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Comparison of Scales, Pectoral Fin Rays, and Otoliths for Estimating Age, Growth, and Mortality of Lake Whitefish, *Coregonus clupeaformis*, in Great Slave Lake

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Foreword

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ABSTRACT

It has been well documented that otoliths are the preferred hard structure for estimating the age of Coregonids. Additionally, the slower growth due to short growing seasons experienced in populations from the sub-arctic may alter the utility of alternative, non-lethal structures for estimating ages. In this study, scales, pectoral fin rays and otoliths from Great Slave Lake (GSL) Lake Whitefish *Coregonus clupeaformis* (Mitchill, 1818) were compared for differences in processing time efficiency, annular assignments, precision biases and reader uncertainty.

Among the three ageing structures, pectoral fin rays took longest to process followed by scales and then otoliths. Readers' confidence was highest for otoliths, followed by pectoral fin rays and then scales. Annuli in ground and baked otoliths appeared as dark, narrow lines with regular spacing; however, annuli in pectoral fin rays and scales were more variable in appearance. Readings of pectoral fin rays had the highest and largest uncertainty while readings of otoliths had the lowest uncertainty. Within-reader precision was highest for age estimates from otoliths, followed by scales and pectoral fin ray sections. Reader confidence, within reader precision and age estimates themselves, were all affected by age structure and age class.

Pairwise comparisons between age estimates from otoliths and scales, and otoliths and pectoral fin rays found no significant differences when fish were younger than 10 and 12 years, respectively, suggesting that these non-lethal structures could be conservatively used to reliably estimate ages of younger (<10 years) and smaller (≤300 mm) Lake Whitefish.

Derived estimates of growth and total mortality for Lake Whitefish in GSL varied significantly among ageing structures. Mean length-at-age based on otoliths ages was significantly lower than that based on scale ages. Of particular significance is that divergence between scale and otolith age estimates is delayed by 5–6 years relative to more southern populations, and in contrast to southern examples, fin rays do not offer a suitable non-lethal alternative for estimating ages of older Lake Whitefish (>11 years).

Comparaison des écailles, rayons des nageoires pectorales et otolithes dans l'estimation de l'âge, la croissance et la mortalité du grand corégone (*Coregonus clupeaformis*) dans le Grand lac des Esclaves

RÉSUMÉ

Il est bien établi que les otolithes sont les structures dures privilégiées pour l'estimation de l'âge des corégonidés. De plus, la croissance plus lente découlant des courtes saisons de croissance que l'on retrouve chez les populations subarctiques peut affecter l'utilité d'autres structures non létales pour l'estimation de l'âge. Dans la présente étude, les écailles, les nageoires pectorales et les otolithes du grand corégone du Grand lac des Esclaves (GLE) (*Coregonus clupeaformis*) (Mitchill 1818) ont été comparés pour relever les différences dans le traitement de l'efficience du temps, des attributions annulaires, des biais dans la précision et de l'incertitude du lecteur.

Parmi les trois structures pour la détermination de l'âge, les rayons des nageoires pectorales ont demandé le plus de temps à traiter, suivis des écailles et des otolithes. La confiance du lecteur est la plus élevée à l'égard des otolithes, suivis des rayons des nageoires pectorales, puis des écailles. Les anneaux annuels dans les otolithes broyés et cuits forment des lignes sombres et étroites à intervalles réguliers; par contre, dans les rayons des nageoires pectorales et les écailles, l'apparence des anneaux variait davantage. La lecture des rayons des nageoires pectorales présentait l'incertitude la plus importante, alors que celle des otolithes présentait l'incertitude la plus faible. Le taux de précision d'une lecture à l'autre pour l'estimation de l'âge était au plus haut pour les otolithes, suivis des écailles et des rayons des nageoires pectorales. La confiance du lecteur, d'une lecture à l'autre et dans les estimations mêmes de l'âge est toujours influencée par la structure pour la détermination de l'âge et la classe d'âge.

Les comparaisons par paires entre les estimations d'âge faites sur les otolithes et les écailles, et entre les otolithes et les rayons des nageoires pectorales ne révèlent aucune différence importante pour les poissons âgés de moins de 10 et de 12 ans respectivement, ce qui suggère que ces structures non létales pourraient à l'inverse servir à établir une estimation fiable des corégones plus jeunes (<10 ans) et plus petits (≤300 mm).

Des estimations calculées de la croissance et de la mortalité totale du corégone dans le GLE varient de façon importante entre les structures de détermination de l'âge. La moyenne taille selon l'âge en fonction de l'âge des otolithes est beaucoup plus petite qu'en fonction de l'âge des écailles. Il est particulièrement intéressant de noter que l'écart entre les estimations de l'âge des écailles et celles des otolithes atteint jusqu'à 5 ou 6 ans comparativement aux populations plus au sud, et par rapport à celles-ci, les rayons des nageoires pectorales n'offrent pas une solution non létale convenable dans l'estimation de l'âge des corégones plus âgés (>11 ans).

INTRODUCTION

Age estimation is key to assessing stanza-based demographic population attributes such as growth, survival, mortality and recruitment against variable population density, prey supplies and exploitation, as well as for constructing age-structured population models (Ricker 1975; Beamish and McFarlane 1983; Weatherley and Gill 1987). Given the importance of age determination in fisheries studies, age estimates are conventionally based on natural marks on continually mineralized structures, taking into account variations in a series of behavioural and physiological processes of fishes (Simkiss 1974; Brett 1979; Maceina et al. 2007).

Among fish ageing structures, scales have remained popular for Esocids, Centrarchids and Moronids because they are easy to remove and their removal causes little damage to the fish (Hogman 1968, Maceina et al. 2007). However, ageing with fish scales does have disadvantages. Many fish have the ability to re-absorb scales, referred to as the “Crichton effect” (Simkiss 1974), or regenerate them after being damaged or removed, resulting in growth patterns that do not accurately reflect the time span of a fish’s life (DeVries and Frie 1996; Schram and Fabrizio 1998). As well, scales from long-lived salmonid species such as Lake Trout Salvelinus namaycush (Schram and Fabrizio 1998), Bull Trout Salvelinus confluentus (Zymonas and McMahon 2009) and Inconnu Stenodus leucichthys (Howland et al. 2004) are very difficult to interpret, resulting in significantly lower age estimates, confidence and readers agreement than with otoliths and fin rays (Ihde and Chittenden Jr. 2002). In some cases, bony structures such as pectoral fin rays of Alligator Gar Atractosteus spatula (Buckmeier et al. 2012) and African Sharptooth Catfish Clarias gariepinus (Khan et al. 2011), and pelvic fin rays of Inconnu (Howland et al. 2004) have provided better alternative non-lethal structures for these long-lived species. Removal of fin spines and rays does not require sacrificing the fish, while removal of other structures such as opercular bones, cleithra, dentary bones and vertebrae does. Also both fin rays and otoliths usually need to be appropriately prepared before being examined for age. Calcified otoliths have become one of the most preferred structures for ageing fish, and are extensively used for a great number of freshwater and marine fishes worldwide (Pannella 1974; Weatherley and Gill 1987; DeVries and Frie 1996), but the fish studied must be sacrificed. As ageing techniques have advanced, age reading methods have evolved from mainly single structure to multiple structure comparisons to determine the most suitable structures for a particular species or population (Howland et al. 2004; Zymonas and McMahon 2009; Khan et al. 2011; Buckmeier et al. 2012).

Lake Whitefish is a commonly exploited coldwater salmonid that is extensively distributed in North American freshwaters from Atlantic coastal watersheds, westward and northward across Canada and Alaska (Scott and Crossman 1998). Van Oosten (1923) first demonstrated the applicability of scales for ageing known-age Lake Whitefish in aquaria. Since then, many age and growth studies of this species have been carried out based on different ageing structures, including scales (Mills and Beamish 1980; Barnes and Power 1984; Mills and Chalanchuk 2004), otoliths (Barnes and Power 1984; Skurdal et al. 1985; Muir et al. 2008a, b) and pectoral or pelvic fin rays (Mills and Beamish 1980, Barnes and Power 1984, Mills and Chalanchuk 2004, Muir et al. 2008b). Subsequent comparisons among ageing structures for Lake Whitefish have shown that:

1) fin rays are more reliable than scales (Mills and Beamish 1980; Barnes and Power 1984; Mills and Chalanchuk 2004, Muir et al. 2008b),
2) scales result in considerable under-estimates of ages compared to otoliths (Barnes and Power 1984; Skurdal et al. 1985; Muir et al. 2008a,b, Herbst and Marsden 2011),

3) fin ray and otolith ages are not significantly different (Mills and Chalanchuk 2004, Muir et al. 2008b), and
4) otoliths are the most precise ageing material (Herbst and Marsden 2011).

Furthermore, Mills and Chalanchuk (2004) validated pelvic fin ray section ages for Lake Whitefish, and since they and others found no significant difference between fin ray and otolith section ages, indirectly validated the otolith section method. Since the break and burn method with otoliths is considered to be the functional equivalent of the otolith section method (Campana et al. 2008), one can infer that the break and burn method has also been indirectly validated for Lake Whitefish.

Although several studies unanimously indicate the importance of ageing comparisons for southern populations of Lake Whitefish, if possible, comparable studies have not been conducted in more oligotrophic, sub-arctic boreal environments (i.e., greater than 50°N latitude) where Lake Whitefish are expected to have greater longevity and reduced growth (Power 1978; Morin et al. 1982). Annuli on ageing structures from slower growing northern stocks are expected to begin condensing at a younger age, thus extending the crowded area in long-lived populations. Previous studies have shown that crowding of annuli at the edges of ageing structures can lead to difficulties in interpretation and often underestimates of ages, particularly in older fish (Power 1978, Mill and Beamish 1980). Thus, we hypothesize this could lead to greater under-ageing from scales and possible under-ageing from fin ray sections beyond a certain age in northern Lake Whitefish populations. There are consequences of under-ageing to the assessment of fisheries when age structured models are used to inform quota management since all aspects of stock productivity and mortality require reliable estimates of age. For example, individual growth rates and estimates of the rate of increase in biomass are based on age determination. The age at sexual maturity is important in considerations of recruitment overfishing and in general mortality estimates when partitioned between instantaneous fishing mortality (F) and instantaneous natural mortality (M), and is especially influenced by the precision of estimates of the number of older-aged fish. Estimates of F are used directly to determine appropriate sustainable quotas.

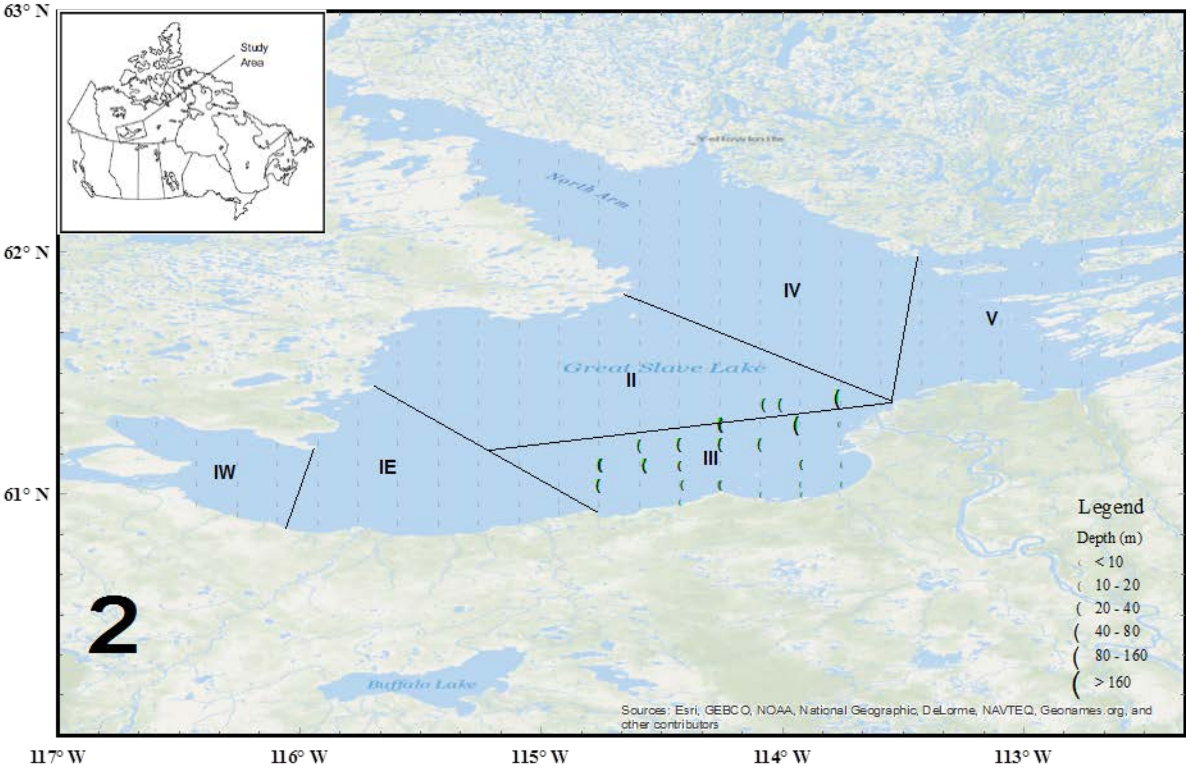
Great Slave Lake (GSL) is the second largest lake in Canada and the deepest lake in North America. Since the 1950s, GSL has sustained the largest commercial and Aboriginal freshwater fisheries for Lake Whitefish in the Northwest Territories, Canada. To monitor and manage whitefish fishery production, age and growth studies based on scale readings have constituted an important component of routine data collection since 1972 (Read and Taptuna 2003). The objectives of this study were to describe and quantify the variation in age estimates from scales, pectoral fin rays and otoliths of Lake Whitefish in GSL and to evaluate the potential effects of this variation on estimates of age-dependent parameters of growth and mortality. It is important to incorporate these quantitative estimates when constructing age-structured models for assessing the sustainability of Arctic fisheries resources that are harvested for commercial and Aboriginal subsistence uses. In particular, we are concerned with three different aspects of Lake Whitefish age and growth-related analyses:

1) which is the best ageing structure among scales, pectoral fin rays and otoliths,
2) If there are discrepancies among ageing structures, at what age do the discrepancies appear, and
3) what are the ageing precision and uncertainty, and the consequent confidence in age estimates derived from each of these ageing structures?

MATERIALS AND METHODS

COLLECTION OF FISH

Between 10 July and 15 August, 2012, a total of 307 Lake Whitefish were sampled using 32 bottom-set experimental gillnets. The nets were deployed in the shallower Resolution Bay area of GSL (latitude 60°52.5′ to 61°22.5′ N, longitude 113°35′ to 114°5′ W) using a random depth-stratified sampling design (Figure 1). In order to include as many size classes as possible, we used multi-mesh gillnets consisting of ten panels with mesh sizes ranging from 13 to 140 mm knot to knot stretched, clear monofilament. Each net was deployed for 18–30 hours to cover day and night periods (Zhu et al. unpubl. rep.). All captured Lake Whitefish were sacrificed and then measured for fork length (mm) and weight (g). Several scales (10–20) were removed from the area of the body ventral to the anterior edge of the dorsal fin and above the lateral line. One or two left leading pectoral fin rays were cut off as close to the body as possible using bone cutters. Sagittal otoliths were extracted using bone cutters and forceps. All structures were deposited into labeled scale envelopes and air dried.



Sources: Esri, GEBCO, NOAA, National Geographic, DeLorme, NAVTEQ, Geonames.org, and other contributors

Figure 1. Map showing sampling locations and fisheries management areas in the main basin of GSL, Northwest Territories. The size of each green dot refers to the depth class, as detailed in the legend. Grey dots are the centers of coordinates by 5-min latitude and 10-min longitude grids.

PREPARATION OF ANATOMICAL STRUCTURES

Scales were cleaned with distilled water and air dried prior to being impressed into acetate plastic slides. To prepare scales for reading, four to five non resorptive scales were placed in a consistent orientation with the external surface facing up on a clean acetate slide. The slide was then passed through an Ann Arbor™ Roller Press (Muir et al. 2008b). For age estimates, the acetate slide was placed impression side up in a Realist Vantage 5 microfiche reader equipped with a 43–51× magnifying lens.

Pectoral fin ray samples were trimmed, set in ColdCure epoxy (Industrial Formulators of Canada Ltd.) and cut into transverse cross-sections using a Buehler ® Isomet™ (Lake Bluff, IL, USA) low speed saw equipped with a 10.16 × 0.012 mm diamond waffering blade. At least three consecutive sections approximately 0.35 mm thick were cut; the first section comprised the most proximal portion of the fin ray. Sections were air-dried and then affixed to labelled slides in sequential order using CytosealTM 280 mounting medium and a cover slip. Pectoral fin ray sections were viewed under reflected light with a dissecting microscope (20–80x).

Otoliths were processed by applying a modified version of the "break and burn" techniques of Christensen (1964) and Power (1978), referred to here as the "grind and bake" technique. On the distal surface, the nucleus of the otolith was marked under a dissecting microscope using an ultra-fine point Sharpie® marker. The marked otolith was then placed on a paper towel and broken slightly anterior to the nucleus along the transverse plane by repeatedly scoring it with an X-acto® knife. The broken surface of the posterior otolith piece was then ground down to the center of the nucleus, maintaining the transverse section plane, using a Foredom® bench lathe (Fordom Electric Co., Bethel CT., USA) fitted with a 19 x 19 × 3 mm (shaft) cylindrical felt bob (medium hardness) wrapped with a strip of 30 μm adhesive-backed lapping film (3M, St. Paul, MN., USA). While grinding, rubber-tipped forceps were used to secure each otolith and care was taken to ensure the anterior-posterior axis of the otolith was held perpendicular to the felt bob. This grind was best done while viewing through a 2.25x magnifying LED ring lamp. This grind step has proven to be quite advantageous when working on otoliths from long-lived, slowing growing Arctic fish species that have outer annuli that are very close together. The grind is consistent to the middle of the nucleus and the ground surface is smooth, resulting in even bakes. After a number of otolith grinds were prepared, they were baked one at a time, sulcus side up, on a Fisher Thermix® hot plate (Fisher Scientific, USA) set at the hottest setting (approx. 400oC). Each bake took 10 to 30 seconds, depending on the size of the otolith piece. The otoliths were baked until a dark brown colour was achieved, then quick-cooled in water. The otolith half was then observed by mounting it in a modelling clay base with the ground surface facing up in a small Petri dish of water. Enough water must be present to cover the otolith half. Otoliths were viewed with a dissecting microscope and reflected light at 20–80x magnification. Usually the best viewing zone for ageing Lake Whitefish otoliths is the ventral side, close to the sulcus.

AGE ESTIMATION

Age samples were examined by independent readers without knowledge of fish size or capture location to minimize observation bias (Casselman 1983). Age estimates from the three calcified structures were carried out by four independent readers in two ageing laboratories. Readings of pectoral fin rays, scales and otoliths were carried out by three independent readers (one reader for each structure) at DFO, Freshwater Institute, Winnipeg, Manitoba; one additional scale reading was conducted by the Ontario Ministry of Natural Resources (as of 2014 the Ontario Ministry of Natural Resources and Forestry, OMNRF) in Dryden, Ontario. For each fish, each ageing structure was read three separate times by each of the individual readers. Reader confidence was assigned a confidence ranking of 1 (very uncertain), 3 (uncertain), 5 (moderately confident), 7 (confident) or 9 (certain), as recommended by Casselman (1983).

Annuli on scales were determined primarily by "cutting over" or breaks in circuli (Lagler 1952) where a completed circulus or ridge forms past the unfinished endpoints of one or more incomplete circuli in both lateral fields of the scale (Jearld 1983). The presumptive annual marks on scales were generally identified by;

1) the origin of multiple secondary radii,
2) a clear, narrow zone in the anterior field, and
3) an additional ridge in the posterior field of the scale in presumably older fish.

An annulus was considered to consist of one wide opaque (light) band and an adjacent narrower hyaline (dark) band (DeVries and Frie 1996; Beamish and McFarlane 2000) (see Figure 2). Separation of annuli near the outer edges of fin ray sections and otolith grinds with more than 10 annuli often required higher magnification (≥60x) and changes in the viewing angle. For simplicity, age estimates derived from otoliths, pectoral fin rays and scales are referred to here as otolith-ages, fin-ray-ages and scale-ages, respectively.

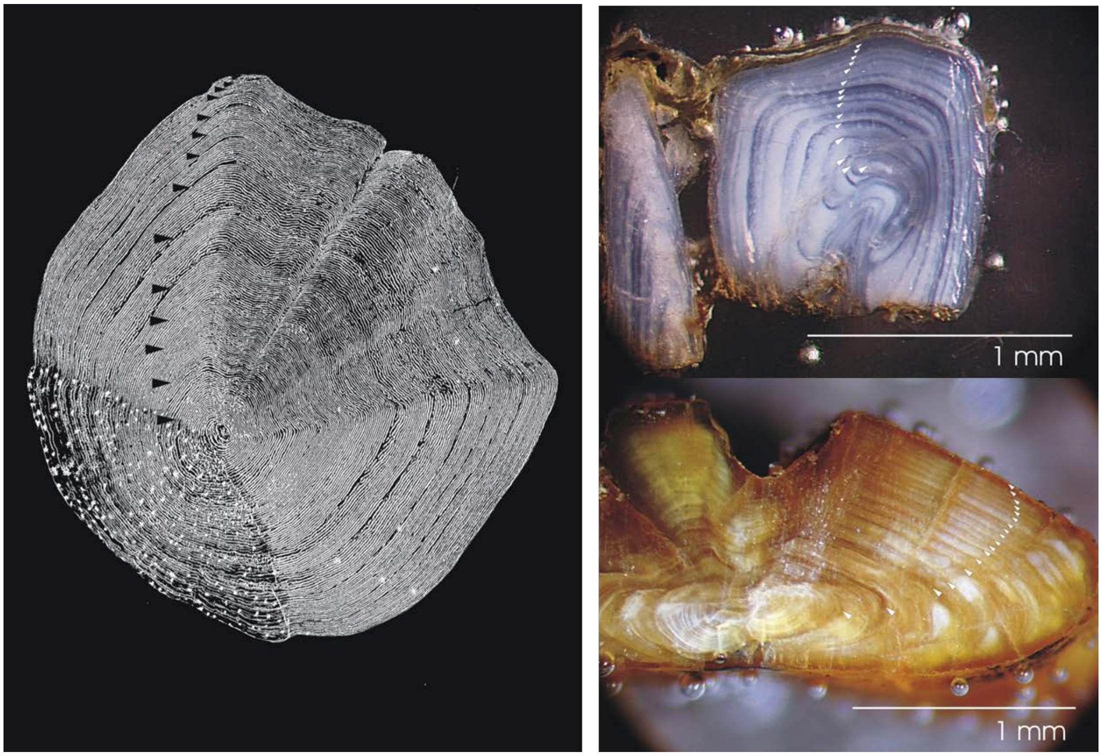


Figure 2. Comparisons of age estimates from a scale (left), pectoral fin ray section (right top) and ground and baked otolith (right bottom) from the same Lake Whitefish from Great Slave Lake, 2012. The fish was a mature male, 411 mm FL and 990 g round weight, scale-age 14, fin-ray-age 15 and otolith-age 18.

STATISTICAL ANALYSIS

Precision is defined as the reproducibility of repeated measurements on a given structure, regardless of whether or not those measurements are accurate (Campana 2001). There are three widely used statistically sound measures of ageing precision: average percent error (*APE*), coefficient of variation (*CV*) and percent agreement (*PA*) between readers and among ageing structures (Campana 2001; Gregg et al. 2006; Muir et al. 2008). To calculate APE we used the formula presented by Beamish and Fournier (1981),

$$APE_j = \frac{1}{R}\sum_{i=1}^{R}\frac{|x_{ij} - x_{j\cdot}|}{x_{j\cdot}} \times 100\%$$

where xij is the ith age determination of the jth fish, xj. is the mean age estimate of the jth fish, and R is the number of times each fish is aged. When averaged across many fish, it becomes an index of average percent error. Chang (1982) agreed that APE was a substantial improvement over PA, but suggested that the standard deviation be substituted for the absolute deviation from the mean age. An estimate of CV was expressed as a ratio of the standard deviation over the mean (Campana 2001),

$$CV_j = \frac{\sqrt{\sum_{i=1}^{R} \frac{\left(x_{ij} - x_{j\cdot}\right)^2}{R-1}}}{x_{j\cdot}} \times 100\%$$

where, CV_j is the age precision estimate for the j^{th} fish. As with the equation for APE_j, it can be averaged across fish to produce a mean *CV*. The index of precision (*D*) is similar to the *CV*, calculated as (Chang 1982),

$$D_j = \frac{CV_j}{\sqrt{R}}$$

One-way ANOVA was employed to:

1) compare reader confidence, precision and age estimates between ageing structures at different ages,
2) analyze among-read variation among ageing structures, and
3) compare age estimates among ageing structures within fork length groups.

Linear regression analysis was then used to assess the relationship between reader confidence and estimated age, while Bonferroni multiple range tests were used to assess how age estimates varied with either ageing structure or age class (Zar 2010). A *t*-test was used to test the null hypothesis that the slope (β) of the linear regression of the counts for the paired ageing structures equaled the coefficient of determination, r^2, which quantifies the amount of variation in *y* associated with variation in *x, y*=α+β*x*. A paired *t*-test was applied to the null hypothesis that the difference between annulus counts between structures is zero and a test of symmetry was used to test the null hypothesis that there is no symmetric difference in annulus counts between the two ageing structures (Hoenig et al. 1995). For all comparisons of annulus counts between ageing structures we made the assumption that ground and baked otolith-ages were accurate, as was determined by previous comparative studies on Lake Whitefish age estimates (Barnes and Power 1984; Skurdal et al. 1985; Muir et al. 2008; Herbst and Marsden 2011). Prior to statistical analyses, the CV data were log transformed. For all statistical analyses differences between pairs of variables were considered significant at a probability level of $\alpha = 0.05$.

Length-at-age from each ageing structure was fit to a von Bertalanffy growth model by non-linear automatic differentiation model builder (ADMB). Instantaneous total mortality (*Z*) was estimated using the slope of a linear regression between log-transformed abundance and ages through a descending limb of scale-, pectoral fin ray-, and otolith-based catch curves (Ricker 1975). All statistical analyses were conducted with Stata version 11 .

RESULTS

SAMPLE SIZE

The fork lengths of fish sampled ranged from 125 to 510 mm with an arithmetic mean of 346.09 ± 4.37 mm, and the round weight ranged from 26 to 2110 g with a mean of 640.03 ± 23.01 g. Of ten mesh-sized panels, samples from small mesh sizes (<51 mm or 2 inches) made up 18% while 82% of the catch was from large mesh sizes (51 to 140 mm or 2 to 5½ inches) (Table 1a). Samples from fork length group 350 to 450 mm accounted for >55% of samples analyzed, reflecting the current dominant length composition of Lake Whitefish in GSL. With respect to round weight, samples were evenly distributed across nine weight groups and 26% of individuals ranged between 625 and 875 g (Table 1b). The average sizes (fork length and round weight) of fish sampled were significantly related to mesh size (fork length: $r = 0.55$, $F = 135.15$, $p < 0.0001$; round weight: $r = 0.56$, $F = 136.31$, $p < 0.0001$), indicating an increase in fish size with mesh size.

Table 1a. Mesh size-specific sample size related to fork length (mm) measurements of Lake Whitefish collected through a fishery-independent gillnet study in the southern part of GSL.

Mesh size (mm)	Fork length (mm)							
	100	200	300	400	500	Total	Mean	SE
13		1				1	217	-
19		1				1	214	-
25	1	1	1			3	243	58
32	2	6	6	9		23	285	22
38		11	9	6		26	275	15
51		9	23	16	1	49	319	11
64		1	38	28		67	337	7
89		1	12	60	1	74	379	5
114			9	39	3	51	390	7
140				11	1	12	432	6
Total	3	31	98	169	6	307	346	4

Table 1b. Mesh size-specific sample size related to round weight (g) measurements of Lake Whitefish collected through a fishery-independent gillnet study in the southern part of GSL.

Mesh size (mm)	Round weight (g)										
	50	250	500	750	1000	1250	1500	1750	2000	n	Mean	SE
13	1									1	95	-
19	1									1	90	-
25	1	1	1							3	225	140
32	8	4	3	5	3					23	422	77
38	9	10	1	3	3					26	328	61
51	3	25	7	2	7	4		1		49	490	58
64		30	12	13	10	2				67	537	40

Mesh size (mm)	Round weight (g)											
	50	250	500	750	1000	1250	1500	1750	2000	n	Mean	SE
89	1	5	15	36	12	4	1			74	758	30
114		6	2	20	12	4	5	1	1	51	898	54
140				1	2	5	3	1		12	1294	69
Total	24	81	41	80	49	19	9	3	1	307	640	23

CHARACTERISTICS OF AGEING STRUCTURES

Scales showed presumed annular marks that often were clear and well defined (Figure 2). However, various inconsistencies often made scales difficult to read and interpret visually. One type of inconsistency in scale marks was the appearance of some degree of “cutting over”, which was present in one lateral field of an individual scale but lacking on the opposite lateral field. In a second type of inconsistency, a well-defined mark was evident on one scale but not on a neighboring scale of the same fish.

Pectoral fin ray sections were very tiny structures, and annular marks were often difficult to read and interpret visually (Figure 2). These marks seemed to indicate age, but early marks were sometimes obscured or consumed by the vascular core of the fin rays. When reading the fin ray sections, the reader indicated that as time went on and more samples were completed, there was a tendency to start counting an extra annulus very near the core that was not perceived to be an annulus in earlier reads. Outer marks were visible only under high magnification and even then were faint and difficult to read. Irregular and unexpected spacing of annuli on the fin ray sections was also a problem. This may be an indication of resorption occurring at different rates in different years for this population.

In comparison, ground and baked otolith sections were of moderate size. Their presumed annual marks were of consistent strength and regular spacing which made them easier to read. The characteristics of different ageing structures of fish were compared in Figure 2, which shows respective annulus counts from scales (14 years old), pectoral fin ray sections (15 years) and otoliths (18 years) of the same fish.

EVALUATION OF PROCESSING TIME AND READER’S CONFIDENCE

Processing time varied greatly among ageing structures. Processing pectoral fin ray sections took 3.23 times longer than the time required for pressing scales into acetate plastic slides, and 1.67 times longer than processing otoliths (Table 2). Read times for each structure were similar. The lowest average time was required for reading pectoral fin ray sections (2.35 min/fish), followed by scales (3.51 min/fish) and otoliths (3.91 min/fish).

Table 2. Time (minutes) used to process and read individual ageing structures as well as reader's confidence rankings for GSL Lake Whitefish.

		Ageing structure			
	Otolith		Fin ray		Scale
Marking	474	Preparing	136	Preparing	708
Grinding	756	Embedding	265		
Baking	135	Sectioning	1885		
Reading #1	1353		875		987
Reading #2	1048		600		1005
Reading #3	922		520		985
Mean processing	4.82		8.08		2.50
Mean reading	3.91		2.35		3.51
		Reader's confidence			
Mean	5.70		5.59		5.47
SE	0.05		0.05		0.04
CV	23.02		24.15		21.85

Reader confidence varied greatly among ageing structures (Figure 3).

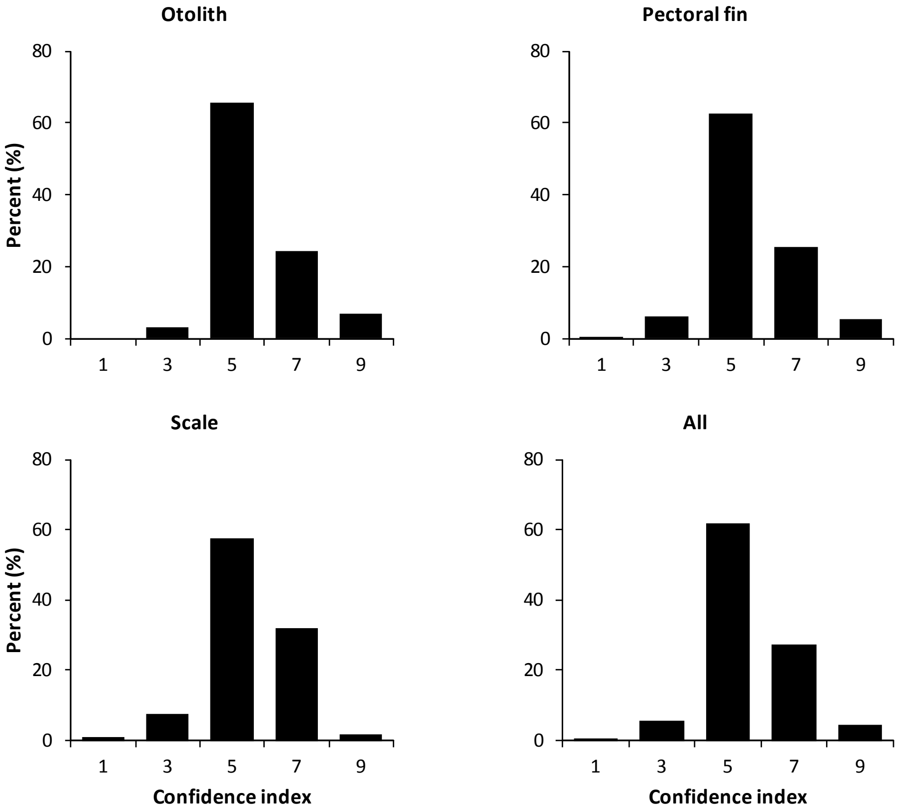


Figure 3. Confidence index percentages for respective ageing structures of GSL Lake Whitefish.

In terms of confidence rankings 1–9 (Casselman 2003), the higher the confidence ranking was, the more certain the reader was regarding what they were interpreting as annuli on the structure (Table 2). Two-way ANOVA results in Table 3a showed that confidence rankings differed significantly among ageing structures (*df*=2, *F*=3.91, *p*<0.0001) and with age class (*df*=16, *F*=11.23, *p*<0.0001), with a strong interaction between structure and age class (Table 3; *df*=32, *F*=3.43, *p*<0.0001). However, there was no significant difference among replicate reads (*df*=2, *F*=2.86, *p*=0.06) and no interaction between read and age class (*df*=32, *F*=1.16, *p*=0.25). Reader's confidence varied among the ageing structures, being highest for ground and baked otoliths (mean ± SE: 5.70 ± 0.05), moderate for sectioned pectoral fin ray sections (5.59 ± 0.05) and lowest for scales (5.47 ± 0.04). Overall, the reading confidence was at the moderate level (5.60 ± 0.03) for all three ageing structures combined. Using Bonferroni multiple comparison tests, no significant differences were found in the confidence rankings between otoliths and pectoral fin rays (*p*=0.24) or between pectoral fin rays and scales (*p*=0.97), but the difference between otoliths and scales was statistically significant (*p*<0.05).

Table 3. Results of multifactorial two-way analysis of variance (ANOVA) identifying factors that influenced a) reader confidence, b) within reader precision and c) age estimates for Lake Whitefish in the southern part of Great Slave Lake in 2012. The factors analyzed included age class (2–18), ageing structure (otolith, pectoral fin ray, and scale) and read (1st, 2^{nd}, 3rd).

Source	*df*	*F*	*p*
a) Reader confidence			
Age class	16	11.23	<0.0001
Ageing structure	2	3.19	<0.0001
Read	2	2.86	0.0574
Age class X ageing structure	32	3.43	<0.0001
Age class X read	32	1.16	0.2506
Read X ageing structure	4	9.44	<0.0001
Age class X ageing structure X read	62	1.42	0.0172
b) Within Reader Precision			
Age class	16	0.63	0.8637
Ageing structure	2	4.14	0.0163
Age class X ageing structure	32	1.55	0.0284
c) Age estimates			
Ageing structure	2	23.16	<0.0001
Read	2	3.57	0.0284
Ageing structure X Read	4	0.93	0.4432

PRECISION AND UNCERTAINTIES

Precision and uncertainty for age estimates were evaluated by means of APE, CV and D with respect to comparing the three ageing structures. Two-way ANOVA results in Table 3b showed that reader precision was strongly impacted by ageing structure (df=2, F=4.14, p<0.02) as well as the interaction between ageing structure and age class (df=32, F=1.55, p<0.03). Age class seemed to have no significant influence on reader precision (df=16, F=0.63, p=0.86). Among-read *APE*, *CV* and *D* were all highest for pectoral fin rays, followed by otoliths and scales (Table 4). Bonferroni multiple comparison tests revealed that among ageing structures, *APE*, *CV* and *D* differed significantly between otoliths and pectoral fin rays (p<0.001) and between otoliths and scales (p<0.01). Fin-ray-ages did not differ significantly from scale-ages in *APE* (t=0.34, p=0.74) or *CV* (t=1.25, p=0.21).

Table 4. Summaries of average percent error (APE), coefficient of variation (CV) and index of precision (D) as well as pair-wise comparisons of APE between ageing structures of Lake Whitefish using a Bonferroni-corrected critical value, α=0.05.

Structure	*APE* (%)		*CV* (%)		*D*		Pair-wise comparison		
	Mean	SE	Mean	SE	Mean	SE	Otolith	Pectoral fin	Scale
Otolith	3.45	0.31	6.07	0.48	3.51	0.28	-	$p<0.001$	$p<0.01$
Pectoral fin	4.83	0.30	8.26	0.48	4.77	0.28	$t=3.46$	-	$p=0.74$
Scale	4.68	0.34	7.45	0.49	4.30	0.29	$t=2.78$	$t=0.34$	-

Consecutive reads of respective ageing structures were highly correlated ($r^2>0.98$ and slope $\beta>0.99$) (Figure 4), assuming the intercept was near zero. Compared with the second and third reads, the slopes were slightly greater in the latter, suggesting that higher ages were assigned by later reads, especially when reading pectoral fin ray sections.

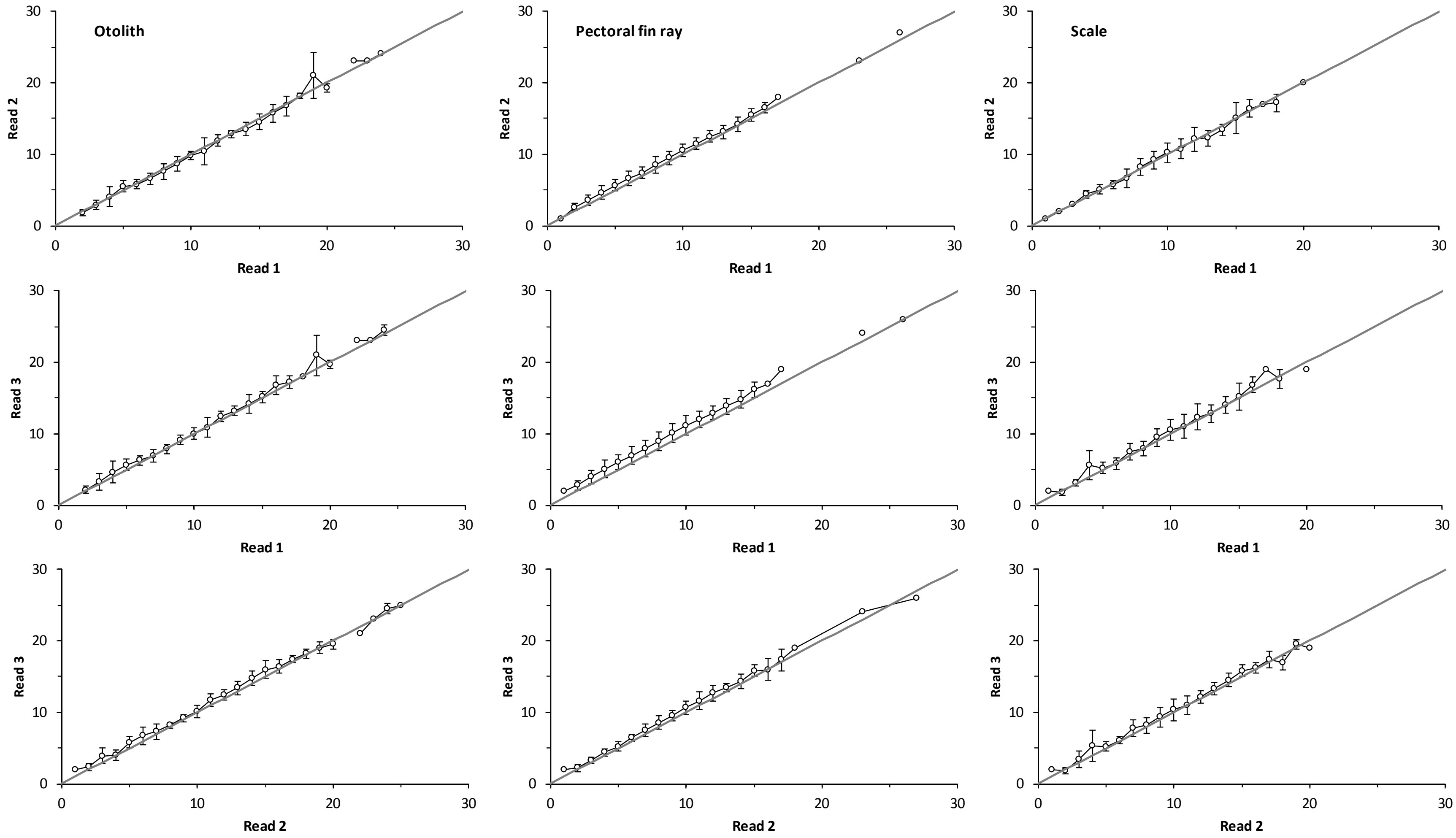


Figure 4. Age bias plots for two independent reads of GSL Lake Whitefish scales, pectoral fin rays and otoliths. Error bars represent one standard deviation. The 1:1 equivalence (solid) line is also included. Points above the line indicate overestimates, whereas points below the line represent under-estimates.

Under-estimated ages were identified in both pectoral fin rays and scales, compared to otolith readings. The counts between age reads differed in otoliths (*p*<0.005) and pectoral fin rays (*p*<0.001) (Table 5), but were similar for scale reads 1 and 2 (*t*=0.82, *p*=0.41).

Table 5. Readers' agreement between age estimates for different ageing structures for GSL Lake Whitefish, using pair-wise t-test.

	Otolith				Pectoral fin ray				Scale			
	Read 1		Read 2		Read 1		Read 2		Read 1		Read 2	
	t	*p*	*t*	*p*	*t*	*p*	*t*	*p*	*t*	*p*	*t*	*p*
Read 2	2.93	<0.005			9.31	<0.001			0.82	0.41		
Read 3	4.37	<0.001	8.41	<0.001	14.71	<0.001	9.65	<0.001	2.90	<0.005	4.36	<0.001

COMPARISON OF AGE ESTIMATES

Two-way ANOVA results in Table 3c revealed that age estimates were significantly influenced by ageing structure (*df*=2, *F*=23.16, *p*<0.0001) and marginally affected by reader (*df*=2, *F*=3.57, *p*=0.03) without a significant interaction between ageing structure and reader (*df*=4, *F*=0.93, *p*=0.44). Of the three ageing structures, age range was greatest from pectoral fin rays (1–27 years), followed by otolith readings (1–25 years) and scale readings (1–20 years) (Table 6; Figure 5). Eighteen percent of the fish were older than 15 in otolith-age, compared with 4% of fin-ray-ages and 7% of scale-ages. Despite the greatest age range being derived from pectoral fin ray readings, mean age was greatest from otolith readings (10.88 ± 0.16 years, CV=43%) and differed significantly between fin-ray-age (9.82 ± 0.13 years, CV=38%; *t*=9.67, *p*<0.001) and scale-age (9.66 ± 0.13 year, CV=40%; *t*=7.42, *p*<0.001). No significant difference in mean age was found between fin-ray-age and scale-age (*t*=1.45, *p*=0.15); age readings were similar between the two structures (Table 6).

Table 6. Comparison of age estimates by ageing structure and reader. The greatest average age was observed with otolith-age and the lowest with scale-age.

	Otolith				Pectoral fin ray				Scale			
	Range	Mean	SE	CV (%)	Range	Mean	SE	CV (%)	Range	Mean	SE	CV (%)
Read 1	2–24	10.86	0.27	42.42	1–26	9.33	0.22	39.65	1–20	9.59	0.22	39.03
Read 2	1–25	10.67	0.28	44.31	1–27	9.81	0.22	38.01	1–20	9.53	0.23	40.32
Read 3	2–25	11.11	0.28	42.71	2–26	10.33	0.23	37.30	1–20	9.82	0.23	40.13
Overall	1–25	10.88	0.16	43.11	1–27	9.82	0.13	38.47	1–20	9.66	0.13	39.81

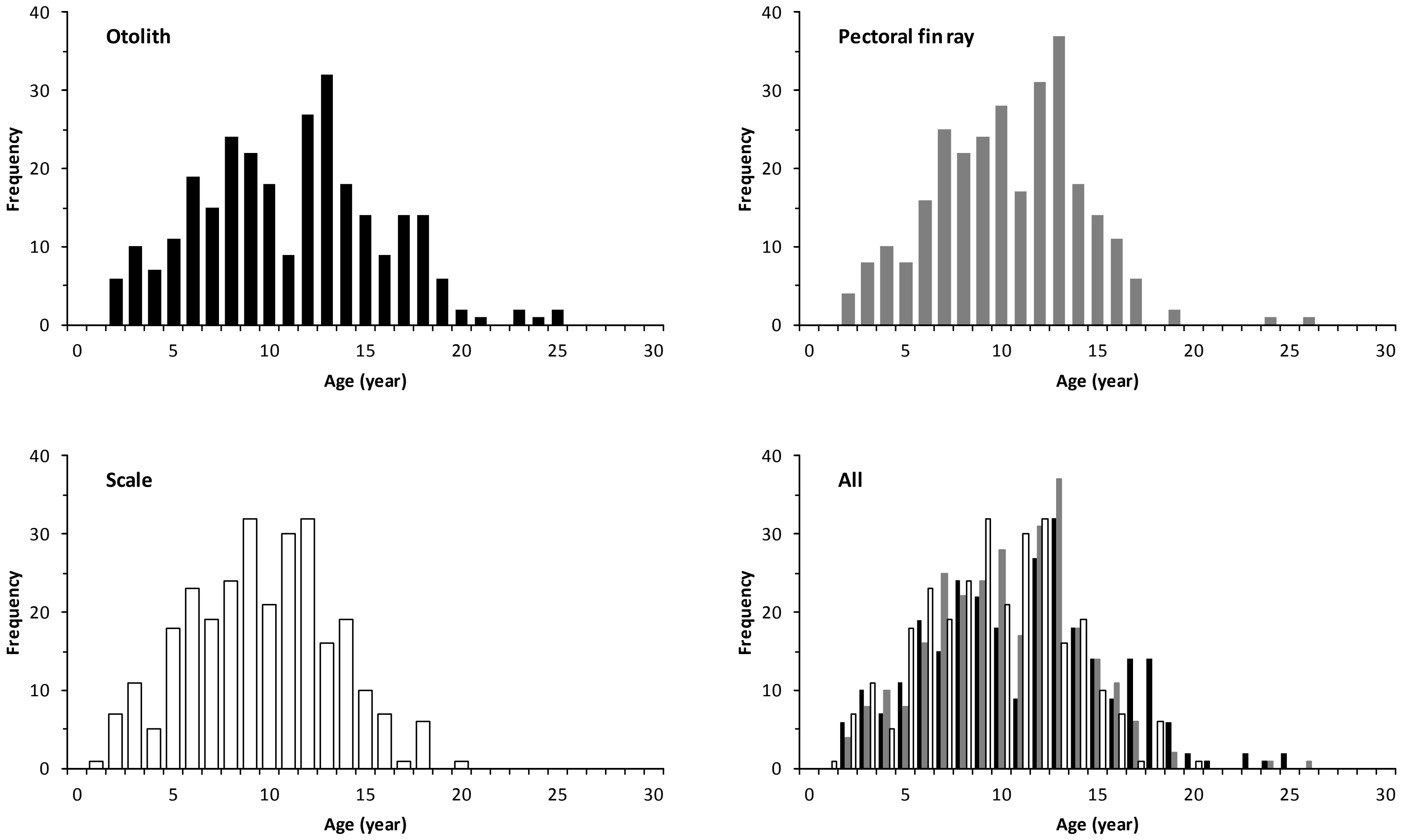


Figure 5. Comparison of age estimate frequencies obtained from three ageing structures of GSL Lake Whitefish. Open bars are for scale-age, grey bars for fin-ray-age and black solid bars for otolith-age.

Differences in age assignments for Lake Whitefish varied with the ageing structures and age classes (Figure 6). Box-Whisker plots demonstrate how changes in age discrepancies varied with respective age classes and between paired ageing structures. In comparison with fin-ray-age, otolith-age was not significantly different until otolith-age 12 (df=167, F=1.97, p=<0.01). Beginning at otolith-age 12, the difference between otolith- and fin-ray-ages increased linearly (slope β=0.38, r^2=0.29, F=57.79, p<0.001). In comparing otolith- and scale-ages, the ages were not significantly different until otolith-age 11 (df=140, F=0.88, p=0.55). From otolith-age 12 on there was a pronounced increase in the difference between otolith- and scale-ages (slope β=0.44, r^2=0.30, F=59.15, p<0.001). A significant difference between fin-ray- and scale-ages could also be detected from fin-ray-age 14 on (df=247, F=1.72, p=0.06) and increased linearly with age (slope β=0.49, r^2=0.21, F=8.63, p<0.01). Overall, ages of GSL Lake Whitefish estimated from pectoral fin rays or scales were underestimates relative to otolith-age and the level of disagreement increased linearly with age.

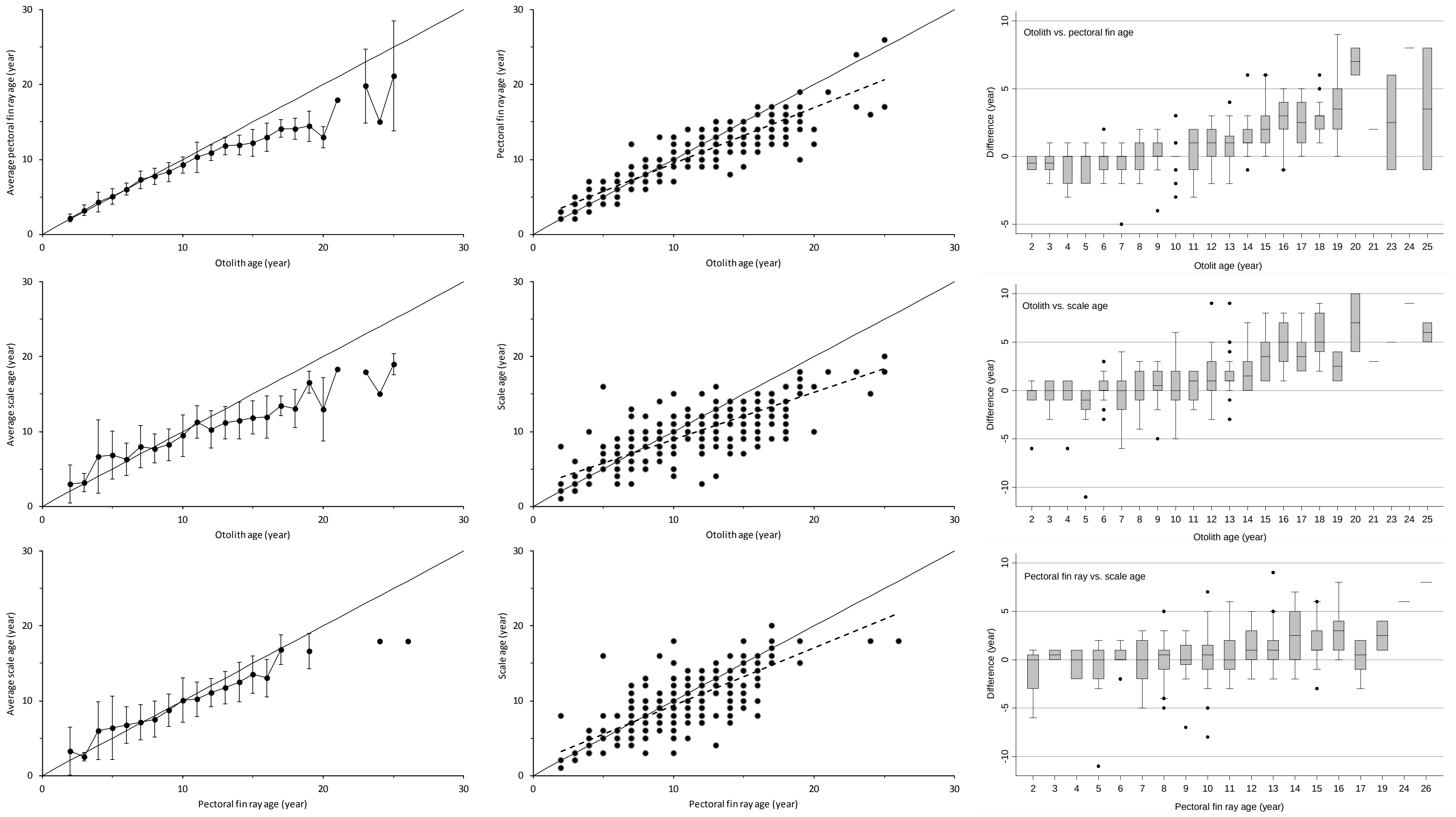


Figure 6. Paired comparison of age bias from the third reads with the average values of the individual structures (left), actual reads (middle), and box-and-whisker plots of age differences between age structures (right). Error bars are one standard deviation. Regression lines (broken) were added to fit the pairwise points and compare with 1:1 equivalence lines (solid line).

The age differences between otolith- and scale-age changed with fish size (Figure 7). Except length group 260 mm, the bias varied within ± 2 years and the mean differences were less than 1 year when fork length (FL) was less than 310 mm (Figure 7a). This suggests there were no age differences between otolith- and scale-ages when fish size was less than or equal to 300 mm FL (*df*=71, *F*=0.25, *p*=0.62). Beginning at length group 310 mm, the age difference increased linearly (*df*=210, *F*=8.58, *p*<0.005). Comparing otolith- and fin-ray-ages, the mean age difference was less than 1.0 when fish size was less than 340 mm FL (Figure 7b) and there were no significant differences between age estimates for fish less than 330 mm FL (*df*=116, *F*=2.66, *p*=0.11). A significant increase in age difference was identified for fish greater than 300 mm FL (*df*=210, *F*=17.67, *p*<0.001). We concluded that fish smaller than 300 mm FL can be aged using any of the ageing structures, scales, pectoral fin rays or otoliths, with equal reliability.

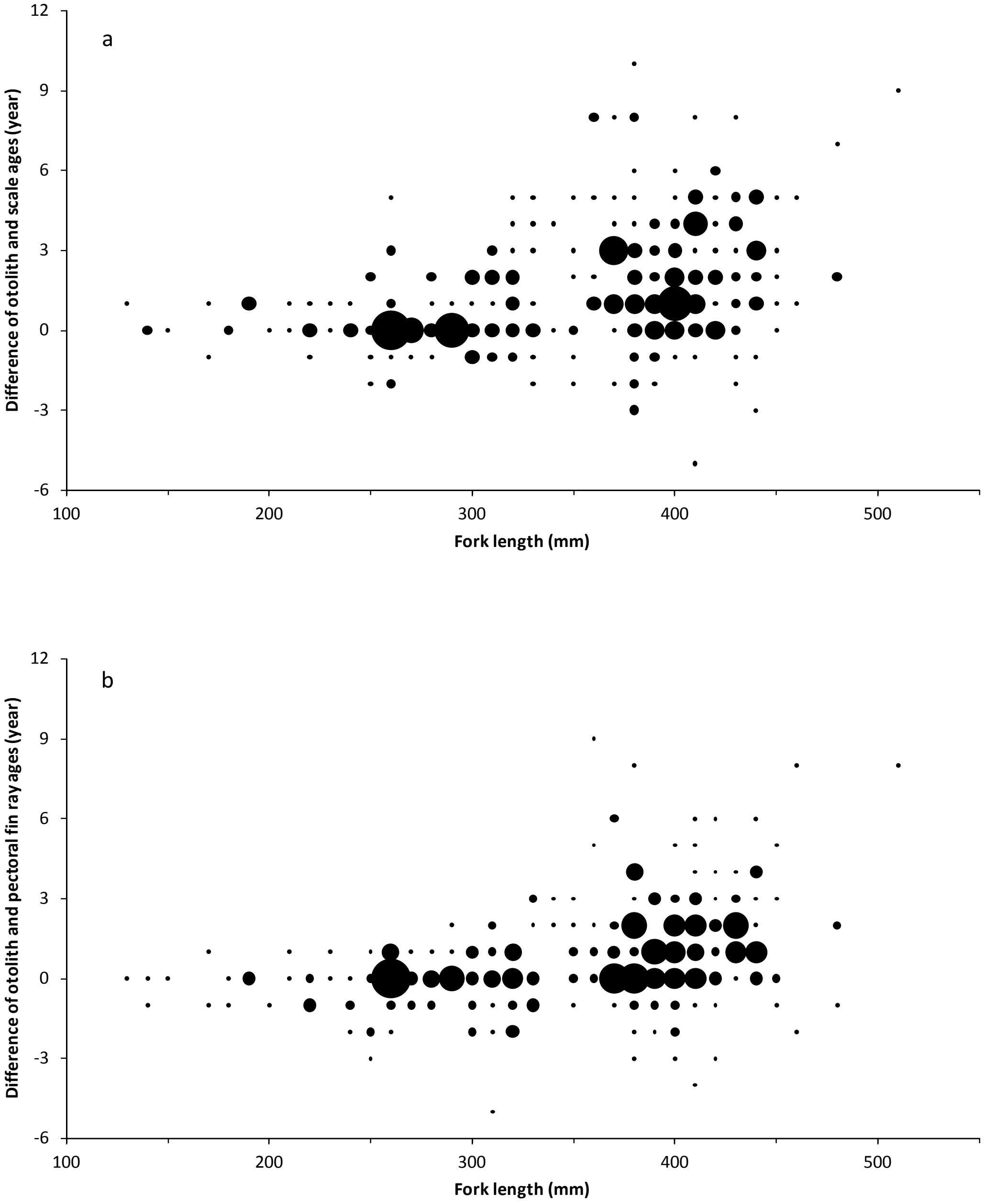


Figure 7. Relationships between FL and differences between otolith-age and scale-age (a) and otolith-age and fin-ray-age (b). For fish smaller than 300 mm FL, scales are suggested for ageing. Otoliths should be used to age fish greater than 300 mm FL.

EFFECTS OF RESPECTIVE AGEING STRUCTURES ON GROWTH AND MORTALITY

Lake Whitefish were estimated to enter the gillnet fishery at otolith-age 12 or fin-ray- or scale-age 11 (Figure 8). Otolith-based total mortality (*Z*), estimated from a catch curve (Ricker 1975), was 0.2154 per year, which was lower than both scale-based (*Z*=0.3625) and pectoral fin ray-based estimates (*Z*=0.6105).

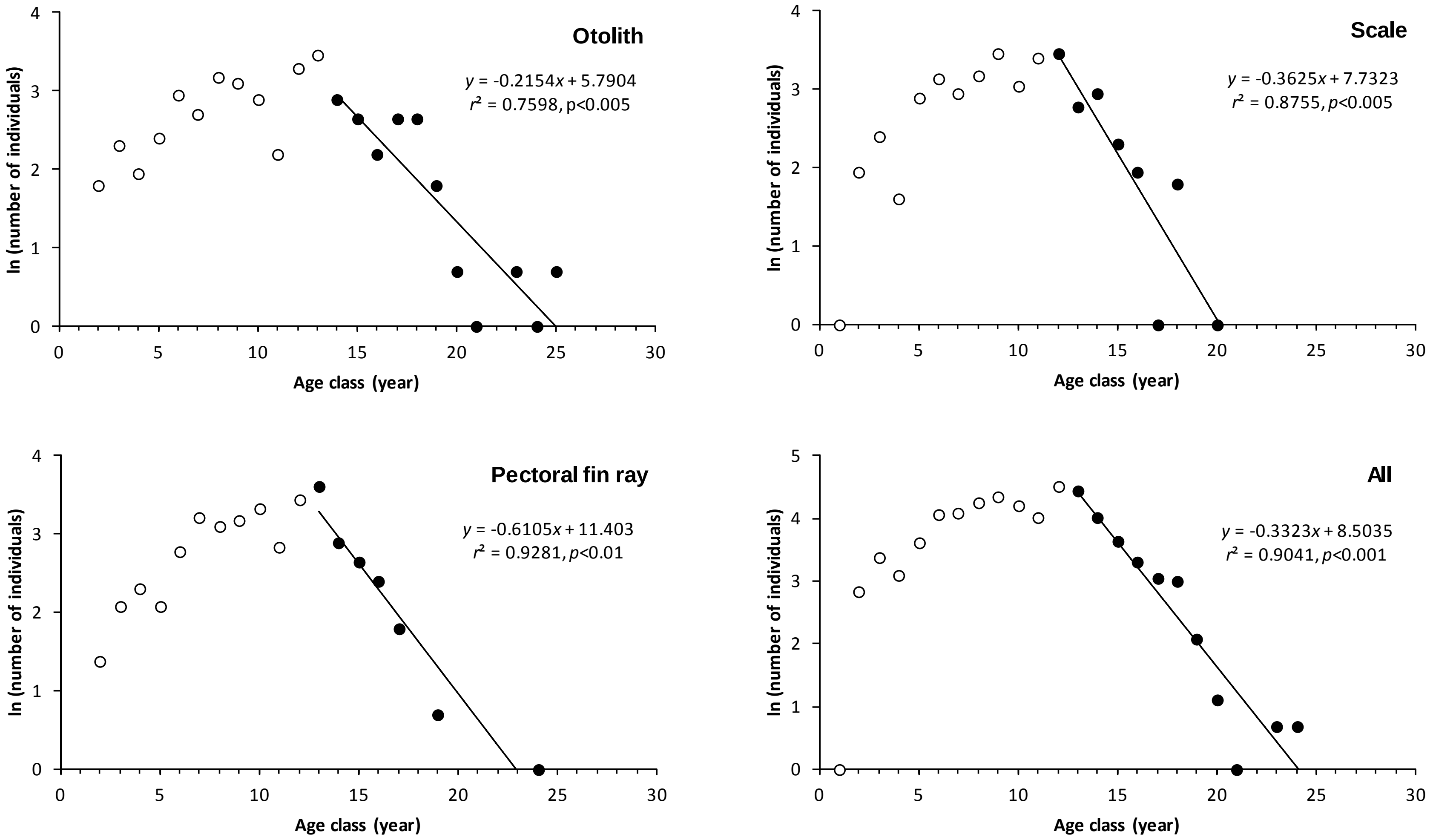


Figure 8. Catch curves for GSL Lake Whitefish based on scale-, fin-ray- or otolith-ages and all combined ages from fisheries independent gillnet studies in the southern part of GSL in 2012. Age at recruitment was 11 years for scale- and fin-ray-ages, and 12 years for otolith-age and pooled results.

The average structure-specific length-at-age values were smoothed using ADMB to fit a non-linear von Bertalanffy growth model for GSL Lake Whitefish (Figure 9).

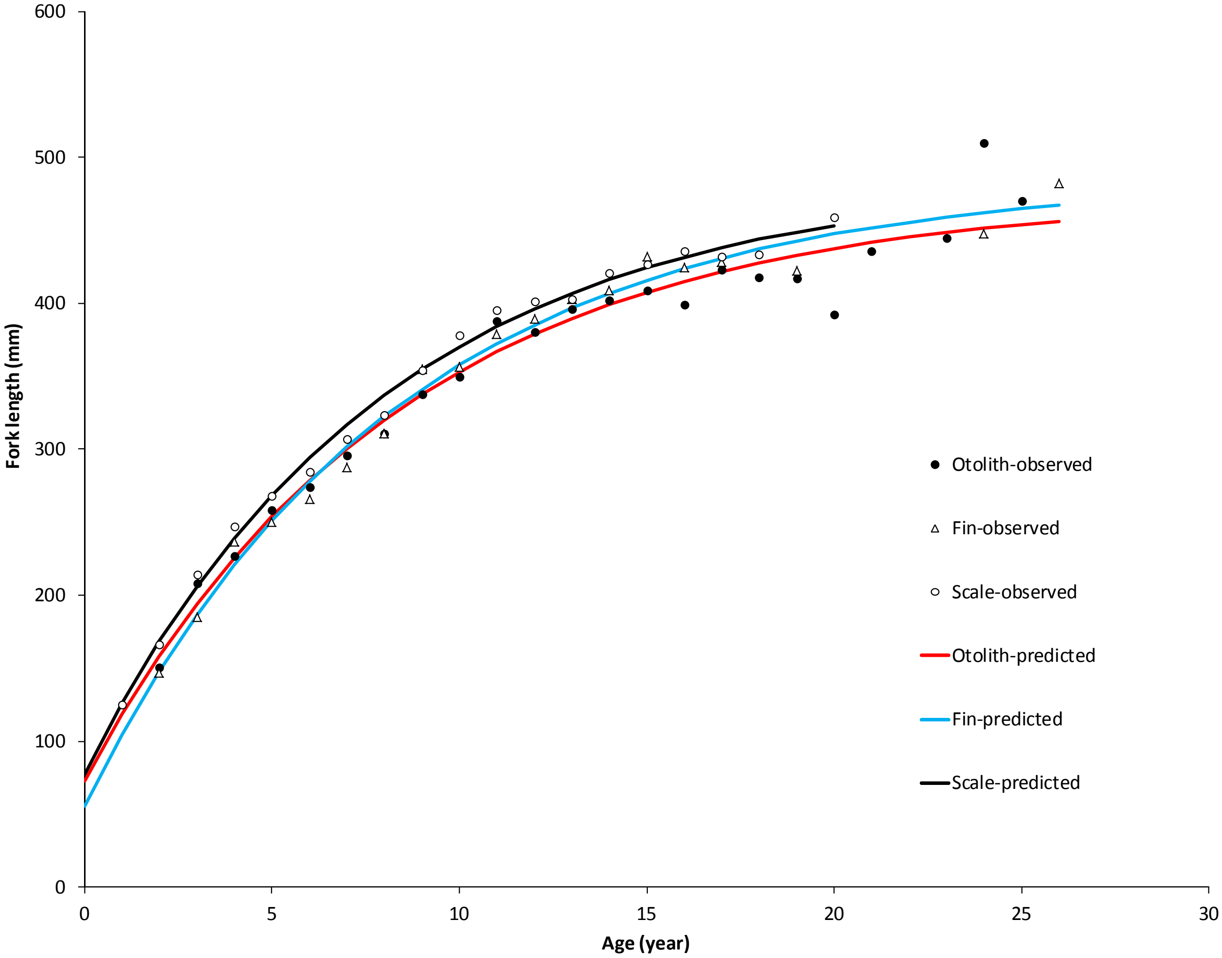


Figure 9. Comparison of model estimated length-at-age growth to observed GSL Lake Whitefish in terms of scale-, fin-ray- and otolith-ages.

As summarized in Table 7, the otolith-based growth model parameters, asymptotic length (L_∞: 473.95 mm), Brody growth rate (K: 0.1198), and age when length was zero (t_0: -1.3976), were the lowest, compared with those from fin-ray- and scale-ages. The values of L_∞ and K from fin-ray-ages were greater by 2.41% and 1.34% than otolith-based estimates, respectively. Similarly, the scale-based estimates of L_∞ and K were 2.55% and 5.18% greater than otolith-based estimates. Between ages 2–20, the annual growth difference in relation to otolith-based growth increased by 1.71 ± 1.86 mm FL (CV=486) and 14.91 ± 0.78 mm FL (CV=23%) for fin-ray- and scale-ages, respectively. All model-based comparisons suggested that growth patterns derived from scale-age were over-estimated while length-at-age growth was best described by otolith-age.

Table 7. Estimated von Bertalanffy model parameters for length-at-age growth by use of respective ageing structures of Lake Whitefish in GSL.

	Otolith		Pectoral fin ray		Scale	
name	Mean	SD	Mean	SD	Mean	SD
L_∞	473.95	1.03	485.36	1.03	486.04	1.02
K	0.1198	1.1175	0.1214	1.0804	0.1260	1.0573
t_o	-1.3976	0.3800	-0.9971	0.2219	-1.3819	0.1236

DISCUSSION AND CONCLUSION

Mills and Chalanchuk (2004) validated the Lake Whitefish fin section method for ageing and by inference, consolidated the otolith section method for ageing fish from the Experimental Lakes Area of Northwestern Ontario. Since the break and burn method is considered to be the functional equivalent of the otolith section method (Campana et al. 2008), one could also infer that the break and burn otolith method has been validated for this species. Although our approaches to these ageing methods were not directly validated, the implications of our study for the northern population of Lake Whitefish are two-fold:

1) different ageing structures can result in biases and uncertainties when generating age compositions, and
2) biased age assignments can greatly influence the effectiveness of estimating fish population dynamics parameters and subsequently formulating precautionary management decisions.

Thus, to select the appropriate ageing structure and method it is important to understand the effects of each option on both the accuracy and precision of age estimates.

SELECTION OF AGEING METHODOLOGY

Selection of the appropriate age estimation method is dependent on the balance between readability (ease of annulus interpretation), consistency (repeatability of age estimates) of ageing structures and considerations for lethal or non-lethal sampling (DeVries and Frie 1996; Ihde and Chittenden Jr. 2002; Herbst and Marsden 2011). In this study readability, based on reader confidence, was found to be influenced by the interaction among processing time, age structure type and age class. Consistency between readers is ensured by following standard ageing methods and criteria that define annual marks and age estimates (Campana 2001).

Of the ageing structures used, we found the processing time for pectoral fin rays was 1.67 times greater than that of ground and baked otoliths, and the shortest processing time was for scales. Ihde and Chittenden Jr. (2002) reported on the longer time required for processing pectoral fin rays (75 min per piece) of Spotted Seatrout *Cynoscion nebulosus*. All of our processing times (2.50-8.08 min per piece) were quite reasonable, but processing time varied with ageing structure. For otolith reading, traditional methods include the use of the unsectioned whole otolith (Buckmeier et al. 2012), broken and burnt (Chilton and Beamish 1982; Barnes and Power 1984; Skurdal et al. 1985; Raitaniemi et al. 1998; Howland et al. 2004; Herbst and Marden 2011), grinding in the transverse plan (Buckmeier et al. 2012) and sectioned (Muir et al. 2008; Zymonas and McMahon 2009). We adopted a grind and bake technique for processing otoliths because of ease of processing and time-efficiency concerns as recommended by Chilton and

Beamish (1982) and Raitaniemi et al. (1998). Although less time was spent processing otoliths, readers' confidence ratings seemed to be higher than for the time-consuming pectoral fin rays. To ensure the ageing protocol was as concise and congruent as possible, we used four readers working in two research agencies and did not provide sample background information for the fish. In comparing *APE*, *CV* and *D*, we found ageing precision varied with ageing structure, but not among reads.

Scales from Lake Whitefish in our study were large enough to read, but it was difficult to distinguish annuli once they became condensed at the outer edge in older fish. This likely contributed to the lower confidence, and, by extension, readability in scale readings beyond age 9. With respect to the consistency of age estimates, we found that precision varied with ageing structure. The highest *CV* was found for otolith readings, suggesting this structure is the most consistent. The suitability of otoliths for age estimation is further supported by the fact that otoliths do not show resorption and their growth is acellular rather than by calcification (Secor et al. 1995). Otoliths are reported to be metabolically inert and thus do not reflect physiological changes that may occur throughout the life of a fish (Phelps et al. 2007).

In comparing age agreement and assignments among structures, scale annuli appeared to be the most inconsistent, which led to lower agreement between readers and produced the most variable results. This is consistent with the findings of other researchers (Mills and Beamish 1980; Muir et al. 2008a; Herbst and Marsden 2011). In particular, Mills and Beamish (1980) advocated that age estimate agreement between fin rays and scales was influenced by fish growth conditions. They reported good agreement (fin-ray- and scale-ages rarely differing by more than 1 year) in populations living in quick-growing environments where age estimates were seldom older than six years. In contrast, precision was higher with fin-ray-age than scale-age in slow-growing populations that were often estimated to be eight years or older (by fin ray).

When fin-ray- and otolith-age estimates were compared in more southern stocks, no significant differences were found (Mills and Chalanchuk 2004; Muir et al. 2008b). Our study, however, found a divergence between age estimates from these two structures, with fin-ray-age being significantly lower (on average by >1 year) in fish beyond otolith-age 11, and this divergence increased with age. This result was not unexpected given that fin ray growth is directly related to somatic growth, so greater difficulties in interpretation of annuli are likely to occur with increased age. Although Mills and Chalanchuk (2004) validated the fin section method for all age groups on a more southern Lake Whitefish stock, our data indicate that this method is not valid for older age groups for this and possibly other more northern stocks.

EFFECTS OF AGEING STRUCTURES ON DEMOGRAPHIC PARAMETERS

The ability to determine ages of fishes with relatively low observational bias is critically important for assessing demographic attributes of exploited fish populations, such as growth (i.e. length- and weight-at-age), size-dependent fishing and total mortality, estimates of year class abundance and biomass, as well as minimum legal fish size for fisheries regulation and management (Quinn and Deriso 1999). Here, we applied three ageing methods to assess

1) age composition,
2) growth patterns, and
3) fishing and total mortality.

Of the three structures, pectoral fin rays produced the largest number of age classes (1–27 years), followed by otoliths (1–25 years) and scales (1–20 years). Despite this, the arithmetic mean age showed structure-specific tendencies. Otolith-age showed the greatest mean age and lowest CV; on average, fish were estimated to be 1 year older relative to fin-ray- or scale-ages.

Using the same set of biological measurement data, we found that fish older than 15 years made up 18% of otolith-ages, 4% of fin-ray-ages and 7% of scale-ages. Thus we suggest that both pectoral fin rays and scales were under-estimating ages beyond age 15. Additionally, when comparing among structures, we found that these differences increased linearly with age, with differences among structures starting at ages 10–12. These results reflected a 6–7 year lag in between ageing structure discrepancies compared to other studies of whitefish. For example, Barnes and Power (1984) studied western Labrador Lake Whitefish and found considerable differences among structures from age 4 or 5 on. Similarly, Skurdal et al. (1985) reported linearly-increasing differences appeared after age 4–5, as estimated by reading otoliths and scales of Common Whitefish (*Coregonus lavaretus*) in Lake Tyrifjorden, Norway. For Lake Whitefish in Lake Michigan, Muir et al. (2008a, b) found that age differences between scale- and fin-ray-ages began at age 5 for the Bailey Harbor stock and at age 6 for the Naubinway and Saugatuck stocks. Between scale- and otolith-ages, differences began to appear at age 5 for the Bailey's Harbor and Saugatuck stocks and age 8 for the Naubinway stock. The 6–7 year lag in our results likely resulted from the effects of the different metabolic processes of slow-growing fish in a typical oligotrophic lake (Simkiss 1974; Healey 1975; Brett 1979). In fact, the growth of Lake Whitefish in our study was slower than in the southern Great Lakes (Kennedy 1953; Rawson 1953; Healey 1975; Cook et al. 2005; Muir et al. 2008b).

Given the magnitude and relevance of the variability associated with multiple ageing structure readings, we investigated the effects of age differences on estimates of growth and mortality parameters. The growth of Lake Whitefish in this study was slower than is observed in the more southerly located Laurentian Great Lakes (Cook et al. 2005; Muir et al. 2008a, b) and likely more typical of arctic and sub-arctic populations of Lake Whitefish that experience a short growing season (Healey 1975; Morin et al. 1982). Under the assumption that the best age estimates were generated from otolith readings (Herbst and Marsden 2011), fish growth attributes were likely over-estimated for Lake Whitefish over fin-ray-age 10 in our study. Use of scale-age resulted in over-estimated growth for all age classes. Furthermore, we used traditional catch-curve analysis to fit age-based abundance to estimate total mortality. This produced total mortality estimates that were 68% higher with scale-age and 1.83 times greater with fin-ray-age compared to otolith-age. In general, fin-ray- and scale-ages produced higher estimates of growth rates and total mortality as a consequence of underestimating ages (Mill and Beamish 1980; Muir et al. 2008).

Our results indicated much lower total mortality estimates (0.22–0.61 per year) than previous studies in GSL (Kennedy 1953; Bond and Turnbull 1973) and other freshwater systems (Muir et al. 2008; Ebener et al. 2010). In GSL, the total mortality of Lake Whitefish, estimated by a catch curve analysis, was 0.51–0.63 during 1947–1949, when the commercial fishery began (Healey 1975). Using data from 12–18 year old fish collected by a five panel multi-mesh experimental gillnet, Bond and Turnbull (1973) reported a value of 0.58. Using a catch-at-age model and cohort analysis, Mohr et al. (2003) estimated total mortalities ranging from 0.39 to 0.44 per year for Lake Whitefish in Lake Huron. Muir et al. (2008) studied the same stocks in Lake Huron and estimated that total mortality ranged from 0.45 to 0.93 per year in the main basin and 0.62 to 1.26 per year in Georgian Bay. Ebener et al. (2010) used tag-recapture models to estimate natural and fishing mortality for four Lake Whitefish stocks in Lakes Michigan and Huron in 2004–2007, and found that the best estimates of total mortality were 0.38–1.14 per year for Lake Michigan and 0.63–1.39 per year for Lake Huron stocks. Potential explanations for the inconsistency among the mortality studies, can be ascribed to

1) observation errors associated with the selectivity properties of individual gillnets,
2) measurement errors derived from different ageing structures and ageing criteria,

3) effective sample size, and most importantly,
4) different levels of fishery exploitation.

Our estimates of lower total mortality ($Z=0.22$) based on otolith readings were considerably optimistic because of the comparison of multiple age structures, sufficient ESS, and the absence of any commercial fisheries in the sampled area.

Based on the use of what we consider to be appropriate age class estimates from otoliths, we found that Lake Whitefish in GSL had a longer age class series and higher average ages, together with lower estimates of length-at-age and size-dependent total mortality, when compared to fin-ray- and scale-ages. We recommend that otoliths be used as the best ageing structure for Lake Whitefish, as suggested by other researchers (Ihde and Chittenden Jr. 2002; Herbst and Marsden 2011). On the other hand, pectoral fin rays produce a comparable number of age classes and reasonable estimates of growth and mortality, and thus provide a better alternative than scales where non-lethal sampling or minimal alteration of sampled commercial catch is desired. A variety of other studies have similarly found pectoral fin rays to be a suitable alternative to scales (Mills and Beamish 1980; Mills and Chalanchuk 2004; Muir et al. 2008a, b), but our results showed that good agreement among the three ageing structures can be assured for fish less than 300 mm FL. Future validation of these two candidate structures is recommended to ensure the effective assessment and management of this important commercial and subsistence fishery.

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