

Precision and Accuracy of Age and Growth Estimates Based on Fin Rays, Scales, and Mark-Recapture Information for Migratory Bull Trout

Abstract

Accurate quantitative descriptions of bull trout (*Salvelinus confluentus*) growth are important for understanding life history and developing reliable stock assessments. In the absence of age validation, important steps are to review the precision of age estimation methods and evaluate whether age estimates yield growth rates consistent with known fish growth based on tag recoveries. We assessed the precision of age estimates using pelvic fin rays and scales for migratory bull trout (297–605 mm total length) from the North Fork Clearwater River, and then compared growth estimates derived from both structures with growth based on tag recoveries. Fin rays produced a lower coefficient of variation ($CV = 5.84$) than scales ($CV = 12.56$). Ages estimated from scales were higher for fish aged < 5 with fin rays and lower for fish aged ≥ 5 . Comparisons of growth estimates derived from 70 tagged bull trout at large from 0.35 to 3.02 years with age-length equations based on fin ray and scale annuli indicated that ages estimated from fin rays ($N = 189$, predicted length of an age 3 fish = 310mm) were closely related to the apparent ages estimated from the mark-recapture model (apparent age of a 310mm fish = 2.9) whereas scales ($N = 65$, predicted length of an age 3 fish = 408mm) were not. This is the first study to assess the precision of structures for modeling growth of larger migratory bull trout. However validation of annuli formation from the recapture of known-age fish is recommended.

Keywords: bull trout; age estimation; growth

Introduction

Accurate age estimates are central to evaluating fish growth, recruitment, mortality, and stock status (Beamish and McFarlane 1983, 1987). The importance of age estimates requires biologists to evaluate both accuracy and precision of the methods of age estimation for different species, populations, and readers (DeVries and Frie 1996, Campana 2001). Small errors in age estimation may have large effects on stock assessments and can result in inappropriate management decisions (Beamish and Chilton 1982, Archibald et al. 1983, Beamish and McFarlane 1983).

Many calcified structures have been utilized to estimate fish ages, including fin rays, spines, cleithra, dentary bones, opercular bones, vertebrae, scales and otoliths (Everhart and Youngs 1981, Beamish and MacFarlane 1987). The acqui-

sition of structures such as otoliths and vertebrae necessitates sacrificing the fish. However, when dealing with threatened or endangered species, options may be limited to structures such as scales or fin rays that can be obtained without sacrificing the fish. Analyses of these structures have generated highly variable results among different species and stocks. For example, fin rays have been found useful in aging lake whitefish (*Coregonus clupeaformis*; Mills and Beamish 1980) and brown trout (*Salmo trutta*; Burnet 1969, Shirvel 1981), whereas other authors have urged caution in utilizing these structures for aging arctic char (*Salvelinus alpinus*; Barber and McFarlane 1987), white sturgeon (*Acipenser transmontanus*; Rien and Beamesderfer 1994), and spotted sea trout (*Cynoscion nebulosus*; Ihde and Chittenden 2002).

Models of fish growth have typically been developed based on age-length data from age estimates (length and age at capture or back-calculated), length-increment data obtained from mark-recapture studies, and length frequency analysis (Isely and Grabowski 2007). Age-length

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relationships are often based on age estimates of annual marks on calcified structures such as fin rays and scales (DeVries and Frie 1996). Ideally, aging methods should be validated for accuracy using known-age fish and verified for precision, or repeatability, of age estimates (Beamish and McFarlane 1983; Campana 2001). In the absence of age validation, two important steps are to review the precision (i.e., repeatability) of methods of age estimation and also evaluate whether non-validated age estimates yield growth rates consistent with growth rates of tagged fish.

Bull trout (*Salvelinus confluentus*), a native char in the northwest United States and western Canada, has multiple life history forms that differ dramatically in growth rates and produce complex age structures (Rieman and McIntyre 1993). They occur as either resident (Chandler et al. 2001, Nelson et al. 2002, Mogen and Kaeding 2005) or migratory forms (Fraley and Shepard 1989, Beauchamp and Van Tassell 2001, Hogen and Scarnecchia 2006). Resident populations generally spend their entire life in headwater streams with adults reaching sizes ranging 150-300mm (Goetz 1989, Buchanan 1997) whereas migratory populations rear in tributary streams for 1-5 years before migrating into large rivers (fluvial) or lakes (adfluvial; Fraley and Shepard 1989) and can exceed 600mm (Fraley and Shepard 1989, Goetz 1989). Bull trout ages have commonly been estimated using scales (Bjornn 1961, Fraley and Shepard 1989, Mogen and Kaeding 2005), however recent studies show higher precision between readers using otoliths (Gust 2001, Zymonas and McMahon 2009) or fin rays (Williamson and Macdonald 1997, Zymonas and McMahon 2009). Williamson and Macdonald (1997) found evidence (based on the analysis of < 10 fish) to support the use of dorsal fin rays rather than scales of bull trout from northern British Columbia. While a recent study assessed the precision of age and growth estimates from pelvic fin rays (through back-calculation) for bull trout < 300mm (Zymonas and McMahon 2009), little research has been conducted on larger migratory forms (> 300mm). The removal of pelvic fin rays, which have been found to not adversely affect bull trout growth and survival for 209-362 mm fish (Zymonas and McMahon 2006), may provide

a suitable structure for non-lethal age estimation and growth modeling of migratory forms.

We assessed and compared the precision of age estimation using pelvic fin rays and scales for migratory bull trout from the NFC, and then compared growth estimates derived from both structures with growth based on tag recoveries. In the absence of age validation, which can require several years to obtain known-age adult fish, a combination of evaluation of aging precision and conformity of mark-recapture data with growth models may provide useful information in this and other bull trout populations.

Methods

Migratory bull trout were sampled by hook and line in the lower reaches of the NFC and river/reservoir transition zones of Dworshak Reservoir during the spring (April-June) of 2000-2008 and fall (October-November) of 2001-2005. All fish (1315 individuals) were measured for total length (TL) to the nearest mm and tagged with passive integrated transponder (PIT) tags for identification upon recapture.

We estimated ages of 189 fish sampled (during the marking phase) in the spring of 2005 and 2007-2008 using pelvic fin rays. Eighty-nine of these fish (sampled in 2007 and 2008) were also aged separately using scales. The first two leading pelvic fin rays were excised as close to the body wall as possible and perpendicular to the fin ray using pliers and surgical scissors. Excised fin rays were wiped clean of mucus and placed in coin envelopes to dry. Fin rays were mounted on wooden craft sticks with high strength epoxy. Transverse cross-sections were then made of dried sections using a Buehler Isomet low speed saw. Due to shape inconsistencies, mounted rays were often adjusted in the vise to provide a section perpendicular to the length of the ray. All sections were glued onto glass slides with clear nail polish and lightly buffed with 1500 grit sand paper.

Scales were sampled from a location above the lateral line and below the posterior base of the dorsal fin (DeVries and Frie 1996). Five to ten scales were collected and placed in coin envelopes to dry. Scales were cleaned with tap water and placed between two glass slides.

Age Estimation

We examined fin ray sections under a compound microscope with 40X magnification. Ages were estimated by counting opaque bands (annuli), which represent slower winter growth, on the ventral hemisegment of the section. The protocol for final age estimation was a double-blind test. In this test, two readers with prior experience in age estimation of bull trout independently assigned an age to each section. If there was no difference between readers, the age estimate was assigned. If there was a difference between readers, each reader independently re-aged the section. If a difference still existed, the readers examined the section together and assigned a final age by consensus. Scales were interpreted with the same double-blind test as fin rays and viewed under a dissecting scope (40x magnification). Only non-regenerated scales (Nordeng 1961) were used.

Fin Ray and Scale Comparison

Precision of ages assigned between readers was measured using the coefficient of variation (CV_j):

$$(Equation 1) \quad CV_j = 100 * \frac{\sqrt{\sum_{i=1}^R (X_{ij} - X_j)^2 / (R-1)}}{X_j},$$

where (X_{ij}) is the i^{th} age estimation of j^{th} the fish, X_j is the mean age estimation of the j^{th} fish, and j is the number of times each fish was aged. We determined an overall index for scales and fin rays by calculating the mean CV across all fish (Campana et al. 1995). We also calculated percent agreement between readers (PA) and percent agreement within one year (PAI).

Pair-wise age bias plots were developed to examine the differences between final ages assigned from fin rays and scales. The plots were developed by plotting the mean final age and 95% confidence intervals estimated from scales corresponding to each of the ages estimated from fin rays (Campana et al. 1995).

Age-length and Length-increment Model Comparison

The von Bertalanffy growth models based on fin ray age estimates, scale age estimates, and

measured growth between tagging and recapture were developed and compared. Measured TL and estimated age at capture were used for the scale- and ray-derived models (no back-calculation). The von Bertalanffy (1938) growth model (LVB) was applied separately to the age-length data derived from analysis of 189 pelvic fin rays and 65 scales. The LVB model takes the form:

$$(Equation 2) \quad L(t) = L_{\infty} [1 - e^{-k(t-t_0)}],$$

where L_{∞} is the asymptotic length, k is a growth coefficient, and t_0 is a hypothetical length at age 0. The model was reformulated and solved for the predicted age (t) from length L :

$$(Equation 3) \quad t = t_0 - (1/k) \ln [1 - L(t)/L_{\infty}].$$

For mark-recapture data, a reparameterized length-increment version of the LVB by Fabens (1965) was applied to 70 mark-recapture events. Time at large in years (Δt) was calculated for each individual recapture. If an individual fish was recaptured more than once, the last recapture event was utilized with initial marking. The Fabens model takes the form

$$(Equation 4) \quad L_r = L_m + (L_{\infty} - L_m)(1 - e^{-k\Delta t}),$$

where L_r is the length at recapture and L_m is the length at marking. Comparisons of estimated growth rates between the fin ray-scale method and the mark-recapture method were assessed by calculating the time at large (Δt) in the length-increment model necessary for a fish to reach the predicted length at age from the age-length models. For example, it should take 4 years for a fish to reach the size predicted for an age 4 fish if estimates are accurate. The apparent age was designated and was calculated by reparameterizing the Fabens model as expressed in equation 4 to

$$(Equation 5) \quad \Delta t = \frac{-1}{k} \ln \left\{ -1 \left[\frac{(L_r - t_0)}{(L_{\infty} - t_0)} \right] + 1 \right\},$$

by substituting L_m (length at marking) with the t_0 (length at age 0) parameter. The t_0 parameter was set to zero to allow for comparisons between models since the Fabens model does not incorporate a length at age zero. Aging bias was evaluated

by assessing differences between predicted and apparent ages.

Results

Fin Ray and Scale Comparison

Pelvic fin rays and scales collected from 89 bull trout (TL range, 297-605 mm) differed in assigned ages between readers. At least one non-regenerated scale was obtained from 73.0% (65/89) of sampled fish. The exact agreement between the two readers

for scales was 33.8% (22/65; mean CV = 12.6) and agreement to within one year was 83.1% (54/65).

Agreement between readers was higher for fin rays than for scales. The exact agreement between readers for the same fish utilizing pelvic fin rays was 58.5% (38/65) and agreement to within one year was 93.8% (61/65). The mean CV between the two readers was 5.8. Ages assigned by reader 1 from scales agreed with the assigned ages from pelvic fin rays 32.3% (21/65) of the time and agreed to within one year only 60.0% (39/65) of the time. The agreement rate between fin rays and scales for reader 2 was 26.2% (17/65) and agreement to within one year was 58.5% (38/65). Estimates from scales were higher for fish aged < 5 by fin rays and lower for fish aged ≥ 5 (Figure 1). Based on these results, pelvic fin rays provided greater precision in age estimates than scales.

Age-length and Length-increment Model Comparison

Ages estimated from the 189 pelvic fin rays ranged from 3 to 11 (mean = 5.5, SD = 1.6) and TL ranged from 274 to 664 mm (mean = 438.3, SD = 82.4). The time at large of the 70 recaptured fish ranged from 0.4 to 3.0 years (mean= 1.2, SD = 0.7) and the mean annual growth rate was 51.5 mm TL (range = 3.9-264.2 mm, SD = 44.7 mm). Both models converged on all parameters and were described as $L_t = 644.71(1 - e^{-0.21\Delta t})$ for the age-length LVB and $L_r = L_m + (681.91 - L_m)(1 - e^{-0.21\Delta t})$ for the length-increment Fabens model (Table 1, Figure 2).

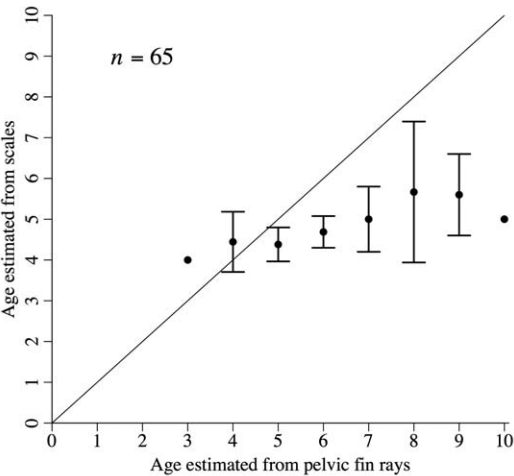


Figure 1. Pairwise age bias plots for migratory bull trout ages estimated from pelvic fin rays (x axis) and scales (y axis) from two independent readers (Reader 1 and Reader 2). Plots represent mean age assigned by scales relative to fin rays. Error bars represent 95% confidence intervals. If no error bar is present then $n = 1$. The line represents a 1:1 agreement between structures.

TABLE 1. Parameter estimation results for age-length and length-increment (Fabens) LVB growth models on NFC migratory bull trout. Age-length data derived from pelvic fin rays and scales.

Parameter	LVB (Fin Rays)	LVB (Scales)	Faben (Mark-Recap)
n	189	65	70
L_{∞}	644.71	561.3	681.91
SE	53.7	255.9	55.51
95% CI	538.8–750.6	49.9–1072.8	601.7–875.3
k	0.22	0.23	0.21
SE	0.06	0.57	0.05
95% CI	0.10–0.34	-0.91–1.38	0.11–0.32
t_0	0.02	-2.66	
SE	0.62	9.19	
95% CI	-1.2–1.23	-21.03–15.71	

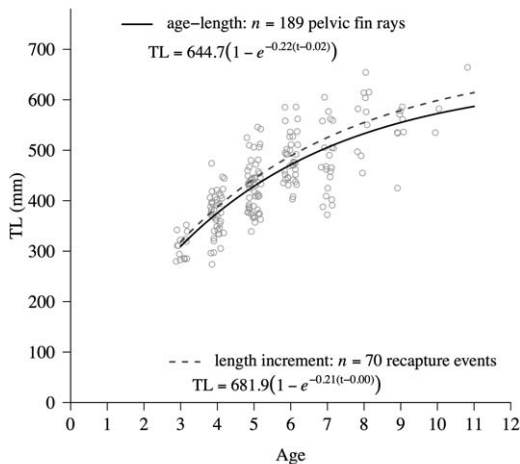


Figure 2. LVB models fitted to age-length data (solid line) and length-increment data (Fabens model, broken line) for NFC migratory bull trout. The age-length model is derived from age estimates from pelvic fin rays collected during the spring of 2005, 2007, and 2008. The length-increment model is derived from mark-recapture events from 2000-2008. Points represent final age estimations from the pelvic fin rays.

Little difference in growth was detected when comparing fin ray data using the age-length model with tag-recovery data using the length-increment model. The differences between the models were associated with differences between ages as calculated by equation 5 and differences in growth rates (Figure 2, Figure 3). The age-length model produced a slightly lower growth rate than the length-increment model (Figure 2). An age-3 fish had a predicted TL of 310 mm from the age-length model while the length-increment model produced an apparent age of 2.9 for the same sized fish. The differences increased with age; by age 7 there was more than half of a year difference (an age 7 fish predicted at 506 mm would have an apparent age of 6.4 years) and by age 9 a full year difference (an age 9 fish predicted at 555 mm would have an apparent age of 8.0 years). These differences were associated with fin rays producing younger ages than the length-increment model for the apparent ages of 9 and older (Figure 3).

Small sample sizes of larger individuals and apparent outliers within the mark-recapture data were associated with differences between the models. The predicted TL of an age-9 fish was

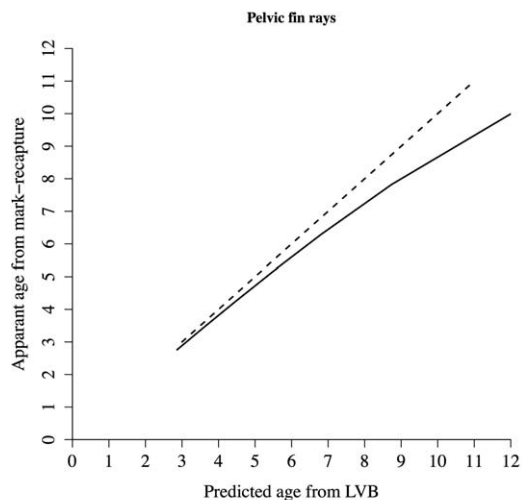


Figure 3. Predicted ages from an age-length LVB versus apparent ages from a mark-recapture Fabens model (solid line). The age-length model was derived from ages estimated from 189 pelvic fin rays of NFC migratory bull trout collected in 2005 and 2007-2008. The Fabens model was derived from 70 mark-recapture events collected from 2000-2008. Apparent ages were calculated by reparameterizing the Fabens model to calculate (change in time) and setting the (length at marking) equal to zero. The broken line represents exact agreement between models.

555 mm. There were only three fish initially marked and subsequently recaptured that were 555 mm or larger upon marking. The growth rates (mm/year) for these three fish were 13.2 (a 627 mm TL fish at large for 728 days), 13.7 (a 604 mm TL fish at large for 389 days), and 42.1 (a 572 mm TL at large for only 186 days). Three other outliers within the recapture data affected model parameters with high growth rates (rates > 3 times higher than the mean growth rate). These fish were initially captured in the spring of 2005 (at 334, 378, and 359 mm) and recaptured in the fall of 2005. They had the highest growth rates of all observations (264, 200, 173 mm of summer growth). When they were excluded and the Fabens model reapplied (Figure 4), the growth estimates for the two models were close; the largest difference between ages (only 0.7 years) occurred at age 10.

Ages estimated from the 65 scales ranged from 3 to 7 (mean = 4.71, SD = 1.06) and TL ranged from 274 to 586 mm (mean = 456.78,

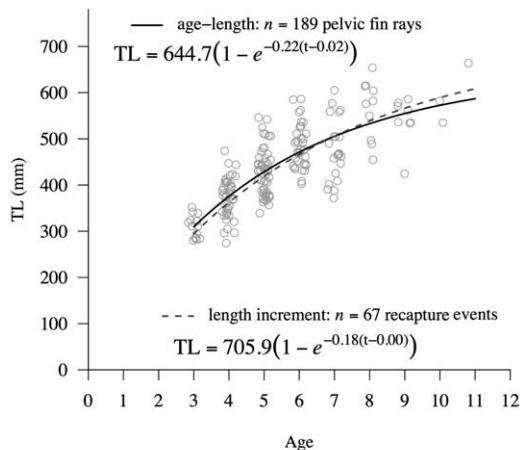


Figure 4. LVB models fitted to age-length data (solid line) and length-increment data (Fabens model, broken line) for NFC migratory bull trout. The age-length model is derived from age estimates from pelvic fin rays collected during the spring of 2005, 2007, and 2008. The length-increment model is derived from mark-recapture events from 2000-2008. Three outliers were apparent in the mark-recapture data (showing higher growth rates) and removed. Points represent final age estimations from the pelvic fin rays.

SD = 74.08). The LVB growth model converged on all parameters for scales and was described as $L_t = 561.33(1 - e^{-0.23(t+2.66)})$. Standard errors for all parameter estimates were high (Table 1, Figure 5). In contrast to results for fin rays, differences in growth between scale age-length and length-increment data and models were apparent across all size classes. An age-3 fish from scales had a predicted TL of 408 mm from the age-length model while the length-increment model produced an apparent age of 4.3 for the same sized fish (Figure 6). We observed the least difference between predicted and apparent ages (0.1 years) at age 6 (485 mm). After age 6, however, differences between models began to increase. An age-7 fish from scales (500 mm) had an apparent age of 6.3 from the length-increment model.

Discussion

Several lines of evidence suggested that pelvic fin rays were a more reliable structure than scales for estimating ages of migratory bull trout. Fin rays provided higher estimates (mean age = 5.9),

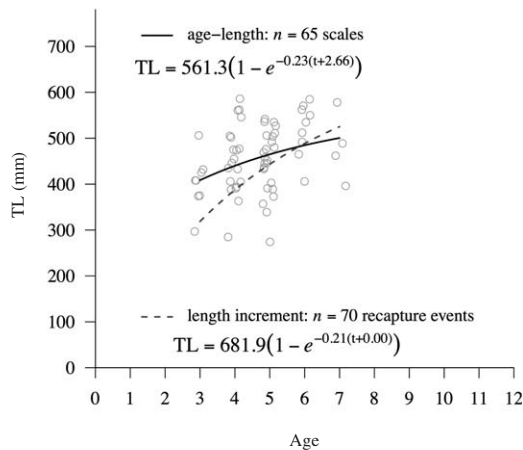


Figure 5. LVB models fitted to age-length data (solid line) and length-increment data (Fabens model, broken line) for NFC migratory bull trout. The age-length model is derived from age estimates from scales collected in the spring of 2007-2008. The length-increment model is derived from mark-recapture events from 2000-2008. Points represent final age estimations from the scales.

higher precision (CV = 5.8), and less between-reader bias (Figure 1) than scales (mean age = 4.7; CV = 12.6). The higher age estimates from pelvic fin rays were associated with age-5 fish and older; much younger estimates were produced from scales. Similar results were reported by Mogen and Kaeding (2005) for migratory bull trout in the St. Mary River drainage, Montana, where validation of annuli formation on scales from recaptured fish found under-aging to occur with age-5 fish and older. Estimates of age-4 fish and younger with fin rays, however, did not tend to be lower than for scales. In our study, only 10 fish (15%) were aged < 5 by pelvic fins (mean age = 3.9) and none under age 3. For these fish, scales produced slightly higher estimates (mean age = 4.2). Although fin ray and scale annuli on younger bull trout (age 4 and under) may present few discrepancies between ages, scale-based age estimates of older charrs (Nordeng 1961) and other species should be interpreted with caution (Beamish and Chilton 1977, Beamish 1981).

Higher precision with fin rays has been documented for bull trout populations in northern British Columbia (dorsal fins; Williamson and Macdonald 1997), the St. Mary River drainage,

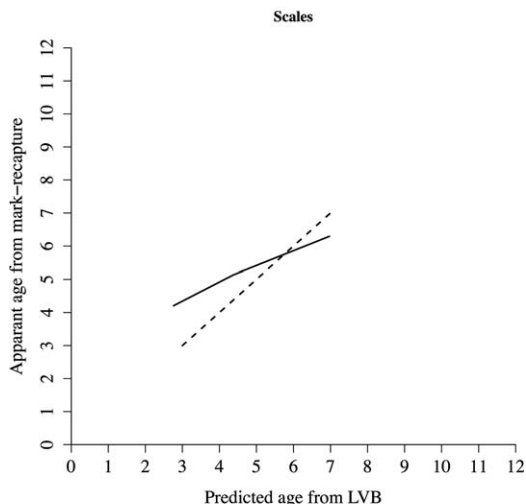


Figure 6. Predicted ages from an age-length LVB versus apparent ages from a mark-recapture Fabens model (solid line). The age-length model was derived from ages estimated from 65 scales of NFC migratory bull trout collected in 2007-2008. The Fabens model was derived from 70 mark-recapture events collected from 2000-2008. Apparent ages were calculated by reparameterizing the Fabens model to calculate (change in time) and setting the (length at marking) equal to zero. The broken line represents exact agreement.

Montana (pelvic fins; Gust 2001), and the Clark Fork River drainage, Montana and Idaho (pelvic fins; Zymonas and McMahon 2009). Gust (2001) and Zymonas and McMahon (2009), however, used a single-reader multiple-round protocol, which does not incorporate between-reader bias. The CV for ages estimated from fin rays in this study ($CV = 5.8$) was higher than 3.4 reported for bull trout by Zymonas and McMahon (2009). Campana (2001) conducted a comprehensive review of measuring precision and stated that many aging studies can be carried out with a CV of up to 7.6.

In addition to higher precision, our results indicate that pelvic fin rays are preferable to scales when used to develop estimates of growth of migratory bull trout (274-664 mm TL) within the NFC drainage. The age-length LVB model derived from 189 pelvic fin rays showed only minimal differences (less than one year) in predicted sizes at age compared to the apparent ages from the length-increment model derived from 70 mark-recapture events. This conclusion

applies even though annulus formation has not been validated nor were the age or timing of first annulus formation documented in the NFC. The similarities in growth models developed from fin rays (age-length) and mark-recapture data (length-increment) suggest that annuli are being produced on a yearly basis and are identifiable by experienced readers for younger and intermediate aged fish (ages 3-7) and only slight differences may have existed for older individuals (ages > 7).

In contrast, scales appeared to be an unreliable structure on which to base growth estimates of migratory bull trout within the NFC. We observed greater differences in predicted and apparent ages from scale data for fish of most size classes. Comparisons of growth models developed from the scales and mark-recapture data indicated differences below and above age 6. Other studies utilizing scales for age and growth estimation of migratory bull trout produced much lower mean lengths at age for younger fish (< 6, Figure 7) (Bjornn 1961, Fraley and Shepard 1989, Salow 2001). Schiff (2004) used scales of NFC migratory bull trout to back-calculate lengths at previous ages and produced a much lower growth rate overall. In this study, ages estimated for smaller fish were slightly older, indicating that annuli were possibly not discernible. Estimates of age and growth of NFC migratory bull trout with scales should therefore be used with caution.

The observed differences in growth between the fin ray age-length model and the length-increment model may be associated with several factors. First, ages were estimated from fin rays collected in the spring (April-June) while the mark-recapture model was developed from fish captured during the spring and fall (October-November) and included fish at liberty for less than one year. Minor differences between models were expected because of seasonal growth variability associated with the mark-recapture model. A fish aged in the spring may not have developed an annulus for that year's growing season and would therefore be closer in size to the next age group (a fish that recently developed an annulus). Secondly, there were small sample sizes of older individuals in the age-length data

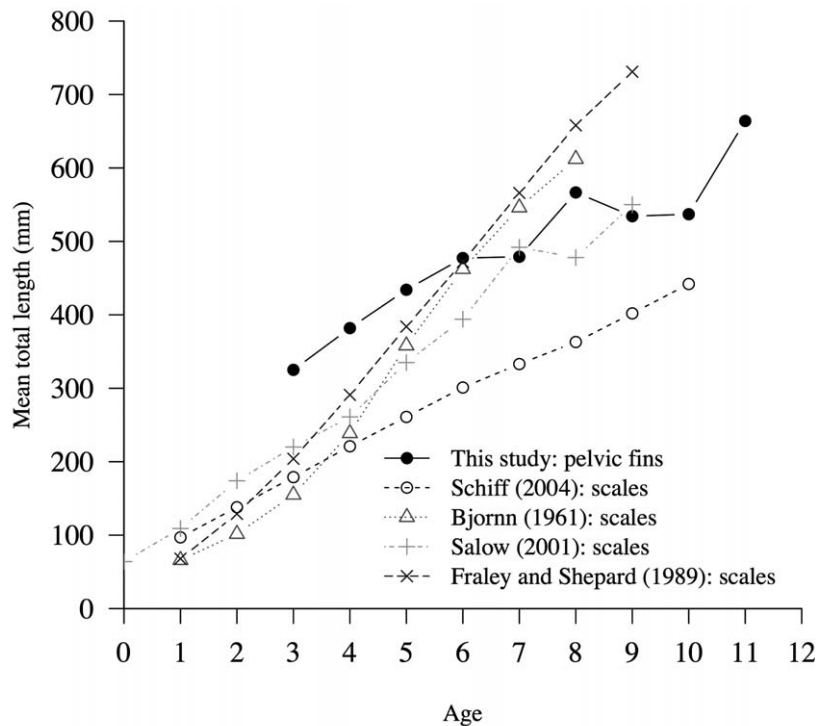


Figure 7. Mean total length (mm) at age for migratory bull trout in various drainages in Idaho and Montana. This study includes estimates from pelvic fin rays from the NFC. Schiff (2004) is based on back-calculation from scales from the NFC. The remaining studies are from scale-based estimates: Bjornn (1961) from Upper Priest Lake, Idaho, Salow (2001) from Boise River, Idaho, and Fraley and Shepard (1989) from Flathead Lake, Montana.

and larger individuals in the mark-recapture data. Haddon (2001) stated that the LVB is inadequate at the curve extremities where sample sizes are often small. Therefore, further research on aging precision of older individuals (> 7) should be attempted. Thirdly, fin ray morphology may have influenced the aging results. For larger individuals, fin ray annuli were often difficult to distinguish near the outer edge of many of the fin ray cross sections because slow growth rates at older ages crowd the annuli. This crowding of annuli was less of a problem for smaller, typically younger, fish. Finally, outliers in the mark-recapture data might explain observed differences between model types. Although, it is unknown whether the outliers were from measurement error, recording error, or just uncommon natural events, when they were removed from the length-increment model the age-length model from fin rays was

even closer in age predictions (largest difference < 1 year). The Fabens model has been found to be susceptible to outliers (Francis 1988). These outliers, however, may be indicative of the high growth variability possible in bull trout populations. In addition to the variability of various life history forms (resident and migratory) present in the NFC drainage (Schiff 2004) and the ability for forms to coexist and give rise to one another (Rieman and McIntyre 1993), other factors such as maturation schedules and age/timing of migrations (migratory form) into more productive waters (such as Dworshak Reservoir) could contribute to growth variability at the population level (Rieman and McIntyre 1983). Growth averaging models such as the LVB, therefore, should be used with caution for bull trout.

This is the first study to assess the precision of age estimates from scales and fin rays for model-

ing growth of adult migratory bull trout. These more accurate age results for fin rays over scales justify their preferential use in growth models. Until actual validation of ages occurs at various localities, it is recommended that our methods be used to evaluate estimates of age and growth for other populations of migratory bull trout.

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