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MANAGEMENT BRIEF

# Evaluation of techniques for estimating the age and growth of known-age White Sturgeon

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**Abstract**

**Objective:** Successful conservation and management of fishes require an understanding of their age and growth. However, methods for estimating the age and growth of long-lived fish species are difficult to validate. The Kootenai River basin has a decades-long mark–recapture program for endangered White Sturgeon *Acipenser transmontanus*. The mark–recapture history information for White Sturgeon allowed for the evaluation of fin rays for age and growth analysis.

**Methods:** Age was estimated from pectoral fin rays of known-age White Sturgeon ($n = 162$) to evaluate ageing accuracy and precision. Lengths were back-calculated using four models and measurements obtained from two fin ray transects (i.e., lateral and posterior).

**Result:** Between-reader agreement for White Sturgeon ages was 58.7%. Consensus age agreement with known ages was poor (30.7%) and decreased with age. Among the four back-calculation models, the Fraser–Lee model provided the lowest root mean square error and percent error. Estimates of mean back-calculated lengths at age derived from the Fraser–Lee model were similar between the two measurement transects. Back-calculated lengths at age were similar to known lengths at age.

**Conclusion:** Ageing of White Sturgeon using fin rays was unreliable, and accuracy decreased with fish age. Back-calculated lengths at age were accurate using measurements from fin rays of known-age fish. Length estimates from the two measurement transects were similar when using the Fraser–Lee method, suggesting that they may be used interchangeably.

KEYWORDS

age and growth, management, threatened and endangered species

## INTRODUCTION

Age and growth information is fundamental for making fisheries management and conservation decisions. Knowledge of age structure provides insight on recruitment dynamics and mortality, whereas information on growth can highlight important abiotic (e.g., physical habitat) and biotic (e.g., density dependence) factors influencing populations (Quist et al. 2012). Collectively, age and growth information provides important insight on fish population dynamics that can be used to guide and evaluate management actions (Mallen-Cooper and Stuart 2003; Shrader et al. 2003; Michaletz et al. 2011). Age and growth information is particularly important for long-lived species, many of which are threatened or endangered due to their sensitivity to anthropogenic disturbance (Boreman 1997; Hamel et al. 2014). Obtaining dependable age and growth estimates for long-lived species can be challenging, and using appropriate methods helps to ensure that management actions are efficient and effective.

For age and growth information to be considered reliable, methods should be verified and validated. Verification is used to describe the repeatability of estimations (e.g., consensus in age estimates among readers), whereas validation describes the accuracy of estimates (Buckmeier et al. 2017). Although verification of calcified structures for ageing is fairly common in the age and growth literature, validation of structures has occurred less frequently (Francis 1990; Quist et al. 2012). The use of unvalidated structures is problematic because it can lead to inaccurate age estimation (Mosegaard et al. 1988; Molony and Choat 1990; Wright et al. 1990). The best method for validation of ageing structures is to use structures from known-age fish (Campana 2001; Buckmeier et al. 2017). However, obtaining ageing structures from known-age fish in a natural environment is resource intensive and it can take multiple years to acquire even a small number of samples. Only a small portion (<20%) of the validation studies reviewed by Campana (2001) used known-age fish. Research that is focused on validation of growth estimates (e.g., length at age) is even less common than research focused on age estimates (Buckmeier et al. 2017). Most growth validation research depends on laboratory or hatchery experiments because validation requires comparisons of known lengths to those predicted by back-calculation techniques (Campana 2001). Validation of growth estimates in natural systems is rare but can be accomplished using information on recaptured fish.

Nonlethal sampling is often preferred to estimate age and growth of vulnerable and long-lived fishes, such as sturgeon (Acipenseridae). Otoliths are usually the best structure for estimating age and growth of fishes, but collection is lethal (Popper et al. 2005; Quist et al. 2012). Additionally, sturgeon otoliths are primarily composed of vaterite, leading to structural irregularities and annuli that are difficult to read (Stevenson and Secor 1999; Hamel et al. 2014; Hupfeld et al. 2023). Several studies have compared age information from otoliths to alternative structures for a variety of species and have found that otoliths and fin rays provide similar estimates (Phelps et al. 2007; Michaletz et al. 2009; Spiegel et al. 2010; Long et al. 2023). However, fin rays can be damaged or resorbed and often produce inaccurate age estimates due to the crowding of annuli in older fish (Johnson and Weston 1995; McFarlane and King 2001; Paragamian and Beamesderfer 2003; Hurley et al. 2004; Braaten et al. 2015). In addition, fin rays commonly display variability in overall condition and morphology (Veinott and Evans 1999). Although there are concerns with the use of fin rays for estimating age and growth, they remain the preferred structure for sturgeons (Paragamian and Beamesderfer 2003; Baremore and Rosati 2014).

**Impact statement**

Validation of age and growth information for long-lived species is difficult. Although age estimates regularly underestimated true age of White Sturgeon, particularly for fish older than age 10, growth estimates were similar to known lengths at previous ages. As such, fin rays are likely suitable for evaluating age and growth of White Sturgeon, but results from such analyses should be interpreted with appropriate caution.

Fin rays used for age and growth are typically sectioned in a transverse plane and then examined (Quist et al. 2012). When back-calculating length at age, increments from sturgeon fin rays are most often measured along a posterior transect (Figure 1; Brennan and Cailliet 1989; Everett et al. 2003; Braaten et al. 2015). The posterior transect extends from the center of ossification of the fin ray to the edge of the longest posterior lobe. Annuli along the posterior transect are typically less crowded than those in other areas of the fin ray. Another transect that has been used is a lateral transect, which extends from the center of the fin ray to the edge following a line perpendicular to the medial axis (Figure 1; Michaletz et al. 2009). Lateral transects may be a useful alternative for fin rays with morphological disfigurations (e.g., accessory fin rays; Brennan and Cailliet 1989) on posterior lobes. Ideally, readers would be able to use either posterior or lateral transects interchangeably to effectively measure individual fin rays. Flexibility in using either transect when back-calculating length at age would reduce the number of fish excluded from analysis, which may be particularly valuable for studies with small sample sizes. However, because back-calculated growth measurements for sturgeon species have rarely been validated, differences in growth estimated from posterior and lateral transects remain unaddressed. Extensive sampling in the Kootenai River system provides a unique opportunity to investigate the validity of age and growth methods for White Sturgeon *Acipenser transmontanus* by using known-age fish. The objectives of this study were to (1) examine reader accuracy in age estimates, (2) evaluate back-calculation methods, and (3) assess differences between growth estimates from lateral and posterior measurement transects on White Sturgeon fin rays.

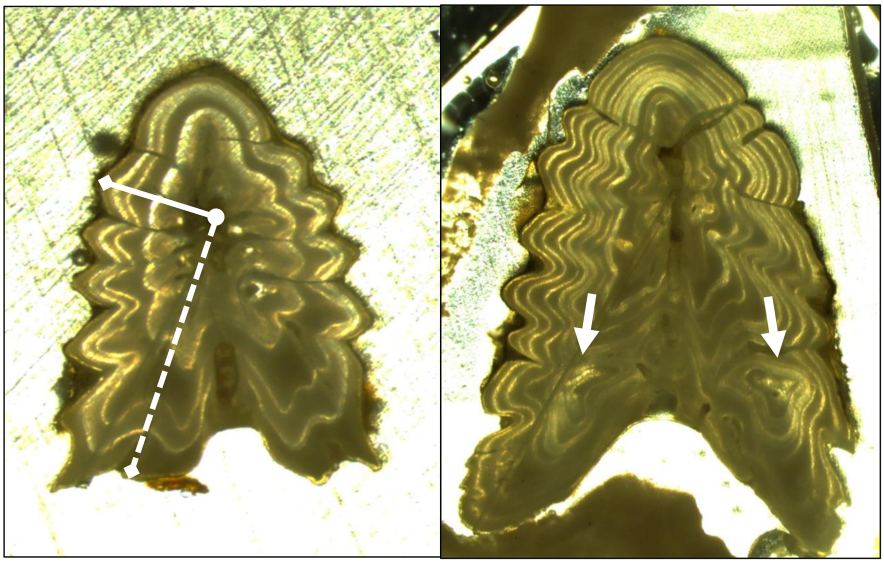

**FIGURE 1** Section of a White Sturgeon pectoral fin ray, identifying the two transects used in this study to measure growth (left panel). The solid line represents the lateral transect, and the dashed line represents the posterior transect. A White Sturgeon fin ray with accessory rays (indicated by arrows) impeding the measurement of growth along the posterior transect is shown in the right panel.

# METHODS

## Study area

The headwaters of the Kootenai River originate in the east Kootenay region of British Columbia. The river flows south into Montana and turns northwest near Libby, Montana. From there, the Kootenai River continues northwest through Idaho and into British Columbia's Kootenay Lake. From the west arm of Kootenay Lake, the river continues west to its confluence with the Columbia River at Castlegar, British Columbia. Natural barriers at Bonnington Falls, British Columbia, and Kootenai Falls, Montana, isolated fishes over 10,000 years ago (Northcote 1973).

## Fish marking and collection

White Sturgeon in the Kootenai River were listed as endangered under the Endangered Species Act in the United States in 1994 and the Species at Risk Act in Canada in 2006. Declines of White Sturgeon in the Kootenai River basin have been mainly attributed to poor recruitment from environmental changes caused by Libby Dam, Montana (Paragamian 2012; Hildebrand et al. 2016). Libby Dam is located 50 km upriver from a natural barrier (i.e., Kootenai Falls) and is the most upstream dam in the Kootenai River. Challenges to recruitment and growth of White Sturgeon in the Kootenai River stem from the compounding effects of several complex issues. The status of White Sturgeon in the Kootenai River has prompted natural resource agencies to implement a variety of conservation activities focused on restoring the White Sturgeon population, including flow augmentation and habitat restoration. Additionally, the Kootenai Tribe of Idaho (KTOI) constructed conservation hatcheries in response to the loss of recruitment. Over 300,000 larval and juvenile White Sturgeon have been released by KTOI into the Kootenai River since 1990 (KTOI 2009). Scutes were removed to identify brood year and rearing location of released White Sturgeon. Every fish released from 1992 to 2004 was marked with a passive integrated transponder (PIT) tag prior to release, 8% of fish released from 2005 to 2007 were marked with PIT tags, and most fish released after 2007 were marked with PIT tags (Hardy et al. 2020). Encounters with recaptured White Sturgeon during annual population surveys have been recorded for over three decades in a multi-agency database. Contributing agencies include KTOI, Idaho Department of Fish and Game (IDFG), British Columbia Ministry of Forests (BCMF), and Montana Department of Fish, Wildlife, and Parks.

White Sturgeon were sampled in the Kootenai River from March 13 to October 26, 2015, by IDFG and BCMF. Fish were sampled using gill nets and setlines as part of annual monitoring efforts (Hardy et al. 2020). Multifilament gill nets had stretch mesh sizes of 2.5, 5.1, and 7.6 cm. Setlines were 23 m long, with six baited hooks of various sizes (12/0, 14/0, and 16/0). Fork length (cm) and weight (kg) were measured from all captured White Sturgeon. All White Sturgeon were scanned for PIT tags. Data from each fish were entered into the shared database as each fish was processed. If a PIT tag identified the fish as being of known age and hatchery origin in the database, a fin ray sample was collected. The furthest anterior pectoral fin ray was cut using side-cutting pliers as close to the body as possible and then approximately 25 mm distally from the first cut (Koch et al. 2008). Fin ray samples were stored in coin envelopes and allowed to air dry.

## Age validation and verification

Fin rays were mounted in epoxy, and 0.5-mm-thick sections were cut using a Buehler low-speed saw (Koch and Quist 2007). Sections of fin rays were sanded with 400–1200-grit sandpaper until annuli were clearly visible. Fin ray cross sections were viewed with a dissecting microscope using transmitted light, and ages were assigned by three readers. Readers did not have information on fish length or age. Two readers had 1 year of experience in reading sturgeon fin rays, and the third reader had nearly 30 years of experience in reading sturgeon fin rays. After each reader recorded age estimates, a consensus age was agreed upon and recorded for each fish.

Accuracy and precision of age estimates were estimated using the FSA package (Ogle et al. 2022) in Program R (R Core Team 2018). Percent exact agreement (PA-0) and percent agreement within 1 year (PA-1) between readers were estimated. Accuracy of age estimates was assessed by comparing consensus and known ages. Precision for each comparison was calculated using the coefficient of variation (CV):

$$\mathrm{CV} = 100 \times \frac{\sum_{j=1}^{n} \frac{s_j}{\bar{x}_j}}{n},$$

where $s_j$ is the standard deviation of the age estimates for the $j$th fish, $\bar{x}_j$ is the mean estimated age for the $j$th fish, and $n$ is the number of aged fish in the sample (Campana et al. 1995; Ogle 2016). The McNemar test of symmetry was used to test whether the number of individuals that were over-aged was equal to the number of individuals that were underaged (McNemar 1947; Ogle 2016).

## Growth validation and transect comparison

A subsample of White Sturgeon with recapture histories was used to compare back-calculation models. We used 46 recapture observations of length at age from 32 fin rays measured laterally and 43 observations from 31 fin rays measured posteriorly. Incremental growth measurements were recorded for both the lateral and posterior transects of each fish (Figure 1). Posterior transects were measured along the longest lobe. If the posterior transect through the longest lobe included an accessory ray, the transect through the other lobe was measured. If both lobes contained accessory rays, only the lateral transect was measured. Fin ray disfigurement also prevented some lateral measurements. The distance from core to edge and the distance between annuli were measured using Image-Pro Plus (Media Cybernetics, Inc.) by one reader using knowledge of the known age of each fish. Annulus measurements were used to estimate mean back-calculated lengths at age using the Dahl–Lea, Fraser–Lee, body-proportional hypothesis (BPH), and scale-proportional hypothesis (SPH) methods (Francis 1990; Ricker 1992; Quist et al. 2012; Shoup and Michaletz 2017; Table 1). All parameters were derived from the $B_t$–$L_i$ regression (for Fraser–Lee and SPH) or the $L_i$–$B_t$ regression (for BPH), where $B_t$ is the measurement of the radius of the fin ray and $L_i$ is the corresponding body length. All back-calculation models were estimated using both lateral and posterior transect measurements.

The accuracy of back-calculation models was estimated by comparing linear regressions of observed versus predicted lengths of fish with recapture data for each back-calculation model using root mean square error (RMSE). Observed lengths were obtained from historical data in the multi-agency recapture database. Root mean square error was calculated for each model as

$$\mathrm{RMSE} = \sqrt{\frac{\sum (L_i - E_i)^2}{n}},$$

**TABLE 1** Models used for back-calculating lengths at age of White Sturgeon sampled from the Kootenai River in 2015, where $L_t$ is the length at annulus $t$; $L_T$ is the length at capture; $B_t$ is the structure radius at annulus $t$; and $B_T$ is the radius at capture. Parameters $a$, $b$, $c$, and $d$ were derived from the $B_t$–$L_i$ regression (for Fraser–Lee and scale-proportional hypothesis [SPH]) or the $L_i$–$B_t$ regression (for body-proportional hypothesis [BPH]). Parameter values were estimated separately for lateral transects ($a = 16.6$, $b = 314.7$, $c = 0.02$, $d = 0.002$) and posterior transects ($a = 16.5$, $b = 143.1$, $c = 0.04$, $d = 0.004$).

| Model | Equation |
|---|---|
| Dahl–Lea | $L_t = L_T\left(\frac{B_t}{B_T}\right)$ |
| Fraser–Lee | $L_t = a + (L_T - a)\left(\frac{B_t}{B_T}\right)$ |
| BPH | $L_t = L_T\left(\frac{a + bB_t}{a + bB_T}\right)$ |
| SPH | $L_t = -\frac{c}{d} + \left(L_T + \frac{c}{d}\right)\frac{B_t}{B_T}$ |

where $L_i$ is the measured length at age $i$; $E_i$ is the estimated length at age $i$; and $n$ is the number of observations. Absolute percent error (PE) of back-calculated length estimates was also calculated for each model as

$$\text{PE} = 100 \times \left| \frac{E_i - L_i}{L_i} \right|$$

to identify deviation from a 1:1 relationship between predicted and known values (Mayer and Butler 1993; Michaletz et al. 2009). The results for each model were compared between lateral and posterior transects by calculating PE between the estimates from each transect, where $E_i$ was the posterior estimate and $L_i$ was the lateral estimate.

In addition to marking annuli using knowledge of the known age of fish, we also marked annuli along the posterior transect using the consensus age (i.e., no knowledge of true age). The additional analysis provided an opportunity to evaluate error in growth estimates when White Sturgeon ages are unknown, as is typical in most age and growth evaluations. Using information from the growth model analysis described above, the growth model with the lowest RMSE was used to compare estimates of back-calculated length at age (i.e., from measurements using consensus age) to observed lengths at age from recaptured fish. Only annuli with known lengths from recapture events were examined. We estimated RMSE and PE for the model that used annuli measured with consensus ages to provide a comparison with the same model used with known-age estimates. Lastly, PE was estimated as the difference between observed lengths at age and back-calculated lengths at age using measurements with and without knowledge of true age.

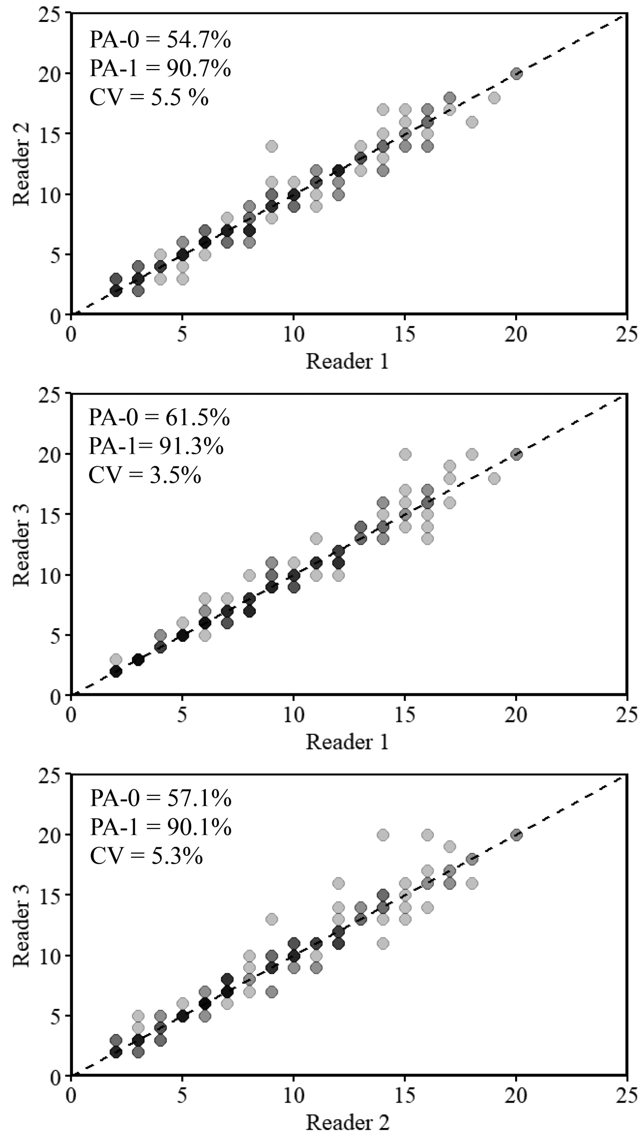


**FIGURE 2** Comparison of reader age estimates (years) from White Sturgeon fin rays ($n = 162$) collected from the Kootenai River in 2015. Percent exact agreement (PA-0), percent agreement within 1 year (PA-1), and mean coefficient of variation (CV) are provided. Shading indicates multiple observations, with darker shades representing more observations.

# RESULTS

## Age validation and verification

In total, 162 White Sturgeon varying from 23 to 112 cm fork length were sampled. Fish varied in age from 2 to 23 years. Between-reader agreement was consistent for each reader pairing (Figure 2). Average between-reader agreement was 57.8% for PA-0 and increased to 90.7% for PA-1. The results of McNemar's test of symmetry indicated that all readers underestimated White Sturgeon ages (McNemar $\chi^2 = 16.4–17.9$, df = 1, $p < 0.05$). Accuracy of the consensus age estimates was poor (PA-0 = 30.7%) and tended to decrease with true age (Figure 3). However, age estimates were not consistently underestimated until after age 10. Percent agreement with known ages was much higher for age-10 and younger fish (PA-0 = 41.8%; PA-1 = 82.3%) than for age-11 and older fish (PA-0 = 18.9%; PA-1 = 45.3%). The CV did not differ considerably between the age-groups (ages 2–10: CV = 12.2%; ages 11–23: CV = 12.8%).

## Growth validation and transect comparison

Estimates that were made using knowledge of true age generally underestimated length at age in all models, but differences were small (Figure 4). All models predicted the lengths of fish more accurately at longer lengths (>50 cm) than when fish were short (<50 cm). The

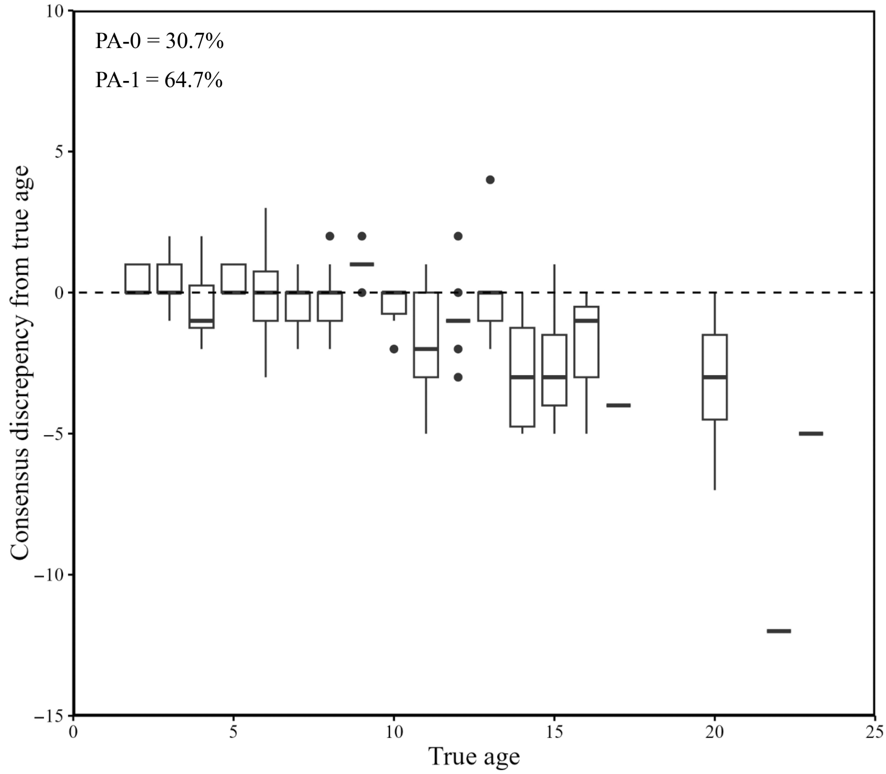


**FIGURE 3** Comparison of consensus age and the true age (years) of White Sturgeon ($n$ = 162) sampled from the Kootenai River in 2015. The dashed line represents exact age agreement. Percent exact agreement (PA-0) and percent agreement within 1 year (PA-1) are provided. The horizontal line in each box represents the median discrepancy in ageing from true age. The top of the box is the 75th percentile and the bottom of the box is the 25th percentile. Whiskers represent the 10th and 90th percentiles, and the black circles represent outliers. Ages that have lines as opposed to boxes contained few observations.

Fraser–Lee model measured along the posterior transect had the highest accuracy (i.e., RMSE = 5.2) among all models and transects. Estimates from the BPH and Fraser–Lee models were similar between lateral and posterior transects (Figure 5). In general, estimates derived from posterior transects underestimated lengths of small fish (<50 cm) to a greater degree than lateral transects.

The Fraser–Lee model measured along the posterior transect had the highest accuracy; therefore, the Fraser–Lee model using increments measured on the posterior transect was used to estimate length at age measured without knowledge of true age. When compared to length estimates using knowledge of true age, RMSE and PE increased slightly for estimates obtained without information on the known age of fish. Percent error in back-calculated length at age was similar on average (PE = 9.2%–12.6%) regardless of whether knowledge of true age was used when marking annuli.

## DISCUSSION

This study evaluated age and growth methods for White Sturgeon using fin rays from known-age fish and multiple decades of recapture data. Although between-reader agreement was moderate, agreement between consensus age and true age was low, particularly for age-11 and older fish. The oldest fish used in this study was age 23 and still considered a subadult in the Kootenai River (Hardy et al. 2020). White Sturgeon in the Kootenai River are known to live over 80 years (Paragamian and Beamesderfer 2003), so the error in ageing an adult fish is likely much greater than that observed in this study. Several other studies have shown that sturgeon fin rays are difficult to age and typically provide underestimates of age and growth. For instance, Rien and Beamesderfer (1994) marked White Sturgeon with oxytetracycline and found that fin rays underestimated the ages of fish in the Columbia River. Age estimates were particularly poor for slow-growing White Sturgeon that failed to form discrete annuli. Bruch et al. (2009) used bomb radiocarbon to validate age estimates from fin rays of Lake Sturgeon *A. fulvescens* in the Lake Winnebago system, Wisconsin. They found that ages were consistently underestimated after age 14 and that error increased with age. Paragamian and Beamesderfer (2003) studied age and growth of wild White Sturgeon in the Kootenai River. Using White Sturgeon of unknown age, they developed two von Bertalanffy models: one that used mark–recapture data and another that used

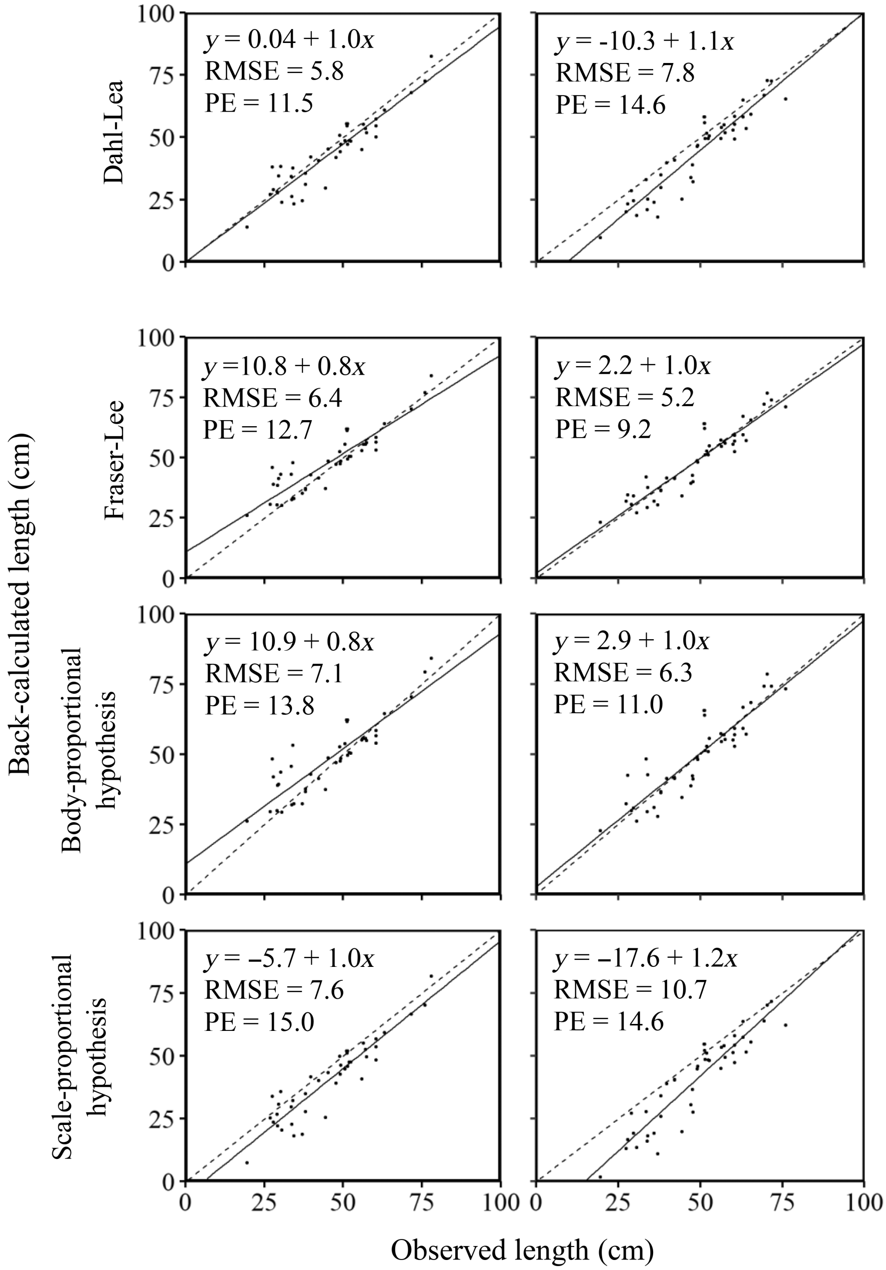


**FIGURE 4** Comparison of length estimates from multiple back-calculation models (using knowledge of true age) to known lengths of White Sturgeon sampled from the Kootenai River in 2015. Measurements were taken along lateral transects (left panels) and posterior transects (right panels). The dashed line represents the 1:1 reference line; the solid line is the regression line. The equation, root mean square error (RMSE), and percent error (PE) are provided for each model.

incremental measurements from fin rays. Comparisons of the two models suggested that both age and growth estimates were underestimated using fin rays. The findings from the current study similarly indicate that ageing White Sturgeon by using fin rays is inaccurate and worsens as age increases.

Growth estimates from White Sturgeon fin rays were relatively accurate. Growth of White Sturgeon was estimated using four back-calculation methods along two distinct fin ray transects; predicted lengths were validated using known lengths from recaptures. For all back-calculation models, error decreased as fish increased in length. For example, Fraser–Lee model estimates using measurements from the lateral transect had a PE of 13.2% for fish less than 50 cm, whereas fish greater than 50 cm had a PE of 1.7%. In general, the models slightly underestimated observed lengths. The majority of sampling for this project was completed during the summer after annuli were likely formed (Rien and Beamesderfer 1994). As would be expected,

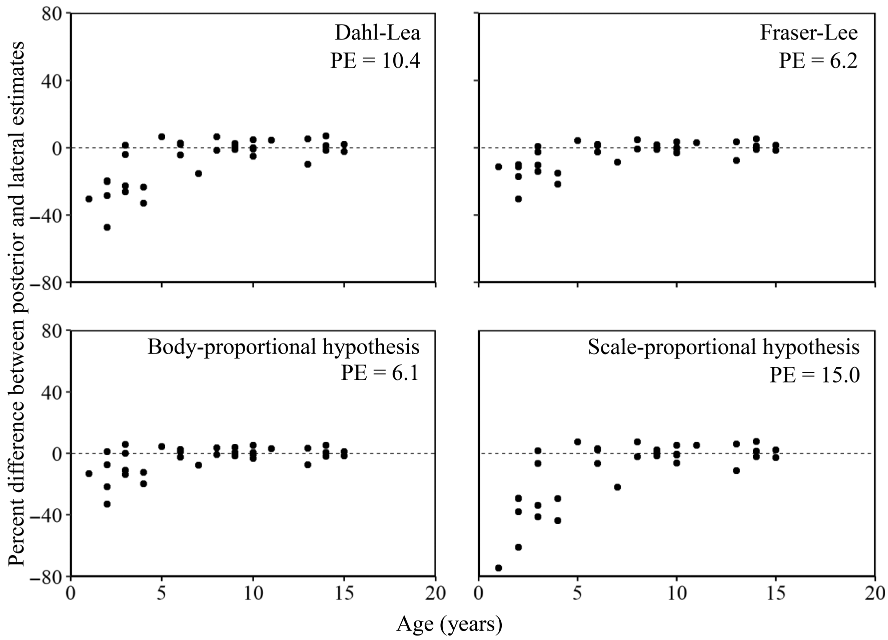


**FIGURE 5** Percent difference between posterior and lateral measurement transects for each back-calculation model of White Sturgeon sampled from the Kootenai River in 2015. Annuli were marked using knowledge of true age. The dashed line represents exact agreement. Error above the dashed line indicates that estimates from posterior measurements are greater than estimates from lateral measurements. Error below the dashed line indicates that estimates from lateral measurements are greater than estimates from posterior measurements. Percent error (PE) is provided for each model.

the estimated length at age (i.e., annulus formation) would be less than an observed length taken later in the same year. In addition to the back-calculation model comparison, another goal of this study was to evaluate differences in length estimates from lateral and posterior transects. To our knowledge, the only other study that has evaluated the differences in transects was that by Michaletz et al. (2009), who found that the lateral transect on Channel Catfish *Ictalurus punctatus* spines provided the most accurate estimates. We found that estimates derived from the lateral and posterior transects were similar. However, the difference between lateral and posterior estimates was lowest when using the BPH (6.1%) and Fraser–Lee (6.2%) models.

Growth estimates derived from measurements made without knowledge of fish age were similar to length estimates from measurements made with knowledge of known ages. Similarity in growth estimates was likely due to the moderately high PA-1 (64.7%). In addition, growth of White Sturgeon—particularly at older ages—was quite slow. As such, errors in marking the correct annulus had little influence on the corresponding back-calculated lengths at age, thereby suggesting that lengths at age estimated from White Sturgeon fin rays of unknown age may still be useful for estimating growth rates. Importantly, investigating relationships between year-specific covariates and increments for particular growth years (Watkins et al. 2017) is problematic.

Ageing sturgeon is challenging given their longevity and relatively slow growth. Overcoming the uncertainty of ageing to complete growth validation was only possible because of the known ages and recapture database for White Sturgeon in the Kootenai River basin. Age estimates by experienced readers were inaccurate, but back-calculated lengths at age closely reflected known lengths from recapture events of White Sturgeon. The Fraser–Lee model for estimating back-calculated lengths at age is likely the best model because it produced the least overall error for both transects and estimates from transects were comparable. Further research using known-age White Sturgeon would provide additional insight on the use of fin rays in age and growth analysis.

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## CONFLICT OF INTEREST STATEMENT

There is no conflict of interest declared in this article.

## DATA AVAILABILITY STATEMENT

Fish data are property of the IDFG but can be made available upon reasonable request.

## ETHICS STATEMENT

This study did not require the direct handling of fish because it used an existing IDFG data set. All fish handling associated with the creation of this data set was performed in accordance with IDFG and American Fisheries Society guidelines.

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