log-transformed weights and lengths.

All statistical tests used $\alpha=0.05$ to determine statistical significance.

Results

No significant bias in estimated ages was detected between readers for thin sectioned otoliths ($p=0.527$) and whole cleared otoliths ($p=0.593$; Figure 3-left). There was, however, a significant bias between readers for whole uncleared otoliths ($p<0.0005$), where Reader 2 (the less experienced reader) provided consistent overestimates for age-1 through age-3 compared to Reader 1 (Figure 3-left). For the same reader (Reader 1) using different structures, no significant bias was detected between whole cleared and whole uncleared otoliths ($p=0.421$) and between whole cleared and thin sectioned otoliths ($p=0.429$; Figure 3-right). A significant bias was detected between thin sectioned and whole uncleared otoliths with the same reader ($p=0.032$), where a higher mean estimated age was given for the whole uncleared otoliths for age-3 fish (Figure 3-right).

The ACV between readers was 6.2 and 14.4 for thin sectioned otoliths and whole cleared otoliths, respectively (Figure 3 left). The ages for the two readers agreed for 64% of the whole cleared otoliths and for 83% of the thin sectioned otoliths (Figure 3-left). For different structures with the same reader, the ACV was 12.4 for whole uncleared and whole cleared otoliths and 9.5 for whole cleared and thin sectioned otoliths (Figure 3-right). Whole cleared and whole uncleared otoliths agreed for 65% of the fish while whole cleared and thin sectioned otoliths agreed for 76% of the fish (Figure 3-right).

The total length of the 393 Rainbow Smelt collected ranged from 38 – 193mm with a mean (\pm SD) of 110.3 (\pm 37.2) mm. The age distribution and mean lengths-at-age for the 393 Rainbow Smelt captured in Whitefish Bay are reported in Table 1.

The length-weight relationship fit to the 393 Rainbow Smelt sampled from Whitefish Bay is $\log_{10}(\text{Weight}) = -5.906 + 3.266\log_{10}(\text{Total Length})$ ($r^2=0.9917$) (Figure 4) or $\text{Weight} = 0.00000124165L^{3.266}$ (Figure 5).

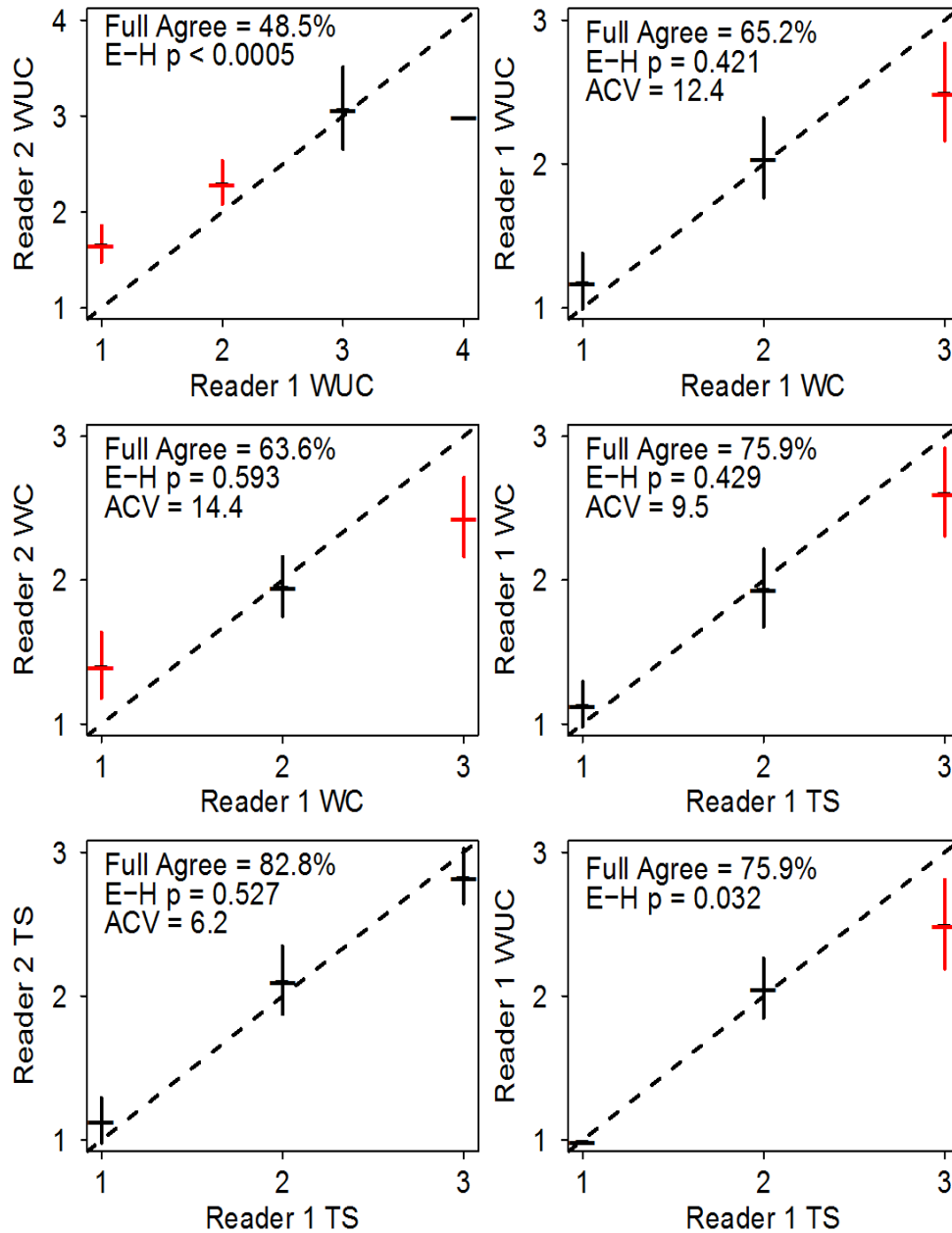


Figure 3. Age-bias plots for whole uncleared (WUC), whole cleared (WC) and thin sectioned (TS) otoliths between readers (left) and between pairs of structures (right). Superimposed on the plot are the percent full agreement (Full Agree), the Evans-Hoenig test of symmetry p-value (E-H p), and the average coefficient of variation (ACV) for Rainbow Smelt captured in Whitefish Bay, June 2015. The red confidence intervals correspond to significantly different age estimates while the black confidence intervals indicate non-statistically different age estimates. The dashed line represents perfect agreement between the ages.

Table 1. Age distribution (percentage), sample size (n), and mean, standard deviation (SD), and standard error (SE) length-at-age (mm) for Rainbow Smelt sampled from Whitefish Bay in June, 2015.

	Age Distribution	n	Mean	SD	SE
Age I	39.9%	157	69.5	15.97	1.27
Age II	28.5%	112	130.6	15.56	1.47
Age III	31.6%	124	143.8	15.52	1.39

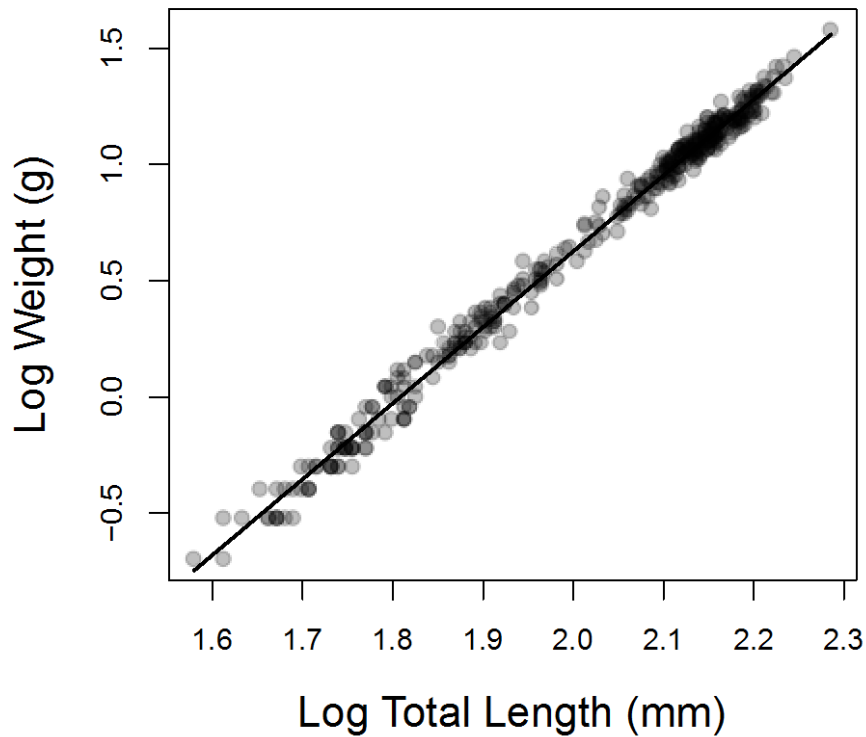


Figure 4. Common log-transformed linear regression of the weight-length relationship for Rainbow Smelt captured in Whitefish Bay, June 2015.

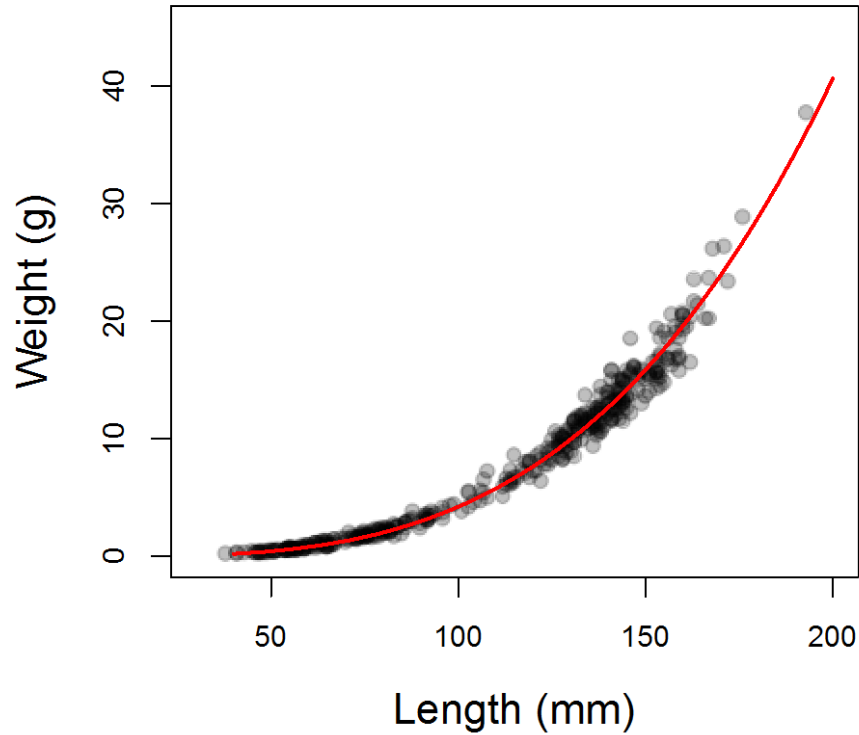


Figure 5. Weight-length relationship for Rainbow Smelt captured in Whitefish Bay, June, 2015.

Removal, preparation, and reading time differed among each methodology ($p < 0.0005$). The amount of effort associated with thin sectioned otoliths (excluding the epoxy cure time) was on average $12.24 (\pm 0.78)$ minutes. For whole cleared otoliths, the amount of effort (excluding the 30 day clearing period) was $7.35 (\pm 0.45)$ minutes followed by $6.68 (\pm 0.4)$ minutes for the whole uncleared otolith methodology (Figure 6).

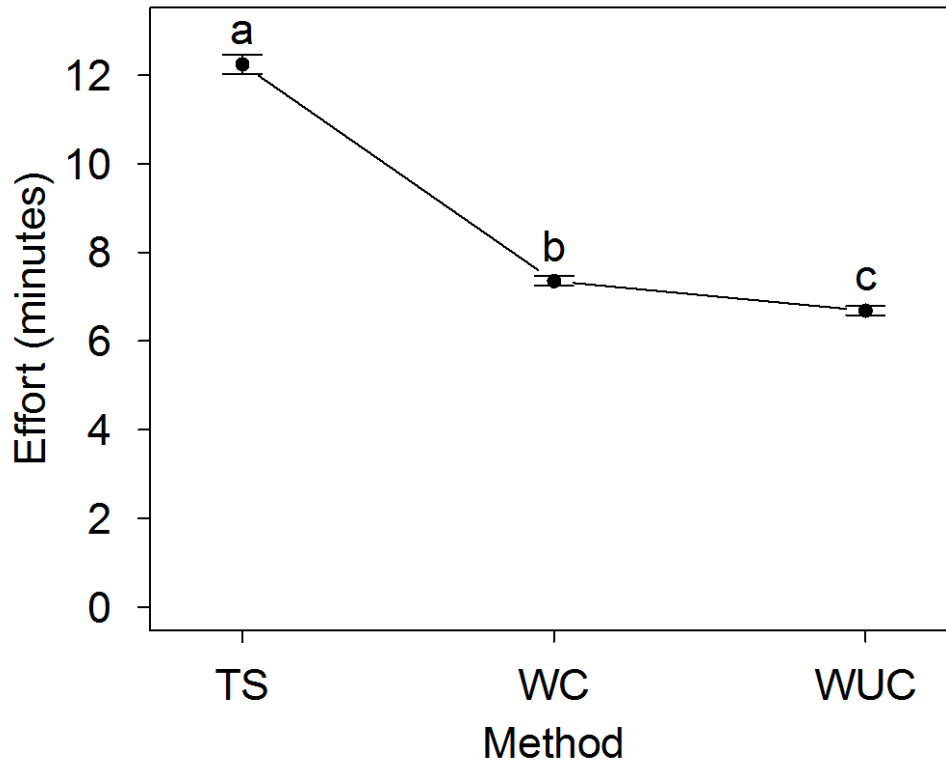


Figure 6. Plot of mean (with 95% confidence interval) amount of effort (minutes) by age estimation methodology (thin sectioned (TS); whole cleared (WC); and whole uncleared (WUC)). Different letters indicate means that are significantly different.

Discussion

For this study, the true age of these Rainbow Smelt cannot be determined, thus validation of the age estimations is impossible. Campana *et al.* (1995) stated that when age estimates cannot be verified, researchers should strive for consistency in age estimation. For the three methodologies proposed in this report, thin sectioned otoliths provided the most consistent (lowest bias, highest precision) between reader age estimates for Rainbow Smelt located in Whitefish Bay. Between whole cleared and whole uncleared otoliths, it was found that whole cleared otoliths provided more precise and less bias age estimates between readers. These results corroborate the findings of Walsh *et al.* (2008) that whole cleared otoliths are better for estimating the age of Rainbow Smelt than are whole uncleared otoliths. Further research should now compare bias and precision for age estimations between thin

sectioned otoliths (most precise in this study) and sectioned fin rays (most precise in Walsh *et al.* 2008 study) for Rainbow Smelt.

Removal, preparation, and reading time varied between the three methodologies, ranging from about 7 minutes for whole uncleared otoliths to 12 minutes for thin sectioned otoliths. These effort results may be used by managers to make decisions about how to allocate time and energy for estimating the ages of Rainbow Smelt. Is funding a limiting resource that would make whole cleared otoliths more ideal or do differences in the ACV create large enough changes in the results to warrant the more time-costly method of thin sectioned otoliths?

To help answer this question, I computed the amount of time and money (based on an hourly wage of \$11.00/hr) associated with various sample sizes of fish to estimate the age of (Table 2). I also applied the age summary methods described previously for thin sectioned otoliths to the other two methods to describe how metrics of growth and age distribution would differ based on the structure used to estimate the ages (Tables 3 and 4). When comparing the two extremes (i.e., the most precise and time costly thin sectioned otoliths and the least precise and time costly whole uncleared otoliths), the age distribution and mean lengths-at-age for age-1 through age-3 are nearly identical with the only striking difference being the single age-4 individual in the whole uncleared otolith sample (Table 3). However, the amount of effort required is 53% greater for thin sectioned than whole uncleared otoliths. The differences in population metrics based on the method used is minimal and does not warrant the use of the significantly more time costly method. However, it is important to note that this population consists of only three (or four) age classes. I would hypothesize that larger discrepancies may arise in the population characteristics if more age classes existed.

Table 2. Time (hours; hrs) and cost (U.S. \$) associated with different sample sizes of fish for the various age estimation methodologies.

# fish	Thin Sectioned		Whole Cleared		Whole Uncleared	
	Time	Cost	Time	Cost	Time	Cost
100	20.4 hrs	\$224.40	12.25 hrs	\$134.75	11.13 hrs	\$122.46
500	102 hrs	\$1,122.00	61.25 hrs	\$673.75	56.67 hrs	\$612.33
1000	204 hrs	\$2,244.00	122.5 hrs	\$1,347.50	111.33 hrs	\$1,224.76

Table 3. Age distribution (percentage) for Rainbow Smelt from Whitefish Bay based on using either whole uncleared or whole cleared otoliths to estimated their ages. Results for thin sectioned otoliths are in Table 1.

	Whole Uncleared	Whole Cleared
Age I	40.7%	40.5%
Age II	30.8%	32.6%
Age III	28.2%	29.5%
Age IV	<1%	--

Table 4. Mean length-at-age (mm) and associated standard error (SE) for Rainbow Smelt from Whitefish Bay based on using either whole uncleared or whole cleared otoliths to estimate their ages. Results for thin sectioned otoliths are in Table 1.

	Whole Uncleared	Whole Cleared
Age I	70.1 (1.42)	70.5 (1.42)
Age II	131.3 (1.37)	130.8 (1.57)
Age III	144.9 (1.43)	144.2 (1.35)
Age IV	160.0 (--)	-- (--)

Taking into account sampling variability, the mean lengths-at-age for Rainbow Smelt sampled from Whitefish Bay in 2015 (based on thin sectioned otolith age estimates) differ from most other studies examined (Table 5). In 2015, age-1 Rainbow Smelt from Whitefish Bay had about half the studies report higher mean lengths-at-age and about half report lower mean lengths-at-age. Mean length-at-age for age-3 fish from Whitefish Bay 2015 were significantly shorter than all other reported findings. However, the mean length-at-age for age-2 fish from this study was the same result produced by three other studies, one of which was Whitefish Bay 1978-1981.

Table 5. Mean length-at-age (mm) and age distribution (percentage) for Rainbow Smelt from various dates and locations around Lake Superior. The standard error derived from the 2015 Whitefish Bay mean length-at-age data is shown in the last row. (Whitefish Bay, WFB; Wisconsin Waters, WI; Lake Superior, L. Sup; Western Lake Superior, W. L. Sup; A, (Bailey 1964); B, (Schaefer 1981); C, (Luey and Adelman 1984)).

Location/Date/Study	Age I	Age II	Age III	Age IV	Age V	Age VI
WFB (Mrnak 2015)	69.5 (40%)	130.6 (30%)	144.3 (30%)	-- (--)	-- (--)	-- (--)
WFB (USGS 1978-1981)	74.2 (48%)	130.6 (32%)	160.4 (15%)	190.3 (3%)	215.6 (<1%)	NA (--)
WI (USGS 1992-2001)	88 (14%)	126 (37%)	151 (34%)	172 (11%)	187 (2%)	226 (<1%)
WI (USGS 1978-1981)	67.8 (52%)	131.8 (20%)	167.3 (17%)	186.7 (9%)	207.5 (2%)	213.2 (<1%)
L. Sup (USGS 1992-2001)	83 (23%)	126 (34%)	156 (27%)	183 (11%)	203 (2%)	229 (<1%)
L. Sup (USGS 1978-1981)	66.2 (58%)	129.9 (20%)	164.6 (14%)	186.5 (7%)	208.5 (<1%)	215.2 (<1%)
W. L. Sup (A; 1958-1960)	66.0 (45%)	151.1 (25%)	190.5 (13%)	210.8 (11%)	228.6 (5%)	248.92 (1%)
W. L. Sup (B; 1976-1977)	101 (11%)	137 (27%)	166 (37%)	186 (20%)	204 (4%)	NA (--)
W. L. Sup (C; 1977-1980)	86.9 (--)	136.8 (--)	169.6 (--)	186.1 (--)	198.3 (--)	204.5 (--)
Standard Error derived from 2015 data set	1.3mm	1.5mm	1.4mm	--	--	--

It is key to note that the standard error (SE) in this study is going to be different than the reference studies due to sample size. My largest sample size was for the age-1 group (n=157), whereas the reference studies used a range of sample sizes from 13,543 fish (USGS; Whitefish Bay 1978-1981) to 86 fish (USGS; Wisconsin Waters 1992-2001). Although the SE is different for each data set, I feel that conclusions can still be reasonably made and based more on practical significance rather than statistical significance. From a practical standpoint, the only major discrepancy is with age-3 Rainbow Smelt sampled from Whitefish Bay in 2015. The mean length-at-age for 2015 age-3 Rainbow Smelt is noticeably smaller than all other reported mean lengths-at-age. Furthermore, while still using the *practical significance* lens, it can be reasonably argued that the mean length-at-age has not drastically changed between locations and times for age-1 and age-2 Rainbow Smelt (two minor exceptions are for age-1 fish in Western Lake Superior in the mid-1970s and age-2 fish in Western Lake Superior in the late 1950s).

It appears that age-3 Rainbow Smelt located in Whitefish Bay during 2015 grow more slowly than most other stocks (past and present) around the lake despite population declines, which in theory would lead to less density-dependent influences upon the stock, resulting in increased growth. Possible contributors to this finding could be a lack of food availability that is targeted by these age-3 fish (e.g., juvenile *Coregonus* species), increased intraspecific competition amongst this age class, or possibly a chemical or nutrient change in the water that has reduced primary production, which may ultimately influence the forage base targeted by these age-3 fish. Research should be conducted to see if the slow growth of Rainbow Smelt age-3 and older is present in other locations and during other times around the lake.

It is also noteworthy that no fish older than age-3 appeared in the 2015 Whitefish Bay sample. Most other studies found Rainbow Smelt up to age-6 and all found age-5 fish (Table 5). The age distribution among all the studies was fairly similar (i.e., age-1 or age-2 fish dominated the sample, except for the Schaefer *et al.* 1976-1977 data set where age-3 fish made up the majority of the sample; Table 5). Older fish (age 5+) make up a very small percentage of these populations ranging

from less than 1% to a maximum of 5% (Table 5). Thus, it could be assumed that if the sampling effort was increased for this study, older Rainbow Smelt might have appeared in the sample. Support for this assumption comes about when looking at the age distribution for the 2015 caught Rainbow Smelt. Age-3 fish make up about 30% of the population with no age-4 fish present. I find it very hard to believe that all 30% of these fish succumb to mortality on an annual basis. Furthermore, all studies used different gear (seines, electrofishing, dip nets, trawls, etc.) so it is reasonable to have different proportions of age classes for each different study due to gear selectivity. I believe that the same possibilities as to why 2015 Whitefish Bay Rainbow Smelt have reduced growth (food, competition, nutrients) could also be contributing to the truncated size structure by not allowing the fish to reach their historic growth and life history potential.

My hypothesis that Rainbow Smelt sampled from Whitefish Bay in 2015 will be older and larger was incorrect. In 2015, Rainbow Smelt from Whitefish Bay exhibited a lower maximum age and slowed growth rates past age-2. A potential explanation for this finding (excluding the general statements above) could be due to Rainbow Smelt being a highly cannibalized species in the absence of readily available resources (Gorman 2008; Feiner *et al.* 2015). These age-3 fish could be feeding upon each other at such a high rate that it is truncating the population (despite the lack of top-down control via Lake Trout), resulting in less older fish. However, cannibalism tends to be felt more by smaller fish (i.e., big fish eat small fish). So, unless Rainbow Smelt exhibit an aggressive feeding behavior similar to Northern Pike (*Esox lucius*; eats very large prey relative to body size), then I do not believe cannibalism is the reason. Pratt *et al.* (2016) noted that Lake Trout abundance has been on the rise in recent years (i.e., 2006-2011) across Lake Superior. The truncated size structure finding could be a result of a newly established Lake Trout stock in Whitefish Bay, which would explain away the slowed growth finding (i.e., Lake Trout are targeting and preying on the big age-3 fish, resulting in the apparent 'slowed growth'). However, cannibalism or predation (or any other form of mortality) would also result in less density-dependent influences, which would lead to increased growth, unless another influence wields a

greater effect on the population (e.g., lack of production). Pratt *et al.* (2016) mentioned that since about 1980, Rainbow Smelt population structure around Lake Superior has shifted towards smaller age-1-2 fish. Moreover, Pratt *et al.* (2016) said that of 35 Rainbow Smelt year classes that have been measured, the eight weakest have occurred in the last 13 years resulting in little recruitment to larger size classes. Gorman (2012) stated that this pattern is consistent with increasing predation pressure. My findings, which are in accordance with Pratt *et al.* (2016) and Gorman (2012), lead me to hypothesize that there is in fact a new population of predators feeding upon these large age-3 Rainbow Smelt at a rather fast rate. Additional studies will be required to determine if this pattern (reduced growth past age-2 and a truncated population structure) is occurring in other years and other locations around Lake Superior and to identify other possible contributors to these findings.

Conclusions

Thin sectioned otoliths are statistically superior to uncleared and cleared whole otoliths for estimating the age of Rainbow Smelt (most precise and least biased). However, the difference in the 2015 Whitefish Bay Rainbow Smelt population characteristics based on the structure used for age estimation are not large enough to warrant the use of this more time costly method. My recommendation is for the USGS Lake Superior Biological Station to use whole cleared otoliths to estimate the ages of Rainbow Smelt (ideal middle ground), but to also keep in mind that thin sectioned otoliths produce the least biased and most precise age estimates.

Rainbow Smelt from Whitefish Bay exhibited a lower maximum age and slowed growth beyond age-2 compared to many other locations and times. I recommend that Whitefish Bay's limnological characteristics, the prey/predator species abundance (past, present, and future), and the Rainbow Smelt's diet be looked at more in-depth with hopes of explaining these findings.

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“See a job, do a job.” -MRV

References

- Bailey, M.M. 1964. Age, growth and sex composition of the American Smelt (*Osmerus mordax*), of Western Lake Superior. Transactions of the American Fisheries Society. 93:382-395.
- Baldwin, N.S., Sallfeld, R.W., Ross, M.A., and Buettner, H.J. 1979. Commercial Fish Production in the Great Lakes 1867–1977. Ann Arbor, MI: Great Lakes Fishery Commission Technical Report 3.
- Bronte, C.R., Ebener, M.P., Schreiner, D.R., Devault, D.S., Petzold, M.M., Jensen, D.A., Richards, C., and Lozano, S.J. 2003. Fish community change in Lake Superior, 1970–2000. Canadian Journal of Fisheries and Aquatic Sciences. 60:1552–1574.
- Campana, M.C., Annand and J.I., McMillan. 1995. Graphical and statistical methods for determining the consistency of age determinations. Transactions of the American Fisheries Society. 124:131-138.
- Chang, W.Y.B., 1982. A statistical method for evaluating the reproducibility of age determination. Canadian Journal of Fisheries and Aquatic Sciences. 39:1208-1210.
- Dryer, W.R., Erkkila, L.F., and Tetzloff, C.L. 1965. Food of the Lake Trout in Lake Superior. Transactions of the American Fisheries Society. 94:169–176.
- Elzey, S., Centerline, C., and Fischer, J., 2010. Improving Methods to Accurately Age Rainbow Smelt. American Fisheries Society Meeting.
- Evans, G.T., and J.M., Hoenig. 1998. Testing and viewing symmetry in contingency tables, with application to readers of fish ages. Biometrics. 54:620-629.
- Feiner, Z.S., Bunnell, D.B., Höök, T.O., Madenjian, C.P., Warner, D.M., and Collingsworth, P.D. 2015. Non-stationary recruitment dynamics of Rainbow Smelt: The influence of environmental variables and variations in size structure and length-at-maturation. Journal of Great Lakes Research. 41:246-258.
- Fridriksson, A. 1934. On the calculation of age-distribution within a stock of cod by means of relatively few age-determinations as a key to measurements on a large scale. Rapports et procès-verbaux des reunions: Conseil permanent international pour l'exploration de la mer. 86:1-5.
- Gorman, O.T. 2007. Changes in a population of exotic Rainbow Smelt in Lake Superior: Boom to bust, 1974–2005. Journal of Great Lakes Research. 33:75-90.
- Gorman, O.T. 2012. Successional change in the Lake Superior fish community:

- population trends in ciscoes, rainbow smelt, and lake trout, 1958-2008. *Advanced Limnology*. 63: 337-362.
- Henderson, B.A., and Nepszy, S.J. 1989. Factors Affecting Recruitment and Mortality Rates of Rainbow Smelt (*Osmerus mordax*) in Lake Erie, 1963–1985. *Journal of Great Lakes Research*. 15:357–366.
- Isermann, D.A., and Knight, C.T. 2005. A computer program for age-length keys incorporating age assignment to individual fish. *North American Journal of Fisheries Science*. 25:1153-1160.
- Jilek, R., Cassell, B., Peace, D., Garza, Y., and Siewart, T. 1979. Spawning population dynamics of Smelt, (*Osmerus mordax*). *Journal of Fish Biology* 15:31–35.
- Ketchen, K.S. 1949. Stratified subsampling for determining age distributions. *Transactions of the American Fisheries Society*. 79:205-212.
- Kimura, D.K., and Lyons, J.J. 1991. Between reader bias and variability in age-determination process. *Fishery Bulletin*. 89:53-60.
- Landsat. 2007. Lake Superior Nasa. Accessed April 28th 2016. URL http://www.cs.mcgill.ca/~rwest/link-suggestion/wpcd_2008-09_augmented/images/889/88926.jpg.htm
- Lawrie, A.H. 1978. The fish community of Lake Superior. *Journal of Great Lakes Research*. 4:513–549.
- Luey, J.E., and Adelman, I.R. 1984. Stock structure of Rainbow Smelt in Western Lake Superior: Population characteristics. *Transactions of the American Fisheries Society*. 113:709-715.
- McClane, A.J. 1974. *Field Guide to Freshwater Fishes of North America*. Henry Holt and Company, LLC, New York, New York.
- McKenzie, R.A. 1958. Age and growth of Smelt, (*Osmerus mordax*) of the Miramichi River, New Brunswick. *Journal of the Fisheries Research Board of Canada*. 15:1313–1327.
- Morison, A.K., Robertson S.G., and Smith D.C. 1998. An integrated system for producing fish aging: Image analysis and quality assurance. *North American Journal of Fisheries Management*. 18:587-598.
- Myers, J.T., Jones, M.L., Stockwell, J.D., Yule, D.L. 2009. Reassessment of the predatory effects of Rainbow Smelt on Ciscoes in Lake Superior. *Transactions of the American Fisheries Society*. 138:1352–1368.

- NOAA Great Lakes Environmental Research Laboratory (CoastWatch). 2015. Great Lakes Environmental Analysis (GLSEA). URL <http://coastwatch.glerl.noaa.gov/glsea/glsea.html>
- Ogle, D.H., 2015. FSA: Fisheries stock analysis. URL <http://fishr.wordpress.com/fsa/>.
- Pratt, T.C., Gorman, O.T., Mattes, W.P., Myers, J.T., Quinlan, H.R., Schreiner, D.R., Seider, M.J., Sitar, S.P., Yule, D.L., and Yurista, P.M. 2016. The state of Lake Superior in 2011. URL http://www.glfrc.org/pubs/SpecialPubs/Sp16_01.pdf.
- U.S. Geological Survey. 2016. Nonindigenous Aquatic Species Database. Gainesville, Florida. Accessed April, 28th 2016.
- Van Oosten, J. 1937. The dispersal of Smelt, (*Osmerus mordax*) in the Great Lakes region. Transactions of the American Fisheries Society. 66:160–171.
- R Development Core Team. 2015. R: a language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria. URL <http://R-project.org>.
- Ray, B.A., Hrabik, T.R., Ebener, M.P., Gorman, O.T., Schriener, D.R., Schram, S.T., Sitar, S.T., Mattes, W.P. and Bronte, C.R. 2007. Diet and prey selection by Lake Superior lake trout during spring, 1986-2001. Journal of Great Lakes Research 33:104–113.
- Schaefer, W.F., Swenson, W.A., and Heckmann, R.A. 1981. Age and growth and total mortality of Rainbow Smelt in Western Lake Superior. Journal of Great Lakes Research. 7:37-41.
- Scott, W.B., and Crossman, E. J. 1973. Freshwater fishes of Canada. Fisheries Research Board of Canada Bulletin. 184.
- Secor, D.H., Dean, J.M., and Laban, E.H. 1991. Manual for otolith removal and preparation for microstructural examination. Electric Power Research Institute and Belle W., Baruch Institute for Marine Biology and Coastal Research, Milwaukee, Wisconsin and Columbia, South Carolina respectively.
- Selgeby, J.H., Bronte, C.R., and Slade, J.W. 1994. Forage species. In The state of Lake Superior in 1992, M.J. Hansen, ed. Great Lakes Fisheries Commission Special Publication 94-1. Great Lakes Fishery Commission, Ann Arbor, MI.
- Sirois, P., Lecomte, F., and Dodson, J.J. 1998. An Otolith-based back-calculation method to account for time-varying growth rate in Rainbow Smelt (*Osmerus*

mordax) larvae. Canadian Journal of Fisheries and Aquatic Sciences. 55:2662-2671.

Sitar, S., Bronte, C., Ebener, M., Fratt, T., Gebhardt, K., Halpern, T., Mattes, B., Mensch, G., Petzold, M., Schram, S., and Schreiner, D. 2000. Status of Lake Trout in Lake Superior 1993-2000. Special Report: Great Lakes Fisheries Commission, Ann Arbor, MI.

Walsh, M.G., Maloy, A.P., and O'Brien, T.P. 2008. Comparison of Rainbow Smelt age estimates from fin rays and otoliths. North American Journal of Fisheries Management. 28:42-49.

Wilberg, M.J., and Hansen, M.J. 2003. Historic and modern abundance of wild Lean Lake Trout in Michigan waters of Lake Superior: Implications for restoration goals. North American Journal of Fisheries Management. 23:100-108.