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Comparison of pelvic fin rays, scales and otoliths for estimating age and growth of bull trout, *Salvelinus confluentus*

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Abstract The suitability of three anatomical structures to determine age and growth of bull trout, *Salvelinus confluentus* (Suckley), was assessed. Scales and pelvic fin rays collected from recaptured bull trout 96–265 mm TL were used to validate annulus formation and assess the accuracy and precision of back calculation. Ageing precision and agreement of assigned ages were compared among scales, fin rays and otoliths from bull trout 52–711 mm TL. Annulus formation was validated for 88% (14 of 16 fish) of recaptured bull trout using pelvic fin rays and 68% using scales (15 of 22 fish). Annulus formation in fin rays occurred between late April to early June, and the hyaline (non-growth) band began forming in late August. Back-calculated length was not significantly different from measured length at initial capture either for fin rays or scales ($P \geq 0.19$), and absolute percent error was 7.2 ± 1.2 (mean ± SE; n = 14) for fin rays and 8.7 ± 1.9 (n = 15) for scales. Consistency of back-calculated lengths at age between tag and recapture samples for individual fish was similar for fin rays (mean absolute difference = 8.2% ± 0.9; n = 33) and scales (9.4% ± 1.4; n = 40). However, fin rays (87% precision) and otoliths (90%) provided notably higher ageing precision than scales (68%) and closer agreement of assigned ages, particularly for fish older than age 4. Pelvic fin rays appear to offer more accurate and precise age and growth determinations than scales and a non-lethal alternative to otoliths, but further work is needed to validate the accuracy and precision of ageing large, migratory bull trout.

KEYWORDS: age validation, ageing error, back calculation, bull trout, pelvic fin rays, scales.

Introduction

Estimation of age and growth commonly involves analysis of calcified structures such as scales, fin rays, or otoliths (Casselman 1990; DeVries & Frie 1996). Scales have been widely used because they are relatively easy to collect and prepare and their removal is non-lethal, but annuli may be difficult to discern on scales from older fish (e.g. Beamish 1973; Barbour & Einarsson 1987; Nakamura, Maruyama & Watanabe 1998; Braaten, Doeringsfeld & Guy 1999). Bony structures potentially offer greater precision than scales, but lethal sampling for internal bones may be impractical for protected species, fish of high angling value or during mark-recapture efforts.

Fin rays are considered a non-lethal alternative to internal bones (DeVries & Frie 1996; Mills & Chalanchuk 2004; Zymonas & McMahon 2006) and have been validated for ageing brown trout, *Salmo trutta* L. (Burnet 1969; Shirvell 1981), Chinook salmon *Oncorhynchus tshawytscha* (Walbaum) (Chilton & Bilton 1986), lake whitefish *Coregonus clupeaformis* (Mitchill) (Mills & Beamish 1980) and white sucker *Catostomus commersoni* (Lacepéde) (Beamish & Harvey 1969). Ageing was more precise with fin rays than with scales in several studies comparing various structures (Sikstrom 1983; Williamson & Macdonald 1997; Braaten *et al.* 1999), although other investigators rejected fin rays as a result of difficulties with sample preparation, identification of the first annulus and

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distinction between true and false annuli (Maraldo & MacCrimmon 1979; Barber & McFarlane 1987; Hubert, Baxter & Harrington 1987). Thus, suitability of fin rays for ageing may vary among species and potentially among populations.

Despite potential advantages for ageing, few published studies have evaluated soft fin rays for back calculation (Chen & Harvey 1995; Braaten *et al.* 1999; Mills & Chalanchuk 2004; Eitzmann, Makinster & Paukert 2007). In part, this paucity stems from challenges for standardising samples and locating a consistent axis of measurement (Rupprecht & Jahn 1980; Brenden, Hallerman & Murphy 2006). Annuli on cross-sections of fin rays vary markedly in appearance depending on longitudinal position within the ray, and sections taken too far distally from the body may not include early annuli (Beamish 1981; Sikstrom 1983; Ferreira, Beamish & Youson 1999). A search of the literature produced only one published study validating back calculation using soft fin rays. Mills & Chalanchuk (2004) reported overall 1.0 mm error and 7.6 mm absolute error using the leading pectoral fin ray of recaptured lake whitefish. Hard spines and spinous rays have been used more extensively for back calculation (e.g. Sneed 1951; Prince & Pulos 1983; Sun, Wang & Yeh 2002), but structural differences between spines and soft fin rays complicate the direct transfer of techniques. The potential for high variability in age and growth estimation using soft fin rays underscores the need for more detailed assessments of accuracy and precision.

Age and growth of bull trout, *Salvelinus confluentus* (Suckley), a char native to the northwestern US and western Canada, have commonly been assessed using scales (Bjornn 1961; Fraley & Shepard 1989; Connor, Reiser, Binkley, Paige & Lynch 1997; Mogen & Kaeding 2005). However, interpretation of bull trout scales is generally considered difficult, especially for fish aged 3 or older (Fraley & Shepard 1989; Goetz 1989; Connor *et al.* 1997; Williamson & Macdonald 1997; Gust 2001), and some recent investigations have used fin rays or otoliths for ageing (Williamson & Macdonald 1997; Gust 2001; Bahr & Shrimpton 2004; Downs, Horan, Morgan-Harris & Jakubowski 2006; Brenkman, Corbett & Volk 2007). Comparisons of multiple calcified structures of bull trout have indicated higher ageing precision and better resolution of annuli with fin rays and otoliths than with scales, but validation was not included (Williamson & Macdonald 1997; Gust 2001). In these studies, otoliths or entire fins removed at the basipterygial articulation from killed fish were used, but the threatened status of bull trout in the conterminous US imposes constraints on lethal sampling. Although excision of the leading three fin rays immediately distal to the fin insertion had no effect on growth and survival in a laboratory study (Zymonas & McMahon 2006), removal of complete fins at the basipterygial articulation is more invasive and its effect has not been evaluated for bull trout. In this study, excised pelvic fin rays and scales of bull trout were used to validate annulus formation and assess accuracy and precision of back calculation. Additionally, ageing precision and agreement among structures were compared for pelvic fin rays, scales, and otoliths.

Methods

Sample collection and interpretation

Fin rays, scales and otoliths were collected from bull trout captured during 2001–2003 in eight streams in the lower Clark Fork River basin from the Thompson River drainage in Montana to Lake Pend Oreille in Idaho, USA (East Fork Bull River, Vermillion River, West Fork Thompson River, Fish Trap Creek, Graves Creek, Prospect Creek, Rock Creek and Trestle Creek). Bull trout captured by electric fishing or moving downstream into screw traps or weir traps situated in lower tributary reaches were generally small (56–300 mm TL) and potentially included juveniles and small adults, whereas those captured moving upstream into weir traps were larger (>400 mm TL) and presumed to be migratory adults. Migratory and stream-resident life history types occurred within the study streams, but populations or individuals were not classified by life history for statistical analyses.

The leading three rays from one pelvic fin were excised near the base and placed into coin envelopes to dry. Samples were trimmed, set in epoxy, and cut into transverse cross-sections using a Buehler Isomet® (Lake Bluff, IL, USA) low speed saw. At least three consecutive sections were cut, the first section comprising the most proximal available portion of the fin ray. Thickness of sections averaged about 0.5 mm. Sections were polished using 400–1200 grit wet-dry sandpaper, and then affixed to a slide in sequential order using thermoplastic glue. Scales were removed from the area of the body ventral to the anterior edge of the dorsal fin and above the lateral line. Three non-regenerated scales from each fish were pressed into 0.56 mm cellulose acetate using a hydraulic laboratory press at 71 °C and 6800 kg hydraulic pressure for 4 min. Because lethal sampling was avoided, saggital otoliths were only collected from 19 incidental electric fishing and trapping mortalities and from six post-spawn adult mortalities encountered during autumn. Otolith samples were set in epoxy and cross-sectioned to obtain a sample containing the nucleus.

Samples were interpreted without knowledge of fish size, sample date or capture location to minimise bias (Casselman 1983). Annual growth in fin ray and otolith sections consisted of an adjacent pair of hyaline (translucent in transmitted light; associated with diminished growth during winter and counted as the annulus) and opaque (dark; rapid summer growth) bands (Chilton & Bilton 1986; DeVries & Frie 1996). Annuli were only counted if bands were continuous around a majority of the fin ray (Shirvell 1981). The larger, ventral hemisegment of the fin ray was used for ageing because it showed better definition than the dorsal hemisegment. The third fin ray was used for analyses unless the second ray showed appreciably better definition. The first, leading fin ray was not used because it was less consistent in shape and definition of annuli, as was reported for Chinook salmon (Chilton & Bilton 1986). Use of fin ray samples was restricted to the most proximal cross sections in which the shape of the fin ray hemisegment was rounded or slightly comma-shaped, which was a reliable morphological indicator of complete inclusion of the annuli (Zymonas 2006). Scale annuli were identified using standard criteria based on spacing and continuity of circuli around the scale (Jearld 1983). Each fin ray, otolith and scale sample was read by one reader on two separate occasions. If the two ages differed for a fish, the sample was read a third time and assigned a final age or else excluded from analyses if confidence in the assigned age was low.

Back calculation using fin rays and scales was based on distances measured with a digital image-analysis system. The axis of measurement on fin rays (anterior side, perpendicular to annuli; Fig. 1) was selected because it showed relatively clear definition and high consistency among consecutive cross-sections along the ray. The origin of measurement in the nucleus was determined using a reference line connecting the dorsal indentation with the posterio-ventral corner of the fin ray section. For scales, distance between annuli was measured along a trajectory 5 degrees offset from the anterior axis. Annuli were measured at the last closely spaced circulus preceding a region of widely spaced, relatively well-defined circuli (Bilton & Robins 1971). Length at age was back calculated using the intercept correction (Fraser–Lee) procedure (DeVries & Frie 1996). For pelvic fin ray samples from bull trout <300 mm TL, the intercept parameter ($\alpha = 20$) was obtained from a body-fin ray relation ($y = 863.37x + 19.306$; $r^2 = 0.93$) established using a random selection of 341 fin ray samples that included up to 20 (if available) samples from each 10-mm body length interval between 50 and 300 mm TL. For scales, random selection of up to five samples in each 10-mm TL interval was used for lengths <300 mm to generate a body-scale radius relation ($y = 863.37x + 12.5$; $r^2 = 0.84$; $n = 65$). Back calculation was conducted only using scales and fin rays and was restricted to bull trout <300 mm because few otoliths were available and few usable samples were collected from larger fish.

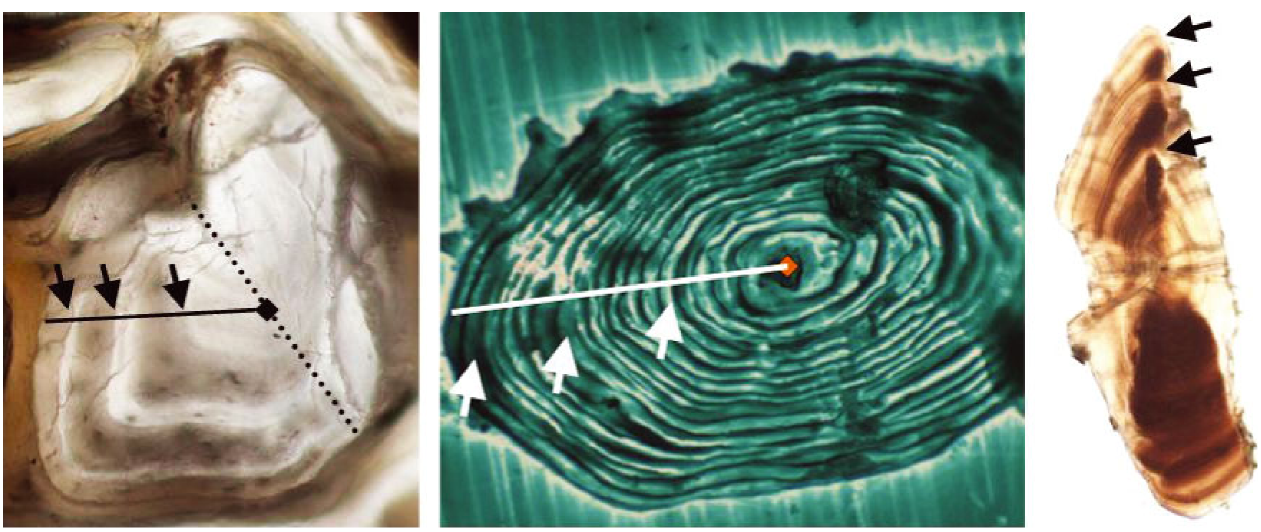
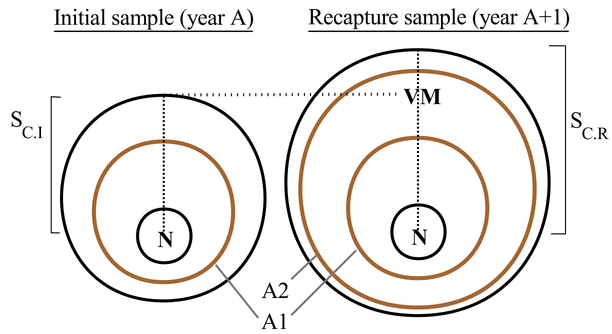


Figure 1. Pelvic fin ray, scale and otolith from a bull trout (172 mm TL) collected on 3 May 2002. Arrows indicate annuli. Measurement axes depicted for fin ray and scale; dotted line on fin ray indicates line of reference for origin of measurement.

Validation of annulus formation

To confirm the formation of a single annulus, age estimates were compared for fin ray pairs and scale pairs from 25 bull trout collected by electric fishing and passive integrated trnasponder tagged in summer 2002 (range 96–249 mm TL; mean ± SE = 155 ± 9 mm) and subsequently recaptured in summer 2003 (range 136–265 mm TL; mean ± SE = 195 ± 8 mm) (herein referred to as the tag–recapture samples). Fin rays were removed in 2003 from the pelvic fin opposite of that excised in 2002. Fin ray pairs from 16 fish and scale pairs from 22 fish were determined to be of suitable quality (no evidence of regeneration, fin ray section sufficiently proximal to include first annulus). Complete sets of suitable tag–recapture samples for both fin rays and scales were available for 14 fish. During age estimations, these samples were interspersed among other fin ray and scale samples and interpreted without knowledge of their membership in the tag–recapture set. Validation of annual increment formation required assigned age at recapture to exceed assigned age at initial capture by exactly 1 year. Number of cases for which age estimates increased by 1 year was compared between fin rays and scales using Fischer's exact test to accommodate small expected cell counts (Zar 1996).



$S_{C.I} = S_{A1.I} * (S_{C.I} / S_{A1.I})$ $\quad S_{VM} = S_{A1.R} * (S_{C.I} / S_{A1.I})$

$L_{VM} = [(L_{C.R} - a) / S_C] * S_{VM} + a$

VM = Virtual mark
A = Annulus
a = Intercept parameter
L_C = Length of fish at capture
L_{VM} = Back-calculated length of fish at virtual mark
N = Nucleus
S_{A1} = Radius of hard part at first annulus
S_C = Radius of hard part at capture
S_{VM} = Radius of hard part at virtual mark

Subscript specifies initial (.I) or recapture (.R) sample

Figure 2. Representation of virtual mark procedure for fin rays and scales, based on initial capture at age 1 and recapture at age 2. Notation modified from DeVries & Frie (1996). S_{VM} is a calculated value used to back-calculate L_{VM} by Fraser–Lee formula shown. Back-calculation error = $[(L_{C.I}-L_{VM})/L_{C.I}]$.

Back-calculation accuracy and precision

Accuracy of back calculation with fin rays and scales was assessed using tag–recapture samples and a virtual mark (VM) procedure whereby the radius of the structure at the time of initial capture was modelled on the recapture sample (Fig. 2). The more common approach of assuming measured body length of fish captured during winter to represent body length at annulus formation (e.g. Mills & Chalanchuk 2004) was not possible in this study because fish were captured during the summer growth period. To account for recent opaque-zone deposition since the last annulus on the initial capture sample, the total radius of the initial capture sample was represented as a VM on the recapture sample. The actual radius measurement from the initial sample was characterised as a proportional distance past the last annulus to account for variability among samples from an individual (i.e. multiple scales, fin ray cross-section locations). Upon locating the corresponding (second-to-last) annulus on the recapture sample, this proportional relationship was used to calculate the distance from the origin to the VM along the axis of measurement. The additional deposition in the ageing structure beyond the VM was assumed to correspond to growth in body length since the initial capture, and the back-calculated length to the VM was compared with observed length at initial capture to assess accuracy of the back-calculation procedure for pelvic fin rays and scales.

Tag and recapture samples were also used to evaluate precision of back calculation beyond the single year addressed with the VM procedure. Back-calculated lengths at age were compared between tag and recapture samples for all ages common to both (e.g. lengths at ages 1 and 2 for each individual that was age 2 when tagged and age 3 when recaptured). Samples were limited to those for which both structures matched the expected age increase of one year.

Differences between back-calculated and actual lengths at initial capture were evaluated with a paired t-test. Mean difference and mean absolute difference (Mayer & Butler 1993) between actual and back-calculated lengths at initial capture and between length-at-age estimates for tag and recapture samples were calculated for fin rays and scales. Wilcoxon rank-sum tests were used to test for significant differences in absolute percent error in accuracy and absolute percent difference in precision between fin rays and scales.

Ageing precision and structure agreement

Ageing precision (first vs second readings) and agreement of assigned ages among different structure types from individual fish were evaluated to further compare age estimation with fin rays, scales and otoliths. Matched sets of all three structures were available only from a limited number of incidental and post-spawning mortalities (19 juveniles 52–173 mm TL, mean ± SE = 111 ± 8; four large adults 465–520 mm TL) because the threatened status of bull trout precluded lethal sampling. Paired fin rays and otoliths, without usable scales, were available from two additional fish (504, 711 mm). Paired samples from 328 bull trout (64–716 mm TL; mean ± SE = 165 ± 6) were additionally used to compare assigned ages between fin rays and scales. Percent agreement and the coefficient of variation were used to assess precision for each structure as well as agreement of age among matched fin rays, scales and otoliths (Chang 1982; Campana, Annand & McMillan 1995). Chi-squared tests on the numbers of precisely (first and second readings agreed) and imprecisely (first and second readings disagreed) aged samples were used to assess difference in ageing precision between structure types.

Results

Alternating opaque and hyaline zones were readily discernable in fin rays and otoliths from bull trout <300 mm TL. Fin rays and otoliths collected throughout the study area indicated formation of an annulus between late April and early June, and a hyaline (translucent) edge was present in some fin ray samples collected as early as late August. Formation of the first annulus was apparent in fin rays collected in April and May from Trestle Creek bull trout that were too large (52–81 mm TL) to be newly emerged fry but highly unlikely to be age 2 based on length frequency data. All three structure types from large migratory bull trout showed regions characteristic of tributary growth (narrow opaque zones in fin rays and otoliths; narrow circuli spacing in scales) followed by main-stem river or lake growth (conspicuously wide opaque zones or wide circuli spacing) after 1–3 years of age. Identification of annuli on fin rays and otoliths was more difficult for the region inferred to have formed after emigration from tributaries, whereas highly variable circuli spacing and high incidence of partial cutting-over made reliable identification of annuli difficult in all regions of scales.

Validation of annulus formation

Formation of an annulus was confirmed for 88% (14 of 16) of fish using fin rays and 68% (15 of 22 fish) using scales (Fischer's exact test: $P = 0.25$). Considering the 14 fish for which both structures could be assessed, annulus formation was identified on 86% of fin ray pairs and 64% of scale pairs (Fischer's exact test: $P = 0.39$). In the two cases where assigned ages of fin rays did not match the expected the expected age (i.e. the assigned age at recapture should be 1 year older than the assigned age at initial capture), fin ray samples were excised at a relatively distal point from the insertion and the position of the first annulus was difficult to determine.

Back-calculation accuracy and precision

Back-calculation accuracy was similar between fin rays (mean percent error ± SE = 4.1 ± 2.0, absolute percent error = 7.2 ± 1.2; $n = 14$ fish) and scales (percent error = 0.2 ± 3.0; absolute percent error = 8.7 ± 1.9; $n = 15$ fish). Measured length did not significantly differ from back-calculated length to the VM for fin rays (paired t-test: $t = 1.38$, d.f. = 13, $P = 0.19$) or scales ($t = 0.104$, d.f. = 14, $P = 0.92$). Considering the fish for which both fin ray and scale sample sets were available, absolute percent error for fin rays (mean ± SE = 6.5 ± 1.5, $n = 7$) was about half that of scales (12.7 ± 3.4), although the difference was not statistically significant (Wilcoxon rank-sum test: $Z = -1.52$, $P = 0.13$).

Comparisons of multiple back-calculated lengths at age between tag and recapture samples from individual fish indicated similar precision for fin rays (mean percent difference ± SE = −6.0 ± 1.4, mean absolute percent difference ± SE = 8.2 ± 0.9; $n = 33$) and scales (mean percent difference ± SE = −1.7 ± 2.0, mean absolute percent difference ± SE = 9.4 ± 1.4; $n = 40$). Where both structure types were compared for the same fish, absolute percent difference was generally lower for fin rays (mean ± SE = 8.2 ± 1.7 $n = 7$) than for scales (mean ± SE = 11.3 ± 2.3), but the difference was not statistically significant (Wilcoxon rank-sum test: $Z = -0.94$, $P = 0.35$).

Ageing precision and structure agreement

Ageing precision was greater with fin rays and otoliths than scales and negatively related to fish length for all ageing structures. Agreement between first and second readings for fin rays was 87% (CV 3.4%) overall, 90%

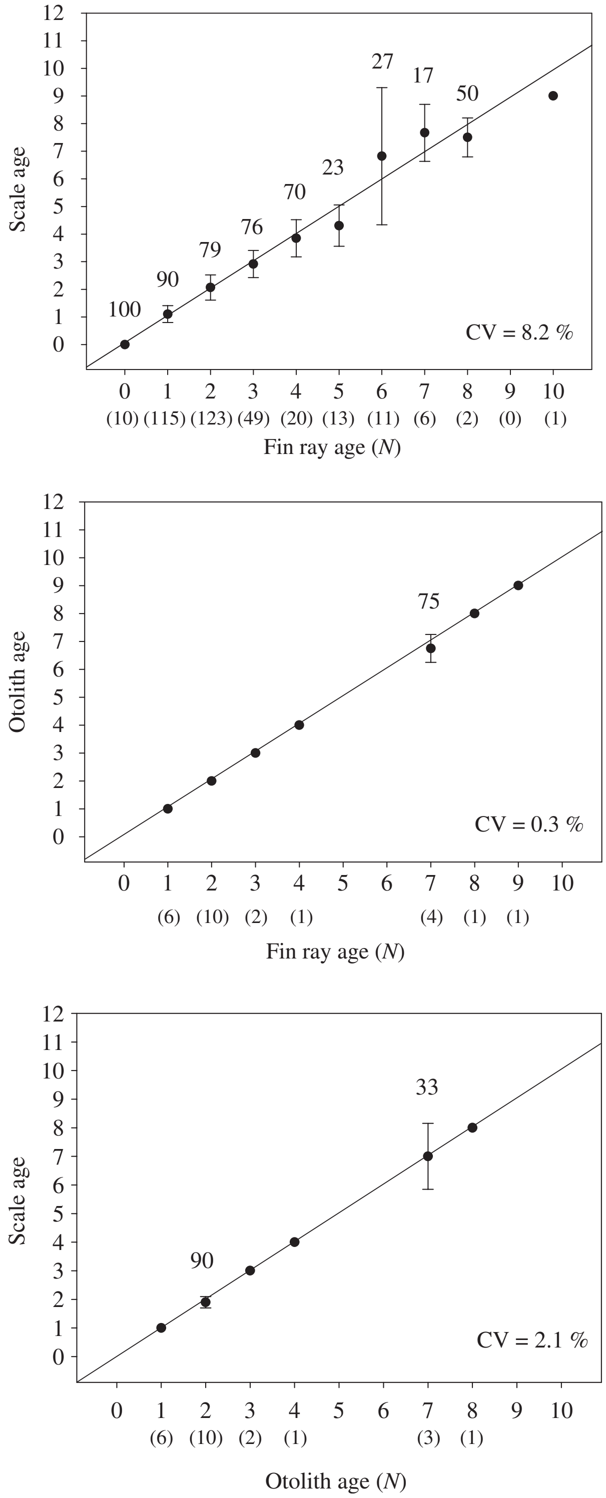


Figure 3. Agreement of assigned ages for paired fin rays, scales and otoliths. Data points and error bars indicate mean ± 2 SE. Percent agreement listed above data points if < 100%. Diagonal indicates line of complete agreement. Sample sizes in parentheses on x-axis. Coefficient of variation (CV) provided for each set of comparisons.

for fish < 250 mm (n = 682) and 67% for fish ≥250 mm (n = 58). For scales, first and second age readings agreed for 68% (CV 7.4%) of fish overall, 71% for fish < 250 mm (n = 142) and 55% for fish ≥250 mm (n = 33). Agreement of first and second readings for otoliths was 100% for fish ≤ 173 mm (n = 19) and 50% for fish ≥465 mm (n = 6).

Agreement of assigned ages between structure types was highest between fin rays and otoliths and negatively related to fish age (Fig. 3). For small bull trout captured while outmigrating from tributaries (ages 1 through 4; ≤ 173 mm; n = 19), agreement between assigned ages was 100% for fin rays and otoliths, 95% for scales and fin rays, and 95% for scales and otoliths. Overall, age agreement was 77% (n = 351) between fin rays and scales and no directional bias was evident, although disagreement increased markedly at age 5 and greater. For fish ≥465 mm, assigned ages agreed for 83% (5 of 6) of otolith–fin ray comparisons, 50% (2 of 4) of otolith–scale comparisons, and 33% (6 of 18) of fin ray–scale comparisons.

Discussion

Selection of the appropriate method for age and growth determination in fishes often requires balancing precision and accuracy of the method with sample size limitations (DeVries & Frie 1996). Lethality of collection poses an important consideration, particularly for threatened species. Results from this study indicate that pelvic fin rays of bull trout offer more accurate and precise age and growth determinations than scales and provide a non-lethal alternative to otoliths.

Higher precision of ageing with pelvic fin rays than scales in this study supports previous investigations reporting higher ageing precision with pelvic fin rays (Gust 2001) and dorsal rays (Williamson & Macdonald 1997) of bull trout and soft or spinous rays of other species (e.g. Beamish & Harvey 1969; Burnet 1969; Sikstrom 1983; Braaten *et al.* 1999) than with scales. Annulus formation in pelvic fin rays of tagged tributary-resident bull trout recaptured after 1 year at liberty was validated in 88% of samples, with discrepancies arising from difficulty discerning the first annulus in fin rays cut distally from the body rather than from inconsistent annulus formation. Validation of annulus formation was considerably lower for scales (68%) because inconsistent patterns in circuli spacing and absence of complete cutting-over led to greater interpretive subjectivity. Differences in validation were not statistically significant between fin rays and scales, but the statistical power of this analysis was low (0.34) because of small sample sizes stemming from low recapture rates of a rare species.

Ages determined from otoliths, fin rays and scales were in overall close agreement through age 4. However, fin rays and otoliths provided better precision than scales from a wider length range of bull trout in this study, as was also documented in previous investigations comparing the three structures (Williamson & Macdonald 1997; Gust 2001). In contrast to previous studies on bull trout, in which whole fins were removed from killed bull trout, the results of this study demonstrate the practicality of non-lethal sampling involving excision of the leading three pelvic fin rays just distal to the insertion for obtaining age and growth information. In combination, the results of the annulus validation, ageing precision and structure agreement analyses in this study support the use of fin rays or otoliths rather than scales for ageing bull trout.

Few studies have reported accuracy and precision of back calculation using soft fin rays, but the results of this study suggest that pelvic fin rays of bull trout offer an appropriate alternative to scales or internal bones. Both pelvic fin rays and scales of bull trout provided high accuracy ($<5\%$ mean error; 7.2–8.7% mean absolute error) and precision ($\leq 6\%$ mean error; 8.2–9.4% mean absolute error), but higher accuracy and precision of ageing favours the use of fin rays for back calculation. The negative bias in error obtained using fin rays suggests that accuracy and precision could be improved by modifying the point of origin for the axis of measurement. Location of the appropriate origin of measurement in the nucleus is not obvious, particularly for asymmetrical cross-sections of fin rays from the paired fins, and lower error and absolute error would have been obtained by consistently positioning the origin slightly closer to the first annulus along the axis of measurement (see Fig. 1). Results of this study compared well to previous studies that reported mean percent error ranging from near zero to 31%, depending on species and method (generally $<10\%$ using the intercept correction method) (Pierce, Rasmussen & Leggett 1996; Klumb, Bozek & Frie 1999a; Klumb, Bozek & Frie 1999b). Back-calculation accuracy with pelvic fin rays of bull trout was similar to that reported for the leading pectoral fin ray of lake whitefish (7.6 mm absolute error vs 9.6 mm absolute error in this study; percent error not reported) (Mills & Chalanchuk 2004).

The VM procedure used to assess back-calculation accuracy and growth in this study has not been directly tested against other methods (e.g. chemical marking), but it provides a means to gauge accuracy in the absence of known lengths attributable to visible marks. Results of back calculation may vary substantially depending on the specific methodology used (Smale & Taylor 1987; Horppila & Nyberg 1999; Klumb *et al.* 1999b), with potential error also associated with measurement error and variation among multiple samples obtained from the same individual. In this study, tests of consistency between tag and recapture samples indicated that longitudinal variability (i.e. relative distance of the cross-section along the fin ray from the fish body), growth of the fish and sample preparation contributed little error to back calculation with fin rays. Although soft fin rays from tag–recapture sampling have previously been used to assess back-calculation accuracy in salmonids (Mills & Chalanchuk 2004), the VM procedure extends this capability to fish captured during periods of relatively rapid somatic growth and opaque zone deposition. Use of individual-based back-calculation assessments such as chemical marking and tag–recapture sampling is a desirable step in the age validation process because comparison of back-calculated lengths to mean observed lengths for individual age classes cannot distinguish back-calculation error from other size-selective factors (Francis 1990).

Age and size strongly influenced accuracy and precision of age and growth determination. High precision and structure agreement was achieved with structures from fish younger than age 5, but precision, agreement and reader confidence were notably lower for larger, migratory individuals that were captured moving upstream into weir traps during spawning migrations or that died after spawning. Absence of clearly defined annuli and inconsistency in the width and intensity of opaque bands in structures from these large migrants likely reflects the influence of environmental and physiological changes experienced while in the process of migration or while occupying larger downstream waterbodies with more varied growing conditions, as these irregularities were not observed in the ageing structures of smaller individuals of similar age from small tributaries supporting predominantly bull trout of resident life history. The common practice of eliminating difficult-to-age samples from datasets would increase precision but might contribute error to characterisation of age and growth patterns in the population (Beamish 1973). Distinctness of annuli may vary among populations, as migratory bull trout were apparently aged satisfactorily using fin rays, scales or otoliths in other studies (Bahr & Shrimpton 2004; Mogen & Kaeding 2005; Brenkman *et al.* 2007).

Pelvic fin rays potentially provide advantages over other structures for age and growth analysis, but usefulness of fin rays depends on proper collection and preparation. The fin ray should be removed at the insertion to ensure inclusion of the first annulus. Samples adequately including the first annulus were easily obtained for tributary-resident bull trout less than about 300 mm TL, but more than 75% of fin rays from large or old individuals (i.e. >400 mm or >age 7) were excised too far distally from the insertion to provide sections in which the first annulus was identifiable. Measurements to the second or subsequent annuli have been used in procedures designed to circumvent problems with the loss of the earliest annuli in fin ray and spine sections (Surry & King 2003; Penha, Mateus & Petrere 2004), but the extent of variability in early growth within and among populations complicates the use of this approach for bull trout. Nonetheless, the results of this study demonstrated the utility of soft fin rays for determining age and growth of a relatively long-lived, threatened salmonid. Further work is needed to validate ageing and back-calculation methodology for large, migratory adult bull trout and to validate annulus formation for time periods exceeding the 1-year criterion used in this study.

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