

Fish length back-calculation from scales: advancing methodology and correction of bias

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Abstract

Fish length back-calculation from hard structures (e.g., scales, otoliths, spines, etc.) is a commonly used method to reconstruct individual growth rates and sizes at age/stage in the absence of an intensive sampling-resampling timeseries. However, reliable estimates via these methods require the empirical validation of multiple assumptions about the growth of these hard structures. Here, we focus on reducing bias in scale-based back-calculations and validating proposed improvements using archived scales from a wild population of anadromous steelhead trout (*Oncorhynchus mykiss*). We first describe a series of back-calculation problems and propose solutions that can be integrated into common back-calculation methods. We then compare back-calculation accuracy, precision, and bias between proposed solutions and traditional forms of two back-calculation methods: Fraser-Lee and Body-Proportional. We discovered that the assumption that rapid growth begins immediately after juvenile steelhead pass downstream of the fish fence (300 m upstream of the ocean) was invalid and required a correction factor to prevent overestimating fish length by an average of 14%. The proposed modified methods we described performed better than traditional back-calculation methods. Overall, these findings can improve estimates of fish length from scale-based back-calculations and illustrate the importance of validating key assumptions.

Key words: back-calculation, measurement error models, salmonids, scales, smolts

Résumé

Le rétrocalcul de la longueur des poissons à partir de structures dures (p. ex. écailles, otolithes, épines) est une méthode fréquemment utilisée pour reconstituer les taux de croissance et les tailles selon l'âge ou l'étape de vie d'individus en l'absence d'une série chronologique d'échantillonnage répété intensif. Des estimations fiables obtenues par ces méthodes requièrent toutefois la validation empirique de différentes hypothèses concernant la croissance de ces structures dures. Nous nous penchons sur la réduction des biais dans les rétrocalculs basés sur les écailles et la validation d'améliorations proposées en utilisant des écailles d'archives issues d'une population sauvage de truites arc-en-ciel anadromes (*Oncorhynchus mykiss*). Nous décrivons d'abord une série de problèmes de rétrocalcul et proposons des solutions pouvant être intégrées à des méthodes de rétrocalcul répandues. Nous comparons ensuite l'exactitude, la précision et les biais du rétrocalcul des solutions proposées et de formes traditionnelles de deux méthodes de rétrocalcul, soit la méthode de Fraser-Lee et la méthode en proportion du corps. Nous relevons que l'hypothèse voulant que la croissance rapide commence immédiatement après le passage des truites arc-en-ciel en aval du barrage (30 m en amont de l'océan) est invalide et nécessite un facteur de correction pour prévenir une surestimation de la longueur des poissons d'en moyenne 14 %. Les méthodes modifiées proposées que nous décrivons donnent de meilleurs résultats que les méthodes de rétrocalcul traditionnelles. Globalement, ces constatations peuvent améliorer les estimations de la longueur des poissons obtenues par rétrocalcul basé sur les écailles et illustrent l'important de valider les hypothèses clés. [Traduit par la Rédaction]

Mots-clés : rétrocalcul, modèles d'erreur de mesure, salmonidés, écailles, smolts

Introduction

Understanding patterns and processes underlying somatic growth and body size is foundational to much of modern ecology and resource management—particularly for species that exhibit indeterminate and nonlinear somatic growth, such as fishes (King 2007). Rate of somatic growth shapes individuals' body size-at-age (or stage), and is associated with life-history

strategies, habitat shifts, migration behaviour, and stochastic processes (e.g., Rooij et al. 1995; Kendall et al. 2015; Wilson et al. 2019). Somatic growth can also indicate fish population density, productivity, and fecundity (Barneche et al. 2018).

Back-calculating fish lengths from hard structures (e.g., scales, otoliths, opercula) is a commonly used method for determining lengths at ages or stages in the somatic growth

Table 1. Fish length back-calculation assumptions (Francis 1990).

Assumption	Description
1	The positions of checks and annuli on hard structures must remain constant through time (i.e., no warping or loss of marks as fish grow).
2	The estimated times of formation of checks and annuli are correct.
3	The back-calculation function describing the relationship between hard structure measures and fish length is accurate.

histories of a wide variety of fishes (e.g., Horppila and Nyberg 1999; Klumb et al. 2001; Heidarsson et al. 2006; Landa et al. 2015; Isermann et al. 2018). For example, two of the fundamental papers on back-calculation by Ricker (1992) and Francis (1990) have been cited 160 and 1021 times, respectively, since they were published (Google Scholar, accessed 20 September 2022). Typically, age or stage can be inferred from hard structures due to seasonal or stage-related changes in somatic and hard structure growth rate, which appear as bands or clusters of rings in hard structures termed annuli or growth checks (Francis 1990). Checks or annuli formed in the past can be used to infer fish length at the time those marks were formed by sampling hard structures that grow in proportion to fish length, and a function that describes the relationship between hard structure measures and fish length (Francis 1990). Thus, fish length back-calculation is a powerful tool that has been used to infer a variety of information including annual somatic growth rates (e.g., Fera et al. 2015), size-selective survival (e.g., Holtby et al. 1990), and links between environmental variables and somatic growth (e.g., Beardsley and Britton 2012).

Back-calculating fish length involves a series of assumptions that bear careful examination. Francis (1990) broke down the validation of fish length back-calculation into three key assumptions (Table 1). Assumption 1 is that the positions of checks and annuli on hard structures remain constant through time. It is extremely difficult to test and rarely validated—in fact, we were unable to find a published example of validating assumption 1. Assumption 2 is that the estimated times of formation of checks and annuli are correct. To test this assumption, studies need to verify that the timing of an event (such as migrating to a new habitat), and the formation of a check are synchronized. If there is asynchrony, this leads to under- or overestimation of size at time. Assumption 2 can be validated with a variety of methods, including using tetracycline to create a visible band on hard structures to validate the timing of growth checks (e.g., Holden and Vince 1973), bomb radiocarbon ageing for estimating the year in which a growth check forms (Campana 1997), or laser ablation to track shifts in hard structure chemistry if (a) a growth check should align with a habitat transition that includes a change in water chemistry and (b) there is minimal lag between exposure to new water chemistry and expression of the new chemistry in the hard structure (Ryan et al. 2019). Assumption 3 is that the back-calculation method is accurate. This assumption can be validated by marking and measuring fish at the stages/ages that are being back-calculated, releasing them, and recapturing them later so that back-calculations can be compared with true lengths. Without

validation of assumptions, size-at-age (or stage) can be misestimated (Francis 1990), potentially leading to mismanagement where somatic growth-associated traits are used as indicators of stock status or production. While studies often assert that assumptions of back-calculation procedures have been previously validated in other papers, such validations are seldom performed.

A great deal of effort has been invested into developing and testing various methods of back-calculation to validate assumption 3 (e.g., Whitney and Carlander 1956; Campana 1990; Francis 1990; Ricker 1992; Ashworth et al. 2017). While there are a wide variety of back-calculation functions (Table 2), they can be broadly split into two categories: Scale-Proportional Hypothesis (SPH) versus Body-Proportional Hypothesis (BPH) methods (Francis 1990). Using scales as an example, the SPH considers scale radius $\sim$ body length, whereas the BPH considers body length $\sim$ scale radius (Francis 1990). The SPH and BPH hypothesis methods produce different length estimates in back-calculations, thus Francis (1990) recommended that scientists use the average of both (Table 2). However, Ricker (1992) proposed the use of geometric mean regression (rather than ordinary least squares (OLS) regression) as an alternate solution to the differences in length estimates from the SPH versus BPH methods. Because geometric mean regression assigns error equally among the x- and y-axes, body length $\sim$ hard structure becomes the reciprocal relationship of hard structure $\sim$ body length. Unfortunately, little attention has been paid to Ricker's paper relative to Francis' paper, thus the use of OLS regression and the dichotomy between the BPH and SPH methods remains common. Quantitative approaches that effectively deal with uncertainty are particularly important for scales given the potential for multiple sources of variation. For example, individual-level variation in scale size (Hanson et al. 2019) and scale erosion and resorption (Claiborne et al. 2011) could all introduce variability. Furthermore, there is evidence that body-scale relationships may change with age (Zivkov 1996), but incorporation of age/stage-specific body-scale relationships in scale-based back-calculation is extremely rare. Thus, there is an opportunity to update scale-based back-calculation methodology.

Here, we aim to examine and improve scale-based fish length back-calculations with a series of analytical advances applied against an extensive empirical data set. We begin with an overview of problems that may lead to inaccuracy in scale-based back-calculations (i.e., issues that affect assumption 3), including individual-level variation in scales, nonlinear relationships between body length and scale radius, age/stage-induced shifts in the body-scale relationship,

Table 2. Common fish length back-calculation functions and new derivations.

Method	Function	Associated hypothesis	Reference	Description
Simple Regression	$L \sim \beta S + \alpha + \varepsilon$ $S \sim \beta L + \alpha + \varepsilon$	BPH SPH	Carlander 1981; eqs. 1 and 2 in text	<ul style="list-style-type: none"> – assumes linear relationship – fit regression, then plug in hard structure measure and solve for length – not recommended by Francis (1990) and often used by mistake in place of the Fraser–Lee, Scale-Proportional, or Body-Proportional method
Dahl–Lea	$L_i = \left(\frac{S_i}{S_c}\right) L_c$	SPH/BPH	Lea 1910	<ul style="list-style-type: none"> – assumes linear relationship between hard structure measure and body length that always intersects the origin (when $L = 0$, $S = 0$) – accounts for deviations in body–scale ratios
Monastyrsky	$\ln(L) \sim \beta \ln(S) + \alpha + \varepsilon$; $L_i = \left(\frac{S_i}{S_c}\right)^\beta L_c$ $\ln(S) \sim \beta \ln(L) + \alpha + \varepsilon$ $L_i = \left(\frac{S_i}{S_c}\right)^{1/\beta} L_c$	BPH SPH	Bagenal and Tesch 1978; Francis 1990	<ul style="list-style-type: none"> – linear or nonlinear relationship – fit regression to extract β for use in the second equation – assumes a constant slope in log space, but ignores log space intercept – accounts for deviations in body–scale ratios
Fraser–Lee	$L \sim \beta S + \alpha + \varepsilon$; $L_i = \alpha + (L_c - \alpha) \left(\frac{S_i}{S_c}\right)$ OR $L \sim \beta S + \alpha + \varepsilon$; $L_i = (\beta S_i) \left(\frac{L_c - \alpha}{\beta S_c}\right) + \alpha$	BPH	Fraser 1916; Lee 1920; eqs. 1, 3, and 8 in the text	<ul style="list-style-type: none"> – the two rows of equations are equivalent – fit regression to extract α and (or) β for use in the second equation for both rows – can use biological intercept* in place of α – accounts for deviations in body–scale ratios
Multi-Age/Stage† Fraser–Lee	$L_0 \sim \beta_0 S_0 + \alpha_0 + \varepsilon$; $L_1 \sim \beta_1 S_1 + \alpha_1 + \varepsilon$; $L_i = (\beta_0 S_i) \left(\frac{L_c - \alpha_1}{\beta_1 S_c}\right) + \alpha_0$	BPH	Eqs. 6, 7, and 9 in the text	<ul style="list-style-type: none"> – fit regressions to extract $\alpha_{0,1}$ and $\beta_{0,1}$ for use in the third equation – accounts for age/stage-specific linear body–scale relationships – accounts for deviations in body–scale ratios
Modified†,‡ Fraser–Lee	$\ln(L_0) \sim \beta_0 \ln(S_0) + \alpha_0 + \varepsilon$; $\ln(L_1) \sim \beta_1 \ln(S_1) + \alpha_1 + O_j + \varepsilon$; $L_i = \exp \left\{ [\beta_0 \ln(S_i)] \left[\frac{\ln(L_c) - (\alpha_1 + O_j)}{\beta_1 \ln(S_c)} \right] + \alpha_0 \right\}$	BPH	Eqs. 16–18 in the text	<ul style="list-style-type: none"> – fit regressions to extract $\alpha_{0,1}$ and $\beta_{0,1}$ for use in the third equation – accounts for age/stage-specific nonlinear body–scale relationships – accounts for deviations in body–scale ratios
Scale-Proportional	$S \sim \beta L + \alpha + \varepsilon$; $L_i = \left(-\frac{\alpha}{\beta}\right) + \left[L_c - \left(-\frac{\alpha}{\beta}\right)\right] \left(\frac{S_i}{S_c}\right)$	SPH	Hile 1941; Francis 1990	<ul style="list-style-type: none"> – fit regression to extract α and β for use in the second equation – can use biological intercept in place of $-\alpha/\beta$ – accounts for deviations in body–scale ratios
Body-Proportional	$L \sim \beta S + \alpha + \varepsilon$; $L_i = (\beta S_i + \alpha) \left(\frac{L_c}{\beta S_c + \alpha}\right)$	BPH	Whitney and Carlander 1956; Francis 1990; eqs. 1 and 4 in the text	<ul style="list-style-type: none"> – fit regression to extract α and β for use in the second equation – can use biological intercept in place of α, where α is included as a fixed variable when fitting the regression – accounts for deviations in body–scale ratios
Multi-Age/Stage† Body-Proportional	$L_0 \sim \beta_0 S_0 + \alpha_0 + \varepsilon$; $L_1 \sim \beta_1 S_1 + \alpha_1 + \varepsilon$; $L_i = (\beta_0 S_i + \alpha_0) \left(\frac{L_c}{\beta_1 S_c + \alpha_1}\right)$	BPH	Eqs. 6, 7, and 10 in the text	<ul style="list-style-type: none"> – fit regressions to extract $\alpha_{0,1}$ and $\beta_{0,1}$ for use in the third equation – accounts for age/stage-specific linear body–scale relationships – accounts for deviations in body–scale ratios
Modified†,‡ Body-Proportional	$\ln(L_0) \sim \beta_0 \ln(S_0) + \alpha_0 + \varepsilon$; $\ln(L_1) \sim \beta_1 \ln(S_1) + \alpha_1 + O_j + \varepsilon$; $L_i = \exp \left\{ [\beta_0 \ln(S_i) + \alpha_0] \left[\frac{\ln(L_c)}{\beta_1 \ln(S_c) + \alpha_1 + O_j} \right] \right\}$	BPH	Eqs. 16, 17, and 19 in the text	<ul style="list-style-type: none"> – fit regressions to extract $\alpha_{0,1}$ and $\beta_{0,1}$ for use in the third equation – accounts for age/stage-specific nonlinear body–scale relationships – accounts for deviations in body–scale ratios

Note: S = hard structure measures (e.g., scale radius), L = fish length measures, β = regression slope coefficient, α = regression intercept, ε = normally distributed error, S_i = hard structure measure from the origin to the i th mark, S_c = hard structure from the origin to the outer margin at the time of capture, L_i = fish length at the time of formation of the i th hard structure mark, and L_c = fish length at the time of capture. SPH = the Scale-Proportional Hypothesis, and BPH = the Body-Proportional Hypothesis.

*A biological intercept is measured directly from juvenile fish and is the average body length at which a hard structure forms.

†0 and 1 subscripts represent the life stage for which length is being back-calculated and the life stage at capture, respectively.

‡ O_j is a categorical variable representing age (number of years spent at sea) within stage (adult) for steelhead trout.

sexual dimorphism, and scale erosion/resorption. For each problem, we provide a solution that can be integrated into common back-calculation methods. We then validate the timing of a growth check (assumption 2) and assess whether integrating our solutions in two common back-calculation meth-

ods improves back-calculation accuracy (assumption 3) for an imperiled population of steelhead trout (*Oncorhynchus mykiss*). We show that unvalidated scale-based back-calculations can hide substantial inaccuracy and bias and we then provide a post-validation method for correcting that bias. We also

find that the combination of several solutions to common back-calculation problems improves back-calculation accuracy over traditional methods.

Methods

Introduction to fish length back-calculation functions

At the core of every back-calculation method is a mathematical function typically composed of two parts. The first part is a regression equation that describes the relationship between body length and scale radius, and the second part is the back-calculation equation that uses parameter estimates from the regression, the length and scale radius of a fish at capture, and the scale radius of the fish at a previous age/stage to estimate the length of that fish at the previous age/stage.

While there are many different back-calculation methods, most are underpinned by one of two simple OLS regressions

$$(1) \quad L \sim \beta S + \alpha + \varepsilon$$

$$(2) \quad S \sim \beta L + \alpha + \varepsilon$$

where L is fish length, S is scale radius, β is the slope term, α is the intercept, and ε is normally distributed error. Equation 1 follows the BPH because body length is the dependent variable, while eq. 2 follows the SPH because scale radius is the dependent variable. These are the most common, but they are not the only BPH and SPH regressions—for example, these regressions can be modified to log-log relationships (see the Monastyrsky method, Table 2). While different back-calculation methods may share the same regression (and therefore, follow the same hypothesis), they always use different back-calculation equations (see Table 2 for the common back-calculation methods).

For this paper, we focus on a pair of methods that follow the BPH and use eq. 1 for their regression: the Fraser-Lee method and the Body-Proportional method. We focus on the BPH for two reasons: (1) Ricker (1992) argued that it makes greater biological sense to use the regression of body length $\sim$ scale radius (BPH) than scale radius $\sim$ body length (SPH) because the SPH regression can result in y-intercepts where body length is negative (Ricker 1992); (2) below, we present a solution that nullifies the BPH versus SPH debate identified in the introduction. Although both methods follow the BPH, they differ in how they describe proportional deviation from the average body-scale relationship. Where the Fraser-Lee equation (eq. 3) describes a proportional deviation from the slope of the average body-scale relationship, the Body-Proportional equation (eq. 4) considers the proportional deviation of the observed fish length at capture from the expected fish length at capture given scale radius at capture.

$$(3) \quad L_i = \alpha + (L_c - \alpha) \left(\frac{S_i}{S_c} \right)$$

$$(4) \quad L_i = (\beta S_i + \alpha) \left(\frac{L_c}{\beta S_c + \alpha} \right)$$

where L_i is fish length at previous age or stage i , L_c is fish length at capture, S_i is scale radius at previous stage or age i , S_c is scale radius at capture, and α and β are estimated from the regression in eq. 1. We focus on these two back-calculation methods because they are extremely common and easily modified. However, many proposed solutions to the challenges of back-calculations identified below can also be applied to other back-calculation functions.

Potential back-calculation challenges and solutions

The following section overviews a suite of problems that may lead to inaccuracy in scale-based back-calculation and provides solutions that can individually be integrated into most common back-calculation methods (Table 2), or all simultaneously integrated into the Fraser-Lee (eqs. 1 and 3) or Body-Proportional methods (eqs. 1 and 4). Some solutions can be used in any back-calculation regardless of the hard structure used, while others are specific to scales or explicitly motivated by salmonids. For each solution, we provide the case for their use and commentary on how they fit into the larger picture of fish length back-calculation methods.

Individual-level variation in scales

Across all hard structures used in fish length back-calculation, accounting for error in the dependent (e.g., fish length) and independent (e.g., scale radius) variables of the body-hard structure relationship is crucial to finding the most accurate regression slope and intercept. OLS regression assumes that there is neither measurement error (the difference between the true value and the measured value) nor process error (error arising due to real drivers of variation) in the independent variables (Ahrestani et al. 2013). For example, in the regression of fish length $\sim$ scale radius, process error in the independent variable would be deviation from the mean scale radius for a given fish length due to an outside factor that affects scale radius but not fish length (e.g., scale erosion), and imperfect scale measurement would produce measurement error. By assuming all errors occur in the dependent variable, OLS regression produces shallower slopes than regression methods that account for error in the independent variable, introducing bias into the body-hard structure relationship.

As we noted in the Introduction, Ricker (1992) proposed using geometric mean regression to solve this issue and move past the SPH versus BPH dichotomy. Geometric mean regression assigns error equally to the dependent and independent variables (50% for Y , 50% for X). This likely works well for hard structures that are not repeatedly or variably sampled within individuals and are unlikely to erode—e.g., sampling an otolith, a dorsal spine, the right cleithrum, etc. However, scales can be highly variable at the individual fish level because they vary in size and shape depending on where they are sampled from on the body of a fish (e.g., Ibañez et al. 2009), and they are vulnerable to erosion and damage. Thus, it seems quite likely that scales may be

responsible for more than 50% of the total error in the body–hard structure relationship.

Sampling and measurement methods have been developed to reduce individual-level variation in scales, including strict protocols that explicitly define where on a fish's body scales should be sampled from (e.g., Maher and Larkin 1955), and taking scale radius measurements that are not on the major axis of the scale (the axis that divides a scale in half along its length; e.g., Morita 2001; Bond et al. 2008). However, there are several factors that contribute to individual-level variation in scales that cannot be avoided through improved sampling or measurement techniques. First, there will inevitably be some variation in the sampled body location across many live fish, which can influence scale size or shape (Ibañez et al. 2009). Second, scale loss or damage is common in most fish species, thus scale regrowth is a common feature (Bereiter-Hahn and Zylberberg 1993). Scale regrowth appears as a “blanked out” portion of a scale where circuli and annuli information are lost¹. Multiple scales are often collected to mitigate this risk. However, even with proper methodology applied to sampling scales to reduce individual-level variation, it is possible that geometric mean regression may not accurately reflect the proportion of error attributable to scales in the body–scale relationship. Instead, we recommend using a measurement error model, where the amount of measurement error attributable to individual-level variation in scales is measured and explicitly accounted for.

Here, we present a Bayesian measurement error model² coded in the statistical software *Stan* (Carpenter et al. 2017), where measurement error τ is fixed (i.e., not estimated in the model) as defined:

$$(5) \quad \tau = \frac{\sum_k^n \sigma_k}{n}$$

where σ_k represents the standard deviation of the mean sampled scale radius for the k th fish, and τ is the mean of those standard deviation measures across n sampled fish. We recommend calculating τ using five scales per individual fish for at least 30 fish across the entire size range, which should provide an appropriate balance between statistical sample size, sampling feasibility and fish health³. The estimates of β and α from the Bayesian measurement error model can be directly substituted for β and α from a BPH OLS regression in the Fraser–Lee method, BPH version of the Monastyrsky method, or Body-Proportional method (Table 2). The estimates of β and α from the Bayesian measurement error model should be more accurate than OLS estimates because measurement variation in scale radii is explicitly accounted for. Thus, this eliminates the need for the SPH versions of methods such as the Scale-Proportional method (the SPH version of the Fraser–Lee method) to average with the BPH methods because the appropriate proportion of error has been assigned to each axis of the BPH regression.

The measurement error model we present is relatively specific to scales but would be equally suitable for any hard

structure that varies at the individual level where a suitable number of samples (five or more) can be taken. An alternative approach can be found in Nater et al. (2018), who use a state-space modeling approach to account for measurement error. We recommend using the measurement error model approach when repeated samples are not available for all individuals in a data set, or when time and (or) money constraints make it impractical to measure repeated samples for all individuals in the data set.

Nonlinear relationships

The study of allometry is fundamental to fish length back-calculation. Allometry is a long-standing field of biology that studies how the dimensions of body parts or metabolism scale with organism body size or the size of another body part (Gayon 2000). It is standard practice to log-transform both the dependent and independent variables and use a reduced major axis (RMA) regression (similar to geometric mean (GM) regression, it also assigns equal error to the dependent and independent axes) to infer whether there is an isometric, negative allometric, or positive allometric relationship between two body variables (Gayon 2000; Niklas and Hammond 2014). For the relationship between body length (length) and a hard structure measure (length), the isometric slope = 1, which is linear in non-log space. If the slope of the relationship is greater or less than 1, it is positively or negatively allometric, which is nonlinear in non-log space. Many published scale-based back-calculations assume isometry between body length and scale radius without testing that assumption (e.g., Martinson et al. 2000; Tedesco et al. 2009; Izzo and Zydlewski 2017). Thus, except for authors using the Monastyrsky method (Table 2), scale-based fish length back-calculation is rarely treated as an allometric scaling problem.

Common back-calculation methods (except the Monastyrsky method) can be used with hard structure measure and body length log-transformed for the regression and back-calculation equation, where the final output can be back-transformed to non-log space (Fry 1943). Before using the isometric version of a back-calculation method, one should at least test for isometry using a log–log linear regression. If the RMA or GM log–log regression slope is significantly different from 1, the standard isometric back-calculation is not appropriate.

Log–log regressions can be used to describe body–hard structure relationships for all hard structures used in back-calculations. A caveat to log-transformation is that the back-transformed intercept of log–log BPH regressions forces the origin to be zero (but see the Modified Fry method in Vigliola et al. 2000). This means that the intercept is no longer interchangeable with biological intercepts (the empirical measurement of average body length at formation of the hard structure), a common modification for improving the Fraser–Lee method. For hard structures besides scales, relationships that go through the origin may not be a large issue because hard structures may develop at very small body lengths. For scales, we know that some fishes, such as salmonids, do not begin scale formation until they reach a particular length

¹ See Fig. S1i in Supplementary material A.

² Code available in Supplementary materials B and C.

³ See Fig. S2 for a simulation showing the trade-off between sample size and bias in Supplementary material A.

(e.g., Fry 1943; Walker and Sutton 2016); thus, describing how body length changes with scale size using a single relationship may not be feasible.

Age/stage-induced shifts

Ontogenetic shifts in the body–scale relationship should be common given that fish typically experience multiple stages of somatic growth across their lifespan (Wilson et al. 2018). Furthermore, fish typically do not hatch with fully formed scales—instead, fish form scales after reaching a certain body size, such that their scales must grow at a rate to catch up to body size at formation plus additional somatic growth if their scales provide complete or overlapping body coverage (Carlander 1985). For example, Atlantic salmon (*Salmo salar*) do not begin scale formation until they are ~30 mm long, and their scales do not provide complete body coverage until they are ~50 mm long, at which point their scale growth can decelerate to match somatic growth rate (Warner and Havey 1961). Shifts in the body–scale relationship should also be expected when fish undergo rapid changes in body morphology during stage changes. For example, salmonids experience rapid body elongation during smoltification (McCormick and Saunders 1987) and develop significant secondary sexual characteristics in preparation for spawning (e.g., Hendry and Berg 1999). Scale-based back-calculations rarely account for ontogenetic shifts in the body–scale relationship.

Common scale-based back-calculations (Table 2) assume that a single function adequately describes the relationship between body length and scale radius throughout the ontogeny of fish. However, Zivkov (1996) showed that body–scale relationships can change as fish grow, and suggested that the differences in these relationships may reduce the utility of common back-calculations based on proportional deviation from the average body–scale relationship. To solve this problem, Zivkov suggested characterizing each distinct age/stage with a separate relationship. Here, we expand on this idea by suggesting that ages/stages where sexual dimorphism occurs may require sex-specific body–scale relationships as well.

Multiple body–scale relationships can be integrated into the Fraser–Lee method and the Body-Proportional method. The Fraser–Lee and Body-Proportional methods both assume that the deviation of an individual from the average body–scale relationship at capture is constant through time and use that deviation to back-calculate body length. The difference is that the Fraser–Lee method uses the deviation of an individual at capture from the average slope of the body–scale relationship, whereas the Body-Proportional method uses the deviation of the length at capture from predicted length at capture based on scale radius⁴. Below, we present versions of the Fraser–Lee and Body-Proportional methods that have been modified to incorporate multiple body–scale relationships:

$$(6) \quad L_0 \sim \beta_0 S + \alpha_0 + \varepsilon$$

⁴ See Figs. S3i and S4i in Supplementary material A.

$$(7) \quad L_1 \sim \beta_1 S + \alpha_1 + \varepsilon$$

where L is fish length, S is scale radius, β is a slope term, α is an intercept, and ε is normally distributed error. Variables with the 0 subscript belong to the body–scale relationship for the age or stage at time i , and variables with the 1 subscript belong to the body–scale relationship for the age/stage of the fish at capture. Subscripts i and c represent the age/stage of back-calculation and the age/stage of capture, respectively. Equations 6 and 7 are modifications of eq. 1 and are the two age- or stage-specific BPH regressions needed for back-calculation with multiple body–scale relationships.

$$(8) \quad L_i = (\beta S_i) \left(\frac{L_c - \alpha}{\beta S_c} \right) + \alpha$$

$$(9) \quad L_i = (\beta_0 S_i) \left(\frac{L_c - \alpha_1}{\beta_1 S_c} \right) + \alpha_0$$

$$(10) \quad L_i = (\beta_0 S_i + \alpha_0) \left(\frac{L_c}{\beta_1 S_c + \alpha_1} \right)$$

Equation 8 shows an alternate but mathematically equivalent version of the Fraser–Lee method that produces identical L_i values. We developed this alternate version because we were unable to modify the original equation to incorporate multiple body–scale relationships due to the absence of β . Equation 9 shows the alternate Fraser–Lee back-calculation modified to back-calculate from the age/stage at capture c to the age/stage at time i . Equation 10 shows the version of the Body-Proportional method modified to back-calculate from the age or stage at capture to the age or stage at time i . Note that the L_0 and (or) L_1 regressions in eqs. 6 and 7 can be split into sex-specific relationships if sexual dimorphism is present⁵.

The modifications we made to the Fraser–Lee and Body-Proportional methods could also be used for other hard structures besides scales. In fact, Morita and Matsuishi (2001) used a similar modification to the Scale-Proportional method for back-calculating fish length at age from otoliths to account for decoupling between otolith increments and fish length. Other approaches that reflect shifts in the body–hard structure relationship for otoliths can be found in Bervian et al. (2006) and Ashworth et al. (2017).

Scale erosion and resorption

When anadromous salmonids return to freshwater to spawn, depending on how long they have spent in freshwater, their scales can experience some degree of resorption and erosion (e.g., Claiborne et al. 2011), where material is lost from the outer edge of the scale. This results in overestimating size at previous ages or stages. The severity of the

⁵ See Figs. S3 and S4 in Supplementary material A for a graphical illustration of back-calculation using the traditional and modified versions of the Fraser–Lee and Body-Proportional methods.

problem it causes for back-calculation depends on when and how scales are sampled and can be avoided if fish are sampled early in their migration close to the river mouth. In the case of minor resorption or erosion, regression solutions like those presented in the previous section could be used. For example, one could add a distance-from-ocean or date-of-capture variable to the regression shown in eq. 7 and incorporate that parameter into eqs. 9 and 10. However, in more severe cases, we recommend stepping back to basic regression methods (see Table 2) as used by Siegel et al. (2018).

Validation with steelhead trout

The solutions presented above appear theoretically sound, but do they produce back-calculation methods that perform better than their traditional versions? Here, we validate the proposed solutions integrated in the Fraser-Lee and Body-Proportional back-calculation methods for assumptions 2 and 3 and compare the results to the traditional Fraser-Lee and Body-Proportional methods using scales from an intensively monitored steelhead trout population. Specifically, we validate back-calculation from steelhead adults (returning to the river to spawn) back to smolts (juvenile steelhead migrating from their natal river to the sea). Although we do not directly validate assumption 1, according to the Program Manager of the Department of Fisheries and Oceans Sclerochronology Laboratory (Pacific Region), Pacific salmonid scales and otoliths are not reworkable; thus, once annuli or checks are deposited, they do not move around within the structure (S. Wischniowski, personal communication, 2021). For assumption 2, we test that the “saltwater check” (the circulus on the scale that is assumed to mark the boundary between freshwater and saltwater scale growth) truly indicates the transition from freshwater to saltwater. For assumption 3, we compare the accuracy, precision, and bias of our modified Fraser-Lee and Body-Proportional back-calculations to their traditional versions (Table 2 and eqs. 16–19).

Steelhead scale data

All scales used in the following analyses were sampled from winter-run steelhead trout captured at the Keogh (Giyuxw) River, BC, Canada, within the traditional territory of the Kwakwaka'wakw First Nation between 1976 and 2014. Steelhead smolts (juvenile fish migrating from their natal stream to the ocean) are sampled annually from April through June using a full-width-of-river fish fence located 300 m upstream of the river mouth. Similarly, adults are sampled using a combination of fence capture and angling, with dates of fence operation and angling varying through time but generally spanning from January through April (Bailey et al. 2018). Since 2013, a subset of smolts have been individually marked with subdermal 5 mm PIT-tags (passive integrated transponders), with all returning adults scanned for PIT-tags to monitor for recaptures. Scales were sampled from a standardized region between the posterior insertion of the dorsal fin and the anterior insertion of the anal fin, 3–4 scales above the lateral

line (Maher and Larkin 1955). Multiple scales were sampled from each fish.

For each set of scales in a sample from a single fish, we selected the clearest scale with the least regrowth. Scales were sandwiched between glass slides with a scale bar and photographed using a Leica dissecting microscope with an integrated Moticam 3.0 + camera and Motic Images Plus software. We identified the centroid of each scale and drew a line from there to the outer margin along the long axis and added two more lines at 15 degrees to the left and right of the long axis (Hopelain 1998; Bond et al. 2008; Fig. 1) using the vector graphics editor Inkscape (“Inkscape” 2020). Radii were measured using ImageJ (Rasband 2020). For smolts and adults, we measured from the centroid to the outer margin of the scale to determine whole scale radius, and we also measured from the centroid to the saltwater growth check in adults to estimate their smolt scale radius, hereinafter referred to as the “saltwater check radius” (Fig. 1). In all cases, we used the average of the pair of 15-degree radial measures to reduce individual-level scale variation.

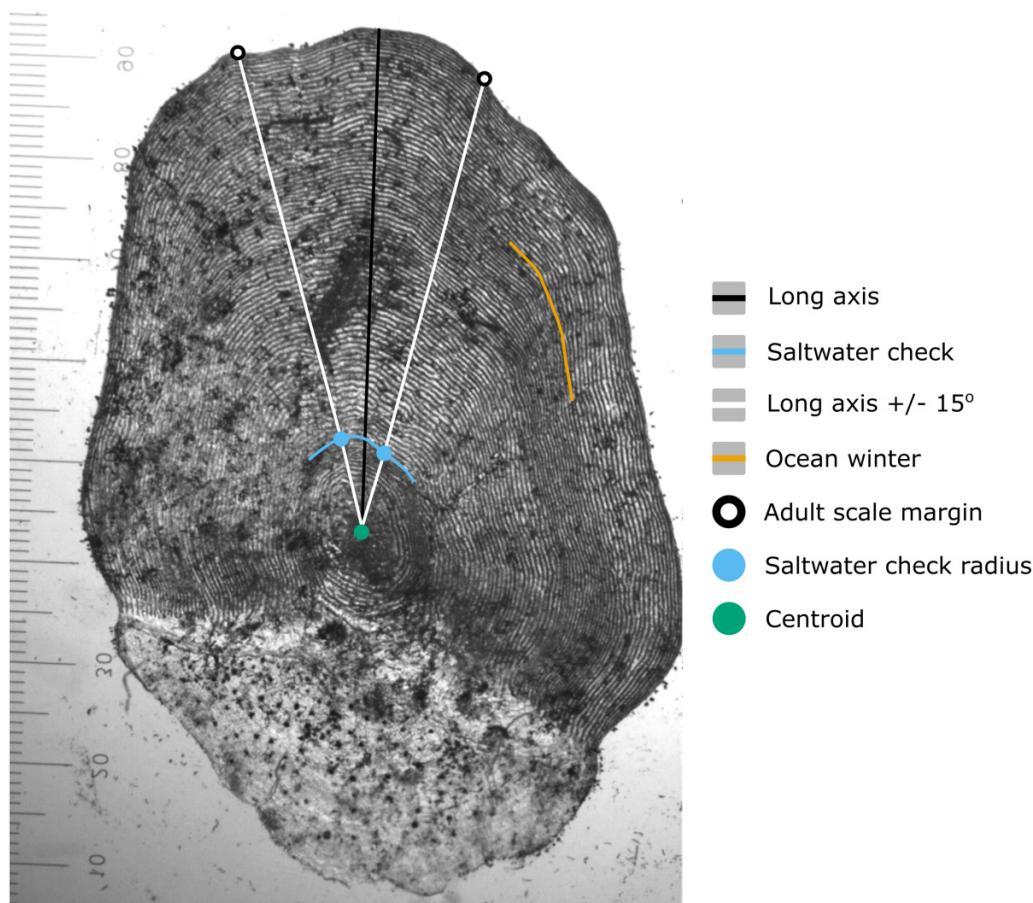
Saltwater checks on adult scales were identified using the standard assumption that salmonid smolts begin rapid somatic growth relative to freshwater somatic growth as soon as they enter the ocean (e.g., Hooton et al. 1987; Connor et al. 2005; Peyronnet et al. 2007), which appears as an abrupt shift in circuli spacing between densely spaced freshwater circuli and widely spaced marine circuli⁶. Scales were aged by identifying and counting annuli (rings of densely spaced circuli relative to average freshwater or saltwater scale growth; Fig. 1). The position of the saltwater check and the age of each scale were determined independently by two different people trained to age steelhead scales from the Keogh River. Discrepancies between ages and saltwater check identification were then tie-broken in discussion with a third scale ager, and scales that we could not agree on were discarded (typically due to excessive scale damage and (or) regrowth).

Saltwater check validation

We used visual and mathematical methods of validating assumption 2. Visual validation involved comparing a smolt and an adult scale from the three recaptured steelhead for which both scales were available. Specifically, we compared the saltwater check radius of each adult scale to the observed radius of the corresponding smolt scale, the circuli counts of the previous summer through winter up to the saltwater check (adult scale) and up to the margin of the smolt scale, and circulus spacing in the same region. This provided preliminary information on whether the saltwater growth check in the adult scale represented the true radius of the smolt scale, and if not, whether that difference may be due to scale warping (i.e., circuli counts are the same in both scales but circulus spacing is different) or due to slow initial somatic growth at sea (i.e., circulus counts are greater up to the saltwater check radii within adult scales).

⁶ See Fig. S1ii in Supplementary material A for an example of a saltwater check.

Fig. 1. An adult steelhead scale from the Keogh River, BC, Canada. The units for the scale bar visible on the left are tenths of a millimetre. Saltwater check radii were measured from the centroid to the blue dots where the white lines intersect the saltwater check marking the theoretical transition from freshwater to saltwater when a fish was a smolt. Adult scale radii were measured from the centroid to the outer margin of the scale at the open black circles. Radii measures from each side of a given scale were averaged to calculate the adult or estimated smolt scale radius. The orange line is placed on the outside of an ocean annulus (a series of relatively densely spaced circuli denoting slower growth). The fish this scale was sampled from spent 1 winter at sea before returning to spawn in the following winter. [Colour online.]



Mathematical validation involved comparing the calculated smolt scale radius (i.e., an estimate of the true smolt scale radius within an adult scale calculated using true smolt length, true adult length, and adult scale radius) to the saltwater check radius (i.e., measured by reading an adult scale and estimating the position of the saltwater check in recaptured fish). To find the calculated smolt scale radius, we fitted back-calculation method-specific body-scale relationships and used steelhead recaptured as adults that were initially captured and measured as smolts just before they entered the ocean. There were 12 steelhead recaptures where a smolt length, adult length, and a readable adult scale were available.

To compare the traditional Fraser-Lee and Body-Proportional methods to our modified versions, we fit body-scale relationships for adults and smolts combined (traditional methods) as well as separate body-scale relationships for smolts and adults (modified methods; details on fitting body-scale relationships can be found in the next section on validating assumption 3). Estimated coefficients

from these fitted relationships (i.e., slope and intercept) were used to parameterize traditional and modified back-calculation equations (Table 2 and eqs. 3–4 and 18–19), which were then rearranged, so that calculated smolt scale radius was a function of measured smolt length, measured adult length, and measured adult scale radius.

$$(11) \quad S_i = \frac{S_c (L_i - \alpha)}{L_c - \alpha}$$

$$(12) \quad S_i = \frac{\left[\frac{L_i (\beta S_c + \alpha)}{L_c} \right] - \alpha}{\beta}$$

$$(13) \quad \ln(S_i) = \frac{[\ln(L_i) - \alpha_0] [\beta_1 \ln(S_c)]}{[\ln(L_c) - (\alpha_1 + O_j)] \beta_0}$$

$$(14) \quad \ln(S_i) = \frac{\left\{ \frac{\ln(L_i) [\beta_1 \ln(S_c) + \alpha_1 + O_j]}{\ln(L_c)} \right\} - \alpha_0}{\beta_0}$$

where L is fish length, S is scale radius, β is a slope term, and α is an intercept (see Table 2 for details). Variables with the 0 subscript belong to the body-scale relationship for the age/stage at time i , and variables with the 1 subscript belong to the body-scale relationship for the age/stage of the fish at capture. Subscripts i and c represent the age/stage of back-calculation and the age/stage of capture, respectively. The variable O represents a categorical effect of ocean age j (details on fitting body-scale relationships can be found in the next section on validating assumption 3). Equations 11–14 are the rearranged equations of the Fraser-Lee, Body-Proportional, Modified Fraser-Lee, and Modified Body-Proportional equations, respectively. We determined whether there was consistent under- or overestimation of smolt scale radius by measuring the average residuals μ_r between calculated smolt scale radius and the saltwater check radius averaged across all recaptured fish such that

$$(15) \quad \mu_r = \frac{\sum_k^n (S_v - S_m)_k}{n}$$

where S_v is the saltwater check radius and S_m is the calculated smolt scale radius for the k th individual, and n is the number of recaptured steelhead used for validation. We used an arithmetic difference rather than a proportional difference because there was no evidence that differences in scale radii between calculated smolt scale radius and saltwater check radius on adult scales increased with increasing smolt length. We quantified smolt scale radius misestimation for each back-calculation method because each method produces different misestimation values, and mathematical validation of assumption 2 assumes that each method is accurate (i.e., that assumption 3 is valid). For each back-calculation method, the mean misestimation value (μ_r) can be subtracted from the saltwater check radius to correct for over- or underestimation of the smolt scale radius within adult scales. Hereon, we refer to saltwater check radius measurements that have been adjusted for mis-estimation as “corrected”, while unadjusted saltwater radius measurements are “uncorrected”.

Back-calculation equation validation

We compared back-calculated smolt lengths from traditional versus modified methods using corrected and uncorrected scale radius measurements with observed true smolt fork length from the 12 recaptured steelhead used for validating assumption 2. We assessed the accuracy, precision, and bias of the different methods by quantifying the average difference between back-calculated and observed fork lengths, finding the standard deviation of those differences, and estimating the mean slope of those differences as a function of true smolt fork length. For a final validation check, we also plotted observed smolt fork length and scale radii measures along with back-calculated smolt fork lengths. The observed smolt data are the same data we used to fit smolt body-scale relationships, and the back-calculated smolt fork lengths came from the same adult lengths and scale radii we used to fit the adult body-scale relationships. We used this plot to examine how the scatter and slopes of the back-

calculated smolt fork lengths and scale radii compare to observed smolt fork lengths and radii.

Traditional methods

We used the most common form of the Fraser-Lee and Body-Proportional back-calculation methods, where fish length and scale radii are untransformed, and a single linear OLS body-scale relationship was fit through all available data (i.e., one relationship for smolts and adults). Specifically, we fit fish fork length as a function of scale radius with a random effect of smolt year (the year a juvenile steelhead migrated to sea) to account for multiple fish sampled per year using the *lme4* package in the statistical software R (R Core Team 2018). This regression included scale radii and lengths from 312 adult steelhead and 389 smolts sampled from smolt years 1981, 1983, 1988, 1993, 1999, 2003, and 2008. While adult data were available for more years, we restricted those data to years that matched the smolt data and to a maximum of 50 fish per year, so that random effects of year would include smolt and adult information for every year and to balance the influence of adults and smolts on the slope of the model. The slope and intercept of the regression were used to parameterize β and α in eqs. 3 and 4.

Modified methods

We integrated most, but not all, solutions proposed earlier into modified versions of the Fraser-Lee and Body-Proportional back-calculation methods. Specifically, we fit separate Bayesian mixed effects measurement error models (see paragraph 4 within the “Individual-level variation in scales” section of “Potential back-calculation challenges and solutions” for a description) with a random effect of smolt year for steelhead smolts and adults using natural log-transformed fork lengths and scale radii. Preliminary comparisons of mixed models using AIC (Akaike’s information criterion; Burnham and Anderson 2002) supported the inclusion of ocean age (years spent at sea) as a categorical variable in the adult body-scale relationship but did not support the inclusion of capture method⁷ (a way to potentially account for scale erosion and resorption in adult steelhead that have returned to the river to spawn), spawner history⁸ (first time spawner versus repeat spawner) or sex⁹. Additionally, preliminary analyses did not support the inclusion of smolt age in the smolt body-scale relationship¹⁰. This resulted in the following equations modified from eqs. 6 and 7:

$$(16) \quad \ln(L_0) \sim \beta_0 \ln(S_0) + \alpha_0 + \varepsilon$$

$$(17) \quad \ln(L_1) \sim \beta_1 \ln(S_1) + \alpha_1 + O_j + \varepsilon$$

where L is fish length, S is scale radius, β is a slope term, α is an intercept, and ε is normally distributed error. Variables with the 0 subscript belong to the body-scale relationship

⁷ See Fig. S5 in Supplementary material A.

⁸ See Fig. S6 in Supplementary material A.

⁹ See Fig. S7 in Supplementary material A.

¹⁰ See Fig. S8 in Supplementary material A.

for the age/stage at time i , variables with the 1 subscript belong to the body-scale relationship for the age/stage of the fish at capture, and the variable 0 represents a categorical effect of ocean age j (Table 2). These regressions included scale radii and lengths from 3892 adult steelhead spanning across smolt years 1972–2012 (with no data for 1977, 2006, or 2007), and the same smolt data as were used for the traditional methods.

Body-scale relationships were fit using the Bayesian statistical software *Stan* (Carpenter et al. 2017) using the package *rstan* (Stan Development Team 2020) in R (R Core Team 2018). Individual variation in scales (i.e., measurement error) was incorporated in the smolt and adult models by defining measured scale radius as a normally distributed variable with the mean representing the “true” mean scale radius of an individual fish and a standard deviation of τ . We calculated τ on the natural log scale with eq. 5 using scales from 50 steelhead smolts stratified by size class (small = <170 mm, medium = 170–200 mm, large = >200 mm) randomly selected from 1981, 1983, 1988, 1999, and 2003. We stratified by size class to reduce size-bias in the estimation of τ , and we only used smolt scales because there were rarely five or more scales available to measure per adult fish.

Stan models were run using four chains with lengths of 10 000 iterations where the first 1000 iterations were discarded as burn-in. We evaluated model convergence using the Gelman–Rubin’s diagnostic test to determine whether independent chains converged to a common posterior mode, with potential scale reduction factors (Rhat) <1.1 suggesting convergence. All covariates were assigned Gaussian priors with a mean of 0 and standard deviation of 5. These weakly informative priors make the null assumption that none of the covariates have an effect but include a standard deviation that is large enough to detect effects from covariates, if there was sufficient evidence.

Estimated coefficients from the smolt and adult body-scale regressions were used to parameterize the following back-calculation equations modified from eqs. 9 and 10:

$$(18) \quad \ln(L_i) = [\beta_0 \ln(S_i)] \left[\frac{\ln(L_c) - (\alpha_1 + O_j)}{\beta_1 \ln(S_c)} \right] + \alpha_0$$

$$(19) \quad \ln(L_i) = [\beta_0 \ln(S_i) + \alpha_0] \left[\frac{\ln(L_c)}{\beta_1 \ln(S_c) + \alpha_1 + O_j} \right]$$

where L is fish length, S is scale radius, β is a slope term, and α is an intercept (see Table 2 for details). Variables with the 0 subscript belong to the body-scale relationship for the age/stage at time i , and variables with the 1 subscript belong to the body-scale relationship for the age/stage of the fish at capture. Subscripts i and c represent the age/stage of back-calculation and the age/stage of capture, respectively. Equations 18 and 19 represent modified Fraser–Lee and Body-Proportional back-calculation equations adjusted to account for natural log-transformed data and the categorical effect of ocean age (O), with the j subscript denoting years spent at sea (Table 2).

Results

Saltwater check validation

We discovered that assumption 2 (that the previous visual method could correctly identify the location of the transition to saltwater on a scale) was not valid. Both the visual and mathematical validation methods indicated that what has been identified as the saltwater check on adult Keogh River steelhead scales does not precisely represent the time (and thus size) when steelhead smolts enter the ocean. Specifically, true smolt scale radii were smaller than saltwater check radii. In the visual validation, we found that the three smolt scales had on average 18% smaller radii than the saltwater check radii measured on their corresponding adult scales, and that the mean number of circuli from the latest winter leading up to the outer edge of the smolt scales were on average 5.2 fewer than the number of circuli leading up to the saltwater check on adult scales (Fig. 2)¹¹. We hypothesize that this pattern arises because steelhead smolts initially experience slow somatic growth after reaching the ocean before beginning rapid somatic growth and forming the saltwater check in their scales. Thus, a portion of the adult scale between the centroid and the saltwater check represents marine somatic growth, suggesting overestimation of the true smolt scale radius within adult scales when using the saltwater check to indicate when an adult steelhead first migrated to sea as a smolt.

Mathematical validation of 12 recaptured individuals for which we had adult scales, adult lengths, and true smolt lengths also revealed that the calculated smolt scale radius was smaller on average than the saltwater check radius in adult scales, further confirming the violation of assumption 2. On average, the difference between the calculated smolt scale radius and the saltwater check radius was –0.32 mm (95% CI: –0.14 to –0.49 mm), –0.33 mm (95% CI: –0.17 to –0.49 mm), –0.14 mm (95% CI: 0.12 to –0.41 mm), –0.13 mm (95% CI: 0.07 to –0.33 mm) for the traditional Fraser–Lee, traditional Body-Proportional, modified Fraser–Lee, and modified Body-Proportional methods, respectively. While these differences in scale radius may appear small, they can translate to biologically significant differences in back-calculated smolt length (up to 21 mm on average depending on the back-calculation method). Thus, the examination of recaptured individuals provided a rare opportunity to test assumption 2 and revealed that the timing of the formation of the saltwater check does not occur exactly when Keogh River steelhead smolts enter the ocean, thereby violating a key assumption of scale aging.

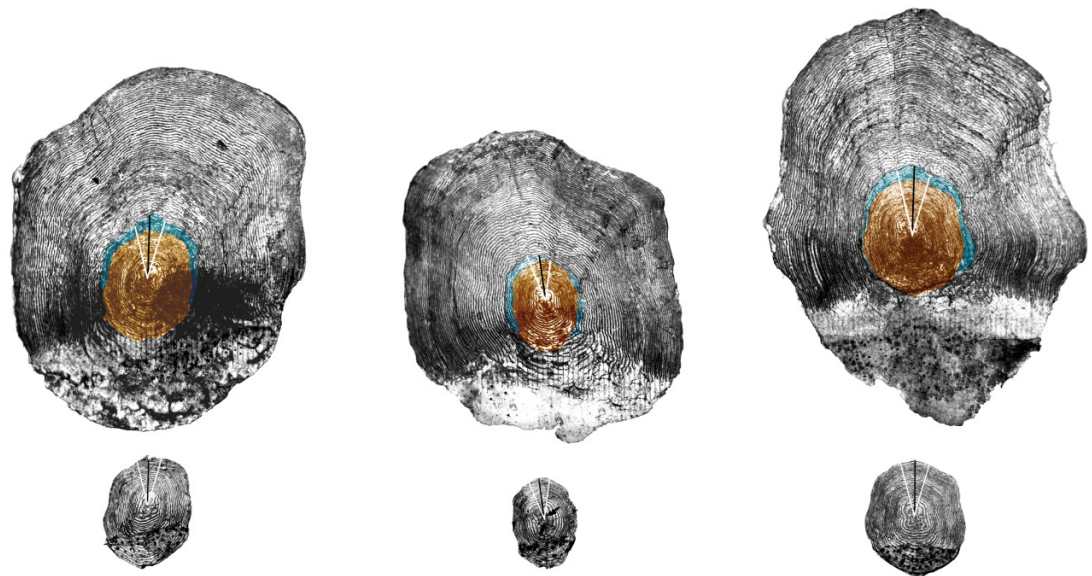
Back-calculation equation validation

Body-scale relationships

We discovered that assumption 3 was better met using our modified regression methods to describe body-scale relationships than using traditional regression methods.

¹¹ See Fig. S9 in Supplementary material A for close-up photos comparing scale pairs from Fig. 2.

Fig. 2. Three pairs of scales sampled from three fish captured as smolts and recaptured as adults. Orange overlays on the adult scales are the footprint of the smolt scales below matched centroid to centroid. The teal margins represent the additional area on adult scales that were estimated to be part of the smolt scale when these fish were smolts based on the saltwater check read on the scale samples from adult fish. Black lines represent the long axes of the scales, and white lines show where radius and circuli measures were taken on the left and right sides of each scale. Estimated values were measured from the smolt portion of adult scales (centroid to saltwater check), and observed values were measured from smolt scales. [Colour online.]



Identity	Recapture 1				Recapture 2				Recapture 3			
	estimated		observed		estimated		observed		estimated		observed	
Smolt scale information												
Side of scale	left	right	left	right	left	right	left	right	left	right	left	right
radius (mm)	1.009	1.144	0.978	0.909	0.986	0.862	0.794	0.822	1.353	1.313	1.062	1.085
circuli count	8	10	5	6	8	7	2	4	9	14	4	4
mean circuli spacing (mm)	0.020	0.019	0.031	0.027	0.020	0.021	0.025	0.019	0.025	0.018	0.030	0.030

Visually, the combined smolt/adult body-scale relationship (Fig. 3) for the traditional back-calculation methods produced worse fits to the data than modified methods based on age/stage-specific body-scale relationships (Figs. 4–5). In the modified methods regressions, the slope of the relationship between body length and scale radius was much steeper for smolts (0.75; 95% CI: 0.69–0.81) than for adults (0.39; 95% CI: 0.37–0.42), suggesting different body-scale relationships. For example, in the separate smolt and adult body-scale relationships, a 0.5 mm increase in scale radius from mean scale radius (mean smolt = 0.8 mm, mean adult = 4.2 mm) resulted in a change in predicted fork length from a mean of 188 mm (95% CI: 151–235 mm) to 270 mm (95% CI: 216–338 mm) for smolts, and from a mean of 697 mm (95% CI: 609–796 mm) to 807 mm (95% CI: 707–923 mm) for adults. We also found weak evidence for a categorical effect of ocean age on the body-scale relationship for adult steelhead (mean effect ranging from 0.99 to 1.27; lower 95% CIs ranging from –3.43 to –3.14, upper 95% CIs ranging from 5.34 to 5.62). Furthermore, variance increases with increasing scale radius providing evidence that the typical regressions for traditional back-calculation methods (which use non-log axes) fail to describe the variance in the data (Fig. 3). Thus, the modifications we made to the traditional regression methods (i.e., fitting separate measurement error models for smolts and adults,

Fig. 3. OLS linear regression describing the relationship between scale radius and body length in steelhead smolts and adults combined.

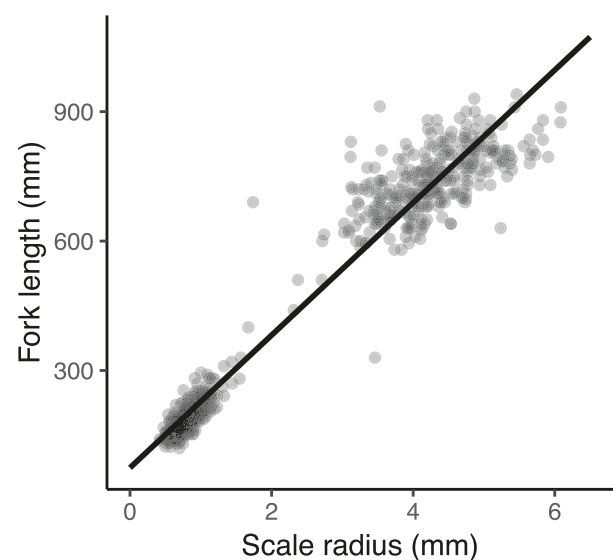
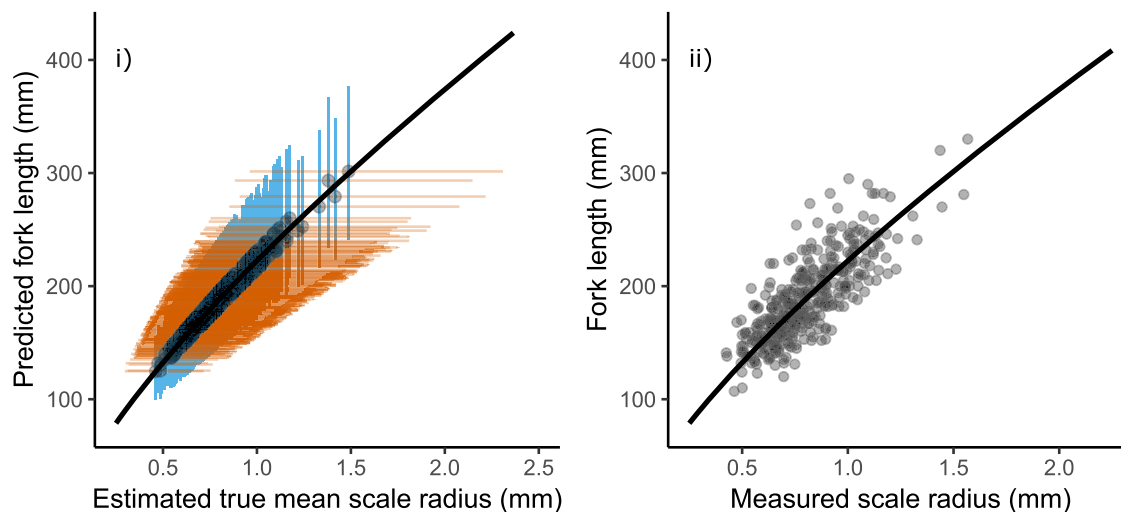


Fig. 4. Bayesian measurement error model fit to steelhead smolt scale radii and fork lengths. (i) Predicted fork length and true mean scale radius estimated by the measurement error model, with blue error bars describing y-axis error (95% credible intervals), and orange error bars describing error in the estimated true mean scale radii for each black point (95% credible intervals). The black line describes the mean relationship. (ii) Black points are raw fish length and scale radius values, and the black line again represents the mean relationship fit by the model. [Colour online.]



using log-log axes, and including ocean age as an explanatory variable in the adult regression) improved the regression fits to our data on smolt and adult body lengths and scale radii.

Accuracy, bias, and precision

Overall, the best back-calculation method for Keogh River steelhead (i.e., the method that best satisfied assumption 3) appeared to be the radii-corrected modified Body-Proportional method (Table 3 and Figs. 6–7). From the mathematical validation, radii-corrected Fraser-Lee methods were on average less accurate and tended to be strongly biased (Table 3 and Fig. 6), and the radii-uncorrected Body-Proportional methods were on average less biased but also much less accurate (Table 3 and Fig. 6). Corrected and uncorrected traditional methods were on average more precise but also more biased than modified methods (Table 3 and Fig. 6). However, among the Body-Proportional methods, the modified version produces the most realistic back-calculated fork lengths (Fig. 7). The scatter and slope of the points produced by the modified Body-Proportional method provide a visibly better match to the scatter and slope of smolt fork lengths and scale radii sampled from smolts collected at the fish fence (Fig. 7). Thus, the use of log-log axes and the integration of an ocean age effect and multiple body-scale relationships (one for smolts and one for adults) to create the Modified Body-Proportional back-calculation equation (eq. 19) most accurately back-cast smolt lengths in Keogh River steelhead.

Discussion

Scientists have been trying to accurately reconstruct individual fish somatic growth using hard structures for over

100 years (e.g., Lea 1910), and several of the original methods are commonly used today (Lea 1910; Fraser 1916). Fish somatic growth is tracked for a variety of reasons, including inferring stock productivity, estimating fecundity, and setting harvest limits (Kuparinen and Festa-Bianchet 2017; Barneche et al. 2018). Scales present an excellent opportunity to reconstruct somatic growth because scale collection is common in many fish sampling programs, it is nonlethal, and causes minimal harm to fish—thus, scale-based somatic growth reconstruction is useful for threatened species and populations. However, scale-based back-calculation poses a series of challenges—for example, scales are vulnerable to damage, erosion, and scale regrowth, vary in size and shape within and across individual fish, and the relationship between scale size and fish length may change with age/stage. Here, we presented a series of solutions to these challenges that can be integrated into commonly used back-calculations. Using archived scales from a wild steelhead population, we also compared traditional and modified versions of two common back-calculations by examining assumptions 2 and 3 of back-calculation (Table 1; Francis 1990).

Examining methodological assumptions revealed biologically significant bias in back-calculated length estimates. Here, we found that the timing of the formation of saltwater checks in Keogh steelhead scales did not match the timing of fish fence passage by steelhead smolts, thus invalidating assumption 2. There are two possible explanations for this discrepancy: the first is that smolts are achieving significant somatic growth in the 300 m section of river between the fish fence and the ocean; and the second is that smolts experience slow initial marine somatic growth. We hypothesize that the scope for somatic growth between the fence and the ocean is likely negligible owing to (a) the fish fence where steelhead smolts were captured and measured is only 300 m from the ocean, (b) the Keogh River is nutrient poor

Fig. 5. Bayesian measurement error model fit to steelhead adult scale radii and fork lengths. (i) Predicted fork length and true mean scale radius estimated by the measurement error model, with blue error bars describing y-axis error (95% credible intervals), and black error bars describing error in the estimated true mean scale radii for each point (95% credible intervals). The lines coloured according to ocean age describes the mean body–scale relationships. Ocean age is the number of winters a steelhead has spent at sea or spawning since initial migration to sea as a smolt. (ii) Points are raw fish length and scale radius values coloured according to ocean age, and the coloured lines again represent the mean relationships fit by the model. [Colour online.]

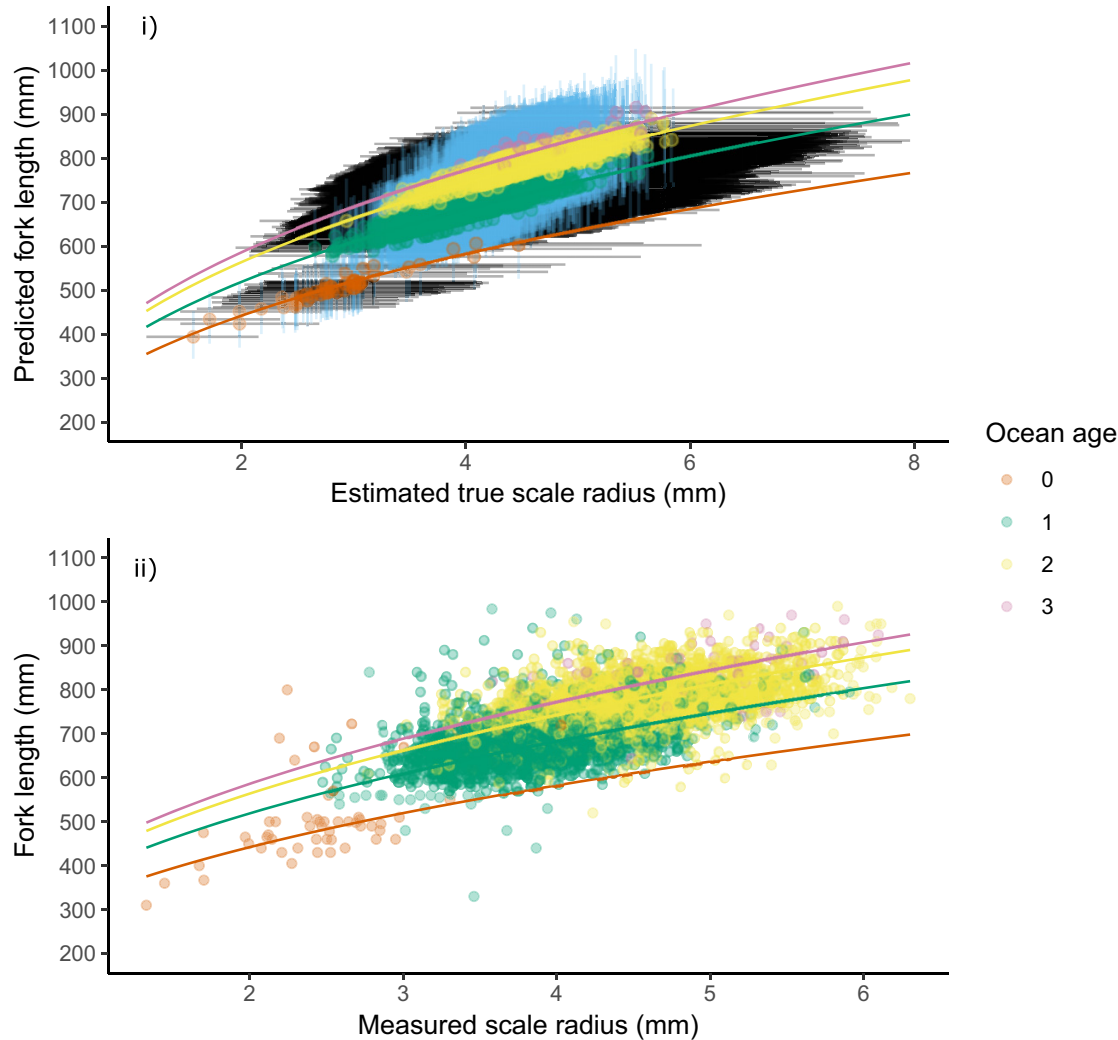


Table 3. Accuracy, precision, and bias of traditional and modified Fraser–Lee and Body-Proportional back-calculation methods using smolt scale radii (measured from the adult scale centroid to the saltwater check) corrected and uncorrected for overestimation using 12 recaptured steelhead trout from the Keogh River, BC, Canada.

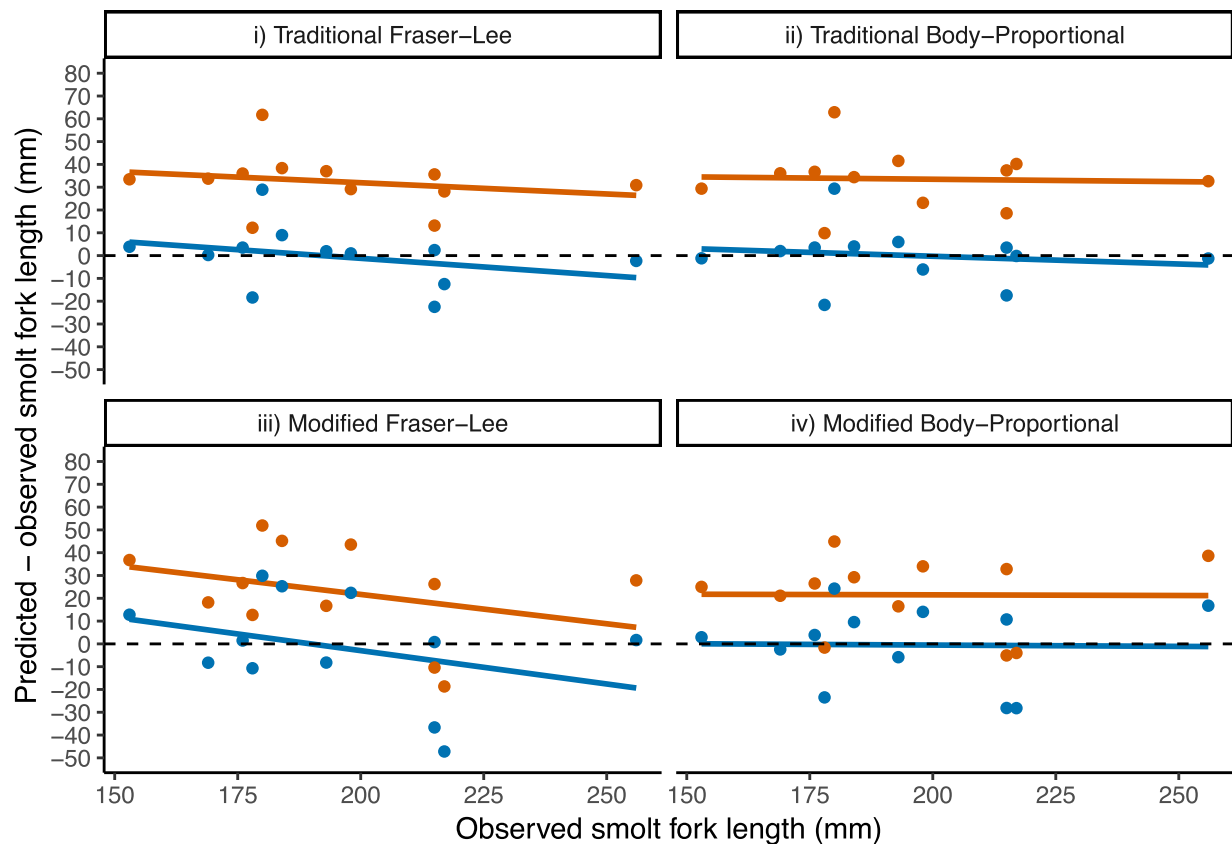
Method	Radii-corrected			Radii-uncorrected		
	Accuracy (mm)	Precision (mm)	Bias	Accuracy (mm)	Precision (mm)	Bias
Traditional Fraser–Lee	−0.4	14	−0.2	33	13	−0.1
Traditional Body-Proportional	0.1	13	−0.07	34	13	−0.02
Modified Fraser–Lee	−1	24	−0.3	23	22	−0.3
Modified Body-Proportional	−0.5	18	−0.01	22	17	−0.006

Note: Accuracy is the average arithmetic difference between estimated and true smolt fork length, precision is the standard deviation of accuracy, and bias is the mean OLS slope of predicted minus observed smolt fork length as a function of observed fork length.

(Johnston et al. 1990) and has functionally no estuary as the river dumps over a sandstone shelf into the ocean, and (c) steelhead trout generally migrate downstream rapidly through the lower parts of rivers (Chapman et al. 2015;

Wilson et al. 2021). Thus, without a correction factor to adjust saltwater check radii measures, all back-calculation methods substantially overestimated smolt fork lengths measured at the fish fence (Fig. 6). We also found differences among

Fig. 6. Validation results for traditional (*i–ii*) versus modified (*iii–iv*) versions of the Fraser–Lee (*i, iii*) and Body-Proportional (*ii, iv*) back-calculation methods using scale radii corrected (blue) and uncorrected (orange) for overestimation of smolt scale radii within adult scales measured from the centroid to the saltwater check. Points are residuals derived from steelhead that were initially captured and measured as smolts, and recaptured, measured, and scale sampled as adults. Points with positive and negative values represent back-calculated smolt lengths that are overestimated or underestimated, respectively. Lines show the OLS correlations between points and true smolt fork length. [Colour online.]

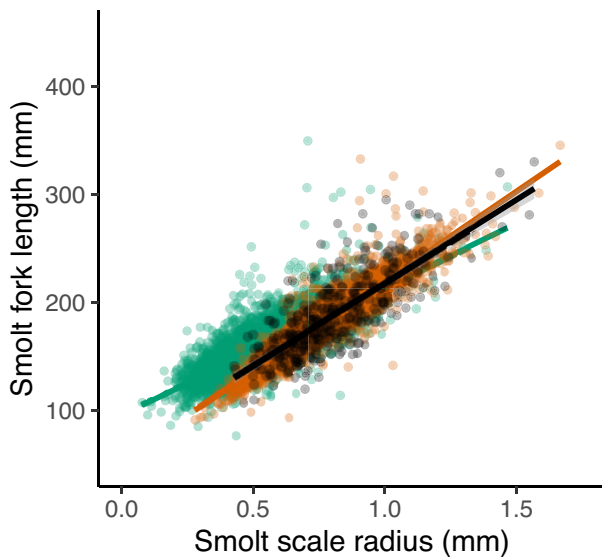


back-calculation methods by examining assumption 3. Of the four methods we validated, the Body-Proportional methods performed better than Fraser–Lee methods, and the modified version of the Body-Proportional method performed best (Table 3 and Figs. 6–7). Traditional and modified Fraser–Lee methods were more biased than traditional and modified Body-Proportional methods (both before and after adjusting the scale radius). Specifically, estimates from Fraser–Lee methods resulted in underestimated body sizes for longer smolts and overestimated body sizes for smaller smolts relative to observed smolt fork length (Fig. 6). Overall, these results demonstrate how substantial inaccuracy can go undetected in standard back-calculations in the absence of validating assumptions.

Back-calculating body sizes when assumption 2 (the estimated times of formation of checks and annuli are correct) is invalid has consequences for back-calculation across fish taxa (including salmonids). First, this finding highlights the general importance of validation. In the absence of validation, we would have overestimated steelhead smolt lengths by an average of approximately 14%—enough to alter the conclusions of scale-based marine size-selection papers such as Ward et al. (1989) and Holtby et al. (1990). Second, we

suggest that back-calculations focusing on size at the time of a habitat transition need to be particularly cautious about validation as there are a variety of factors that may delay expected shifts in somatic growth or somatic growth expression in hard structures. Using salmonid smolts as an example, we hypothesized four different mechanisms that may explain slow initial marine somatic growth, where the potential for smolt size overestimation is dependent on the hypothesized mechanism: (i) In river systems such as the Keogh River where there is little-to-no estuary, the sudden transition to saltwater may have physiological effects that slow somatic growth until fish acclimate to saline water. (ii) The early marine environment may not be productive enough to increase somatic growth rates—for example, the Keogh River drains into Johnstone Strait, a region that is hypothesized to be a slow somatic growth zone for migrating Pacific salmonids (Mckinnell et al. 2014; Journey et al. 2018). (iii) Prey-switching, where salmonid smolts adjusting to new food sources in the ocean may prevent immediate rapid somatic growth—e.g., brown trout foraging efficiency increases with time after introduction to a novel prey resource (Sundström and Johnsson 2001). (iv) There may be a time lag between rapid somatic growth and expression of that growth in hard

Fig. 7. Comparison of smolt fork lengths and corresponding scale radii measured from smolts captured at the Keogh River fish fence (black points) to back-calculated smolt fork lengths with corresponding corrected saltwater check radii using the traditional Body-Proportional method (green points) and the modified Body-Proportional methods (orange points). Lines and shaded gray areas describe the OLS slopes of the body-scale relationship for each group. [Colour online.]



structures. Hypotheses (i) and (ii) are geographically constrained mechanisms, where smolt size overestimation would only occur in watersheds with little or no estuary or that drained into a low productivity marine environment. In contrast, hypotheses (iii) and (iv) would be general with some potential for variation among species. Finding the mechanism behind slow initial marine scale growth would inform the reliability of unvalidated scale-based salmonid marine survival papers.

We also provided a quantitative comparison of the performance of different methods of length back-calculation. The modified Body-Proportional method produced the most realistic back-calculated smolt lengths. This is most apparent in the comparison of back-calculated smolt lengths and sampled smolt lengths as a function of scale radius (Fig. 7) where the slope of the smolt lengths back-calculated using the modified Body-Proportional methods is steeper than the traditional methods and a better match to the slope of the smolts measured at the fish fence. The steeper slope of the points produced by the modified methods can be attributed to the use of multiple body-scale relationships, and accounting for measurement error in scale radii. Using multiple body-scale relationships allowed the steeper slope of the smolt body-scale relationship to be reflected in back-calculated smolt lengths, and accounting for error in independent variables typically increases the slope of the relationship relative to slopes produced by OLS regression. This result confirms Zivkov's (1996) contention that there are age/stage-based changes in body-scale relationships, and mirrors the findings of Morita and Matsuishi (2001), where the

incorporation of an age effect in their otolith-based back-calculation improved estimates of back-calculated fish somatic growth rates. It also supports Ricker's (Ricker 1992) point that OLS regression does not produce the most accurate slopes for body-scale relationships.

Scale-based back-calculation assumptions are rarely validated—it is common practice for publications using back-calculation to cite other papers that have validated back-calculation methods for the same species in place of performing their own validation. Yet, validations typically produce useful information. For example, Heidarsson et al. (2006) discovered that traditional versions of the Dahl-Lea and Fraser-Lee methods overestimated Atlantic salmon smolt length from adult scales, and that there were population-specific differences in the degree of overestimation. Similarly, Hanson et al. (2019) also found the Dahl-Lea method to overestimate smolt length in Atlantic Salmon, and proposed a correction equation to improve their back-calculation. Klumb et al. (1999) showed that the Fraser-Lee and Weisberg methods overestimated smallmouth bass and walleye lengths at previous captures, but that the Fraser-Lee method performed better than the Weisberg method. Conversely, Pierce et al. (1996) demonstrated little difference between a variety of back-calculation methods for pumpkin seed and golden shiners, but this was attributed to body-scale relationships with low error. Thus, unless working with a population for which back-calculation has been previously validated or displays extremely low-variation body-scale relationships, we recommend validating assumption 3 (that the back-calculation function is accurate) if possible. Ideally, practitioners would validate event markers in hard structures for each new population of fish and test different back-calculation methods using recaptured individuals. However, we understand that this is rarely feasible. Even if recaptured individuals are unavailable, a comparison of the slope and scatter of back-calculated fish lengths as a function of scale radius to the slope and scatter of sampled fish lengths and scale radii (e.g., Fig. 7) could prevent the use of back-calculation methods that violate assumption 3. Ultimately, if no validation is performed, papers should include that as a caveat in their discussion.

One potential source of error in fish-length back-calculation that was not accounted for in this study was the capacity for body-scale relationships to change through time and (or) vary with environmental conditions (Smoliński and Berg 2022). Back-calculation methods inherently account for variation in the body-scale relationship among individual fish by using individual deviation from the mean body-scale relationship in the back-calculation process. In this study, we took this further by accounting for age- and stage-based shifts in the body-scale relationship. However, if the slope or intercept of the underlying mean body-scale relationship varies through time or with environmental conditions, length back-calculations for fish that experienced unusual environmental conditions or lived during time periods with large deviations from the long-term average body-scale relationship may be compromised. Smoliński and Berg (2022) provided evidence that body-scale relationships in herring may differ across time periods and as a function of sea

surface temperatures. Their result appears plausible when placed in the context of work by Beakes et al. (2014) that found that scale growth is a function of water temperature and somatic growth, where somatic growth is a function of temperature and food availability. However, Smoliński and Berg's findings assume a linear relationship between scale radius and fish length across age classes and do not account for individual-level variation in scale radius. Thus, it is difficult to determine how much of the variation in their body-scale relationships is explained by time period and sea surface temperature when growth trajectories can alter significantly as fish age and scale radii can vary considerably within individuals even when sampled from a standardized location. Future work should investigate temporal and environmentally driven variation in body-scale relationships while accounting for ontogenetic shifts in the body-scale relationship and individual-level variation in scale radius.

Conclusion

Back-calculating fish lengths from hard structures such as scales stretches back over a century (e.g., Lea 1910) and remains relevant today (e.g., Ulaski et al. 2020). Although the hard structures used for back-calculation have diversified through time (starting with scales and broadening to otoliths, fin spines, cleithra, and vertebrae; Francis 1990), scales remain useful because they can be sampled nonlethally with minimal harm to fish (excellent for species of conservation concern). Validating fish length back-calculations can have major impacts on fish length at age estimates, such that invalid assumptions may alter the conclusions of publications and change recommendations to fisheries managers. Here, we provided a series of options for back-calculation practitioners to use to improve the validity of assumption 3 (that the back-calculation method is accurate), particularly if validation suggests that assumption 2 (timing of growth checks/annuli) is valid but the back-calculation function itself is not performing well. We also demonstrated how these modifications can improve back-calculation with a wild fish population. Ultimately, we hope this paper provides a roadmap for other scientists seeking to use more effective and accurate scale-based back-calculation.

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Data availability

Data generated or analyzed during this study are available from the corresponding author upon reasonable request.

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The authors declare no competing interests.

Supplementary material

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