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Using scale-derived estimates of body size in analyses of Atlantic salmon life-history variation: a cautionary note

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Abstract

Measurements of individual body length at different life stages are critical in understanding fish ecology and evolution. Such data can be obtained via back-calculation from measurements of fish scales or by using the size of the scale as a direct proxy for body length. Using data from Atlantic salmon, we test key assumptions associated with each approach and their implications for investigating how variation in growth earlier in life is associated with age at maturity. The scaling of scale size approximated isometry and was similar among individuals who matured at different ages—validating a key assumption of back-calculation. However, we observed that individuals genetically predisposed to delay maturation have smaller scales for their body size—challenging a key assumption of the "direct scale-size" approach. Depending on the method of body length estimation, the relationship between body length growth earlier in life and age at maturity was observed to differ. Thus, when using scale material to study the relationship between growth and maturation in salmon, we recommend back-calculation and an assumed allometric scaling coefficient.

Key words: scalimetry, scale reading, scale radius, body size, vgll3, six6

Introduction

Back-calculation of fish body length from calcified structures such as scales and otoliths has been an integral part of investigations that seek to explain variation in survival, recruitment, and life-history traits in fishes (Gross and Charnov 1980; Nicieza and Braña 1993; Morita and Fukuwaka 2006; Kuparinen et al. 2009; Nakayama et al. 2017; Vollset et al. 2022). The back-calculation of individual length from scale size has a long history in fish biology (Dahl 1907; Dahl 1910; Lea 1910). Since the publication of these pioneering studies, many other back-calculation methods have been proposed (for reviews, see Francis 1990; Bailey et al. 2022). Back calculation requires several assumptions, that if not met, risk over- or under-estimating size at earlier ages or developmental stages (Francis 1990; Bailey et al. 2022). One of these assumptions is that the back-calculation function describing the relationship between scale size (referred to hereafter as scale radius) and fish length is accurate. In this context, it is generally assumed that the shape of the relationship between scale radius and body length is consistent among all individuals of the same species or population, whether it be isometric or allometric. In analyses that seek to explain life-history variation within a species using back-calculated estimates of individual length, this assumption may be problematic if the allometry of scale radius and body length differs systematically among the individuals of interest.

As an alternative to back-calculation, some studies have begun to use scale size as a direct proxy for body length when investigating relationships between individual size at age and variation in recruitment or life-history traits (Peyronnet et al. 2007; McCarthy et al. 2008; Hogan and Friedland 2010; Marco-Rius et al. 2012, 2013; Tréhin et al. 2021; Tréhin et al. 2023). This approach, referred to hereafter as the "direct scale-size" approach, assumes that the relationship between growth in body length and growth in scale radius is isometric. Unlike back-calculation methods, the direct scale-size approach does not produce estimates of past body length that are independent of the diameter of the sampled scale, and thus makes the assumption that the relationship between body length and the relative size (i.e., scale radius for a given body length) and therefore the number of scales is consistent among all of the sampled individuals of a given species. Whilst it might seem far-fetched that relative scale size could vary among individuals of the same species, it is not without precedence, as genetic differences have been found to underpin within-species variation in the presence of other hard structures in fish such as vertebrae number (Leary et al. 1985; Billerbeck et al. 1997; Tibblin et al. 2016; Berg et al. 2018). If relative scale size does vary systematically within a species, estimations of body length at earlier ages and life stages based on the direct scale-size approach have the potential to influence the estimated relationship between individual size and the response variable of interest if scale size is correlated with the response variable in some systematic way. Here, using the Atlantic salmon as a study species, we draw upon data from different European populations to address four main research objectives: (1) Do fish scales grow isometrically? (2) Do scale size allometric slopes differ among life-history variants of the same species? (3) Does scale size differ among life-history variants of the same species? (4) Do methods for back-calculation matter in within-species analyses of fish life-history variation?

To our knowledge, the assumptions that (i) scale radius—body length allometries, and (ii) relative scale radius are consistent within a species remain untested. Here, we evaluate these assumptions with respect to the relationship between growth in body length and age at maturity in wild Atlantic salmon. However, it is worth noting that the validity of these assumptions maybe relevant to any analysis of life-history variation requiring the estimation of individual body lengths from scale samples. We begin by briefly describing scale growth in Atlantic salmon and the back-calculation of individual body lengths from scale samples within the context of allometric theory. Next, we show that whilst the slope of ontogenetic allometric relationship between scale radius and body length approximates isometry and is consistent among salmon that mature at different ages, scale radius tends to be smaller among salmon that have a genetic predisposition to mature relatively late in life. We conclude by demonstrating that the choice of body size estimation method (either from directly in the scale or by back-calculation) can influence the statistical relationship between growth in body length and age at maturity in salmon.

Scale growth and the back-calculation of body length in Atlantic salmon

The primary function of fish scales is presumably to form a layer that provides protection from injury and infection. In Atlantic salmon, the scales develop and then cover the body during the first year of life (Jensen and Johnsen 1982). As Atlantic salmon grow in body length (beyond the age at which the body becomes completely covered with scales), no more scales are produced with the exception of regenerated scales that grow rapidly to replace a lost scale. Rather, the existing scales increase in size as clearly defined rings called circuli deposited incrementally from the center of the scale (Todd et al. 2014). The spacing between circuli provides a permanent record of an individual's trajectory of growth in body length because narrower spacings indicate periods of slow growth and wider spacings represent periods of more rapid growth (Peyronnet et al. 2007; Jensen et al. 2012). For example, during juvenile residency in freshwater where growth is relatively slow, narrowly spaced circuli are deposited, being even more narrow during winter than summer (Fig. 1). Then, after smolting, when juveniles enter the marine environment in spring, relatively widely spaced circuli are deposited, reflecting the rapid increase in body length that occurs during this time, before the spacing of circuli narrows again during the period of reduced marine growth that occurs over the first winter spent at sea (often referred to as the first winter annulus). If the individual spends additional years at sea, this pattern in marine growth repeats itself (Fig. 1). Thus, scale radius can also mark key transitions in development.

How can scale growth be interpreted in terms of allometric growth, i.e., the proportional change in size of a given body part relative to the whole (Huxley 1932)? The standard allometric equation is

$$Y = aX^b,$$

where Y is the size of the body part and X is the size of the body, while a and b are coefficients. This relationship is linear on the log scale

$$\log(Y) = \log(a) + b\log(X)$$

where $\log(a)$ is known as the allometric intercept and b is known as the allometric slope or the allometric scaling coefficient. The allometric relationship can be measured within an individual (ontogenetic allometry), across individuals at the same developmental stage (static allometry), and across populations or species (evolutionary allometry) (Cheverud 1982; Pélabon et al. 2013). In the context of body length back-calculation from scale radius, Y would be scale radius and X body length, and b the ontogenetic allometric scaling coefficient. In Atlantic salmon, body length growth trajectories are commonly reconstructed using the back-calculation method proposed by Dahl (1907) and Lea (1910) that assumes isometry (i.e., scale radius increases in direct proportion to body length) and is given by the equation

$$L_i = L\frac{S_i}{S}$$

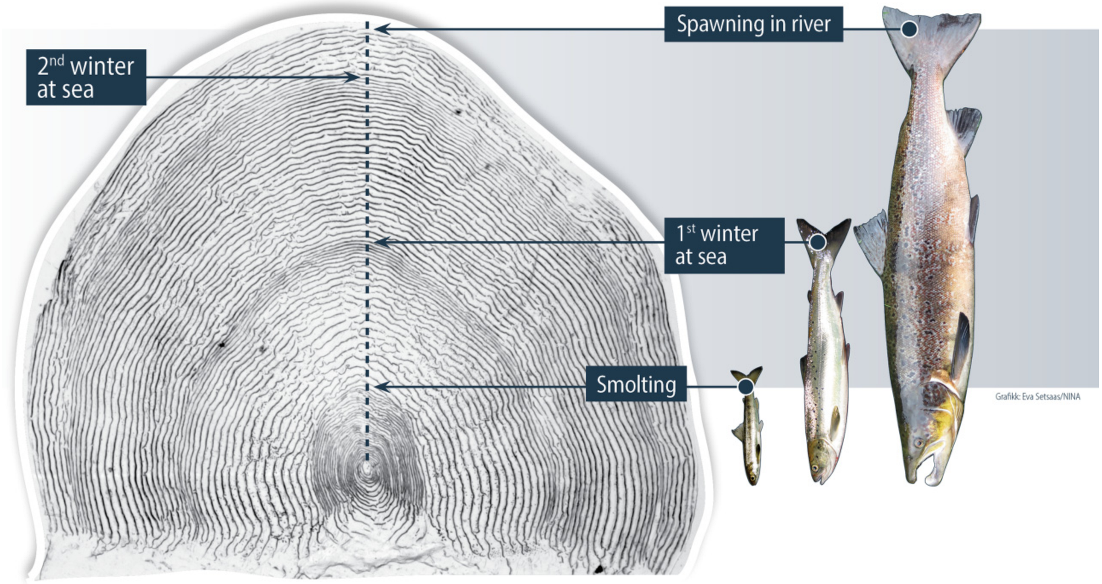
were L_i is the back-calculated length at ontogenetic stage i, L is the total length of the adult fish, S_i is the scale radius of ontogenetic stage i and S is the full diameter of the scale. An allometric version of this back-calculation method has been referred to as the Monastyrsky model (Bagenal and Tesch 1978) and is given by

$$L_i = L\left(\frac{S_i}{S}\right)^{1/b}$$

where b is the assumed allometric slope of scale radius on body length. Thus, values of the exponent b that differ from 1 imply that scale radius increases at a proportionately faster ($b > 1$) or slower ($b < 1$) rate than body length.

There is a diversity of other methods for back-calculation than those described above, where additional parameters are estimated. These have been considered thoroughly elsewhere (see Francis 1990; Bailey et al. 2022) and our intention is not to argue for an optimal method in salmon. Rather, we use the Dahl–Lea method as an example because it will be familiar among those who study reconstructed growth trajectories in this species (Hanson et al. 2019). Once the body becomes completely covered with scales, it seems plausible that the growth in the widest radius of a given scale is approximately isometric with respect to the growth in length of

Fig. 1. Atlantic salmon scale showing patterns of freshwater and marine growth. Typical measurements of scale growth include scale radius at emigration from freshwater (when the individual undergoes physiological preparation for life in saltwater, a process referred to as smolting), which is measured as the distance from the center of the scale to the edge of the tightly clustered group of circuli that mark the departure from freshwater (shown as "smolting" in the figure). Scale growth during the first year spent at sea is measured as the increment in diameter from the edge of the freshwater zone to the edge of the next tightly clustered group of circuli, which marks the reduction in growth experienced over the first winter spent at (i.e., the first winter annulus, shown as "1st winter at sea"). If the individual spends more than 1 year at sea, scale growth during the second year at sea is measured as the increment from the edge of the first winter annulus, to the edge of the second winter annulus (shown as "2nd winter at sea"), and so on. Note, measurements of scale radius are made along the longest axis of the scale. Graphic: Eva Setsaas—Norwegian Institute for Nature Research.



the body. We propose this because one of the primary functions of the scale is protection. Large deviations from isometry would imply either that the scales did not properly cover the body during development (but after the initial phase of scale establishment) or that the scales overlapped each other much more during some stages of development but not others. We note that some deviations from isometry maybe expected. For example, when the head and the tail are included in the measurement of fish length. If growth of the tail or head is non-isometric relative to growth in body length, this could lead to a non-isometric relationship between scale radius and total fish length. This could occur when adults develop exaggerated sexual characters, for example, like the elongated jaw in males, or if the tail becomes eroded with age, which has been observed in repeat spawning individuals.

Materials and methods

Here, we treat each of our objectives as a question and to address these questions, we draw upon data from four different Atlantic salmon populations in Europe. An overview of these datasets and a verbal description of how they were used to address each question and our main conclusions is presented in Table 1.

Description of datasets and statistical approach

The allometry of scale radius and body length

The allometry of the relationship between scale radius and body length in Atlantic salmon was investigated using data from a mark-recapture program in the river Orkla, Norway (63°18′N, 9°49′E). Between 1984 and 1997, repeated measurements of body length were obtained from 431 individuals, first, at the point of smolting and again when the same individuals were recaptured as adults. Most of these individuals ($n = 406$) were hatchery-reared smolts (originating from River Orkla stock) that were tagged and released into the river during the peak smolt emigration period (mid-May). The remaining individuals ($n = 25$) were of wild origin that were captured, tagged, and released back into the river just prior to the peak smolt emigration period (late-April). Recoveries of the tagged adults were reported by recreational anglers in the river Orkla ($n = 92$) and by salmon fishers in the sea (both in Norway, $n = 314$ and the Faroe Islands, $n = 25$). Scale samples were obtained from the recaptured adults, from which scale radius at smolting and recapture was measured and sea age at maturity determined, i.e., the number of years spent by each individual at sea before returning to spawn in freshwater. Individual scale radius—body length allometric slopes—from the time of smolting to adulthood, was obtained by calculating the ratio of the change in

Table 1. Overview of main questions addressed in the current study, our conclusions, and the statistical methods and datasets used to obtain them.

Question and conclusion	Method and dataset
1.Do salmon scales grow isometrically?	*Calculation of scale radius ontogenetic allometric slopes*
Scale radius vs. body length relationship approximates isometry (Figs. 2*b* and 2*c*)	River Orkla, Norway: $n = 431$ fish Rivers Elliðaár and Vesturdalsá, Iceland: $n = 86$ fish
2.Do scale size allometric slopes differ among salmon life history variants?	*Regression of scale radius ontogenetic allometric slope vs. age at maturation*
Scale radius vs. body length allometry does not differ with maturation age (Fig. 2*c*)	River Orkla, Norway: $n = 431$ fish
3.Does scale size differ among salmon life history variants?	*Regression of scale radius vs. body length for different maturation genotypes*
Individuals with a genetic predisposition to delay maturation have smaller scales (Fig. 3)	River Surna, Norway: $n = 1091$ fish
4.Do methods for back-calculation matter in analyses of salmon life history variation?	*Regression of maturation age vs. growth for different body length back-calculation methods*
Age at maturation vs. growth relationship affected by body length back-calculation method (Fig. 4)	River Surna, Norway: $n = 1244$ fish*

*Data from an extra 153 individuals without individual maturation genotypes were included in this analysis.

scale radius to the change in body length (all values transformed to natural log scale). To complement this analysis, we also considered data extracted from Heidarsson et al. (2006) who presented individual data on the relationship between scale radius and body length in two Icelandic salmon populations, Elliðaár (64°06′N, 21°51′W, $n = 53$ individuals, data extractable for 40 of these individuals) and Vesturdalsá (65°44′N, 14°54′N, $n = 52$ individuals, data extractable for 46 of these individuals). In both populations, body length measurements and scale samples were taken from individuals at the point of smolting and again when the same individuals were recaptured as adults in the river when returning to spawn. Heidarsson et al. (2006) presented their data (Figs. 2 and 3 in their article) as a scatterplot of body length ratio (“L_{rat},” fork length at smolting/fork length at recapture) *vs.* scale radius ratio (“S_{rat},” scale radius at smolting/scale radius at recapture). We transformed both variables to the natural log scale and calculated the allometric slope of the relationship between scale radius and body length for each individual as $\ln(S_{\mathrm{rat}})/\ln(L_{\mathrm{rat}})$.

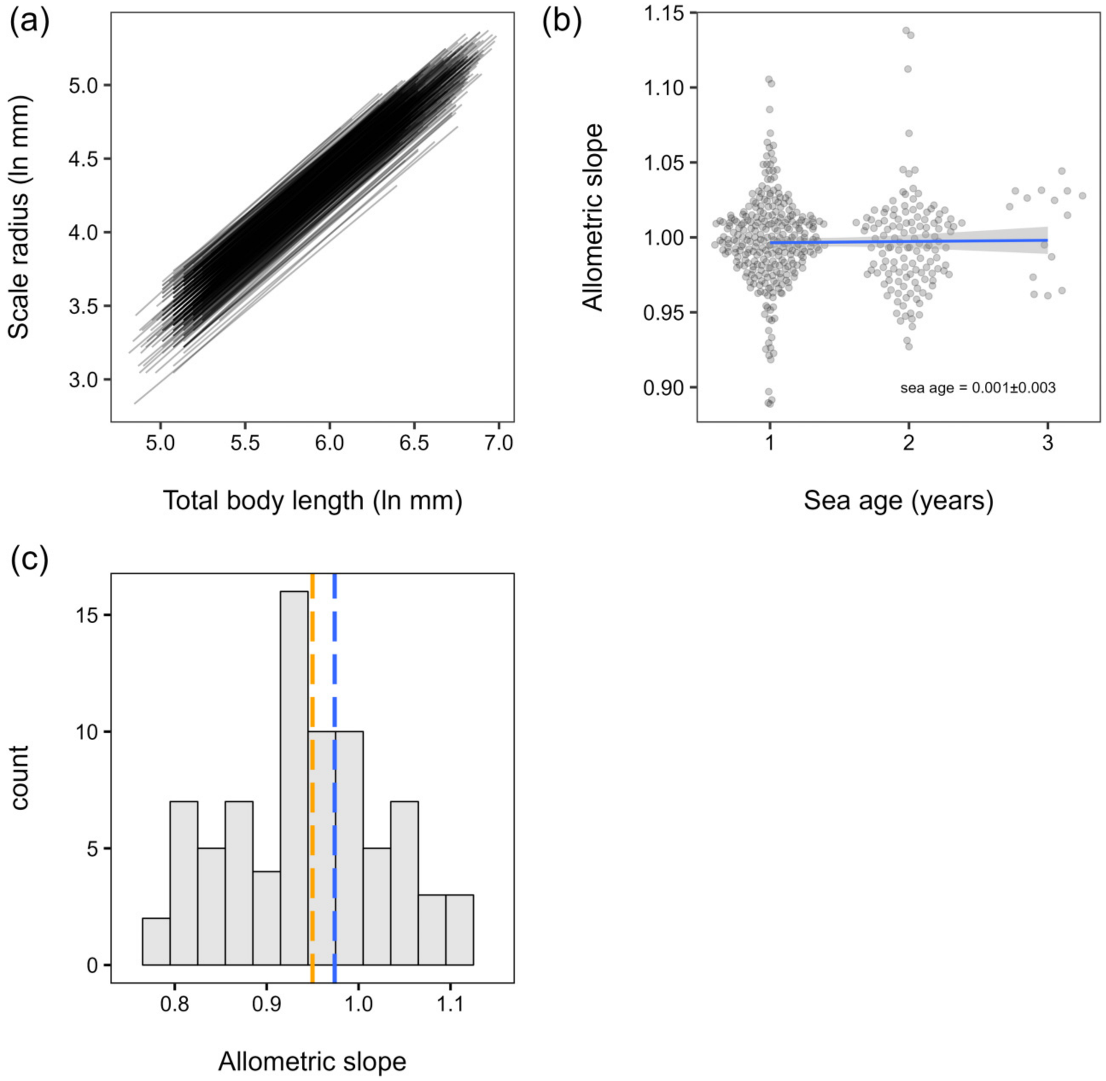
The individual scale radius—body length allometric slopes served two purposes. First, they were inspected to test the assumption made under the direct scale-size approach that the relationship between growth in body length and growth in scale radius in Atlantic salmon is isometric. Second, the allometric slopes derived from the River Orkla dataset were regressed on each individual’s corresponding value for sea age to test the assumption frequently made under back-calculation-based approaches that scale radius—body length allometries are similar among the individuals of interest, which in this case are individuals that mature at different sea ages. Whilst it seems unlikely that the rearing origin of the recaptured individuals (wild or hatchery) might affect the allometry of scale size, salmon recaptured in the river, rather than at sea, may have started to develop exaggerated sexual characters (e.g., more elongated head in males) that might influence the allometric relationship between scale radius and. body length. To test both possibilities, we compared the fit of two regression models (using AIC values). In both models, we fitted individual allometric slopes as the response variable. In the more complex model, we considered the origin (wild *vs.* hatchery) and recapture location (River Orkla recreational fishery, Norway sea fishery, or Faroe Islands sea fishery) for each individual as additional explanatory variables.

Relationship between scale size and genetic predisposition for age at maturity

The relationship between relative scale radius and genetic disposition for sea age at maturity was investigated using scale samples obtained from 1091 wild adult Atlantic salmon captured by recreational anglers in the river Surna, Norway (62°59′N, 8°40′E) between 2014 and 2021. The Atlantic salmon is a rare example of a species where the molecular genetic basis of maturation is well understood. In salmon, variation in sea age is associated with two major effect loci, one in the genomic region of *vgll3* on chromosome 25 and the other in the genomic region of *six6* on chromosome 9 (Ayllon et al. 2015; Barson et al. 2015; Sinclair-Waters et al. 2020; Sinclair-Waters et al. 2022). Homozygosity for early (“EE”) or late (“LL”) maturation alleles at the *vgll3* locus is associated with younger and older sea ages, respectively. However, sex-dependent dominance is observed for heterozygotes (“EL"). Thus, heterozygosity tends to be associated with younger sea age in males and intermediate sea age in females (Barson et al. 2015). At the six6 locus, homozygosity for early ("EE”) and late maturation alleles (“LL”) is associated with younger and older sea ages, respectively, with heterozygotes (“EL”) having sea ages that are intermediate between the two homozygote groups (Ayllon et al. 2015; Barson et al. 2015; Sinclair-Waters et al. 2020; Sinclair-Waters et al. 2022). For each sampled scale, DNA was extracted using the DNEASY tissue kit (Qiagen) and genotyped at the vgll3 and six6 loci on an EP1$^{\mathrm{TM}}$ 96.96 Dynamic array IFCs platform (Fluidigm).

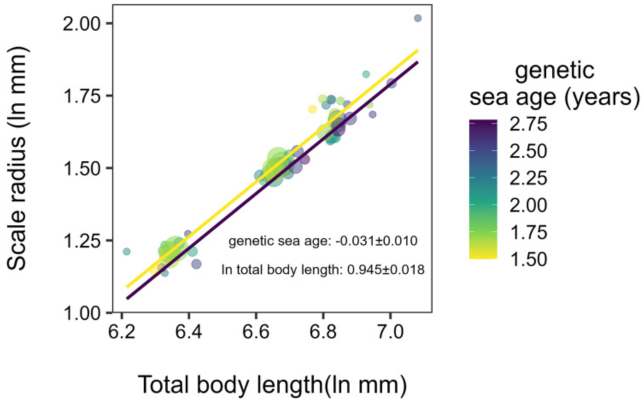
The relationship between relative scale radius and maturation genotype was evaluated in a linear regression with body length and the genetic disposition for sea age at ma-

Fig. 2. (*a*) Ontogenetic allometries of scale radius among 431 Atlantic salmon from the river Orkla, Norway. Measurements of scale radius and body length were obtained at two points in time for each individual: (i) when undertaking the emigration from the river to the sea as juveniles (smolts) and (ii) upon recapture as adults when returning to the river to spawn. (*b*) Ontogenetic allometric slopes for the same individuals and their relationship with sea age. The blue line shows fitted values from a least square regression with shaded ribbon indicating 95% confidence intervals. (*c*) Histogram of ontogenetic allometric slopes for scale radius of Icelandic Atlantic salmon. Measurements of scale radius and body length were obtained at the same points in time for each individual as for the Orkla fish. Data are pooled from two different rivers, Elliðaár and Vesturdalsá. Orange and blue lines show mean allometric slopes for each of these respective Icelandic populations. Icelandic data were extracted from Heidarsson et al. (2006).



turity as covariates. The genetic disposition for age at maturity (referred to hereafter as genetic sea age) was estimated as the sex-specific mean sea age of the nine possible combinations of vgll3 (EE, EL, or LL) and six6 (EE, EL or LL) genotypes. We used mean values for scale radius and body length (both natural log-transformed) in this regression rather than individual-level data because there maybe error associated with measurements of body length (made by anglers), which might result in a downward bias in the slope of the estimated relationship. The strength of this downward bias is determined by the ratio of error variance to total variance in the explanatory variable (Hansen and Bartoszek 2012). Given potential error in individual body length measurements, mean values likely offer more precision, reducing this bias. In addition, given that we can obtain estimates of error in mean body length values but not the individual values, the strength of this bias can be estimated. To do this, we used eq. 13 in Hansen and Bartoszek (2012). Thus, mean values for scale radius and body length were calculated by assigning the fish to 57 different groups, with each group being based upon a given combination of gender and phenotypic sea age (range: 1–5 years) within each of the nine possible values of genetic sea age (i.e., possible vgll3 and six6 genotypes). Lastly, the influence of each datapoint on the resulting model estimates

Fig. 3. Static allometry of scale radius at capture among 1091 adult Atlantic salmon from the river Surna, Norway. Datapoints represent mean values for individuals of the same genetic sea age. Genetic sea age was calculated as the sex-specific mean sea age of the nine possible combinations of vgll3 (EE, EL, or LL) and six6 (EE, EL or LL) genotypes. Mean values for scale radius and body length were calculated by assigning the fish to 57 different groups, with each group being based upon a given combination of gender and phenotypic sea age (range: 1–5 years) within each of the nine values of genetic sea age (i.e., possible vgll3 and six6 genotypes). The size of each datapoint is proportional to the square root of the sample size. The regression lines represent ordinary least squares predictions for the youngest and oldest genetic sea ages present in the data (1.5 and 2.8 years, represented by yellow and purple, respectively). Parameter estimates for the effect of scale radius and body length are indicated in the figure. Due to error in the predictor, the effect of ln total body length was downwardly biased by 1.2% (error-corrected estimate: 0.0956), while there was no detectable bias for the effect of genetic sea age.



was weighted by the number of individuals present within each group.

How does method of body length estimation affect the statistical relationship between age at maturity and growth?

The influence of body length estimation method on the statistical relationship between age and size at maturity (i.e., phenotypic sea age) was investigated using the data from the river Surna described above. However, given that *vgll3* and *six6* genotypes were not required in this analysis, an additional 153 individuals missing such data were made available for consideration. Using ordinary least squares, we regressed individual phenotypic sea age on body length realized at the end of the first winter spent at sea, gender, and their interaction. The residuals of this regression will be far from a normal (Gaussian) distribution, but note here that the least squares method does not require exact distributional assumptions for estimating regression coefficients and their associated standard error. Three separate regressions were performed using values for body length produced by two different methods for the retrospective estimation of body size from scales, the direct scale-size approach, and Dahl–Lea back-calculation assuming isometry ($b = 1.0$) and negative allometry ($b = 0.95$). Theory posits that a developmental threshold, likely a labile trait related to a minimum size, developmental stage, physiological state or combination thereof, must be reached before maturation can proceed (Day and Rowe 2002). Thus, following a theoretical model specific to Atlantic salmon (Thorpe et al. 1998), we chose individual body length at the conclusion of the first winter at sea as the proxy for this labile trait. We also considered the interaction between gender and body length in each of these regression because age at maturity has clear gender-specific implications for fitness in Atlantic salmon, as delaying maturation (and thus increasing body size and thereby fecundity) likely has a greater effect in increasing reproductive success for females rather than males (Fleming 1996). We first transformed body length values (this includes values estimated by the direct scale-size approach) to the natural log scale before centering them on their respective capture year means to remove the influence of an among-year effect on the estimated relationships. Natural log transformation of the explanatory variables is advantageous for several reasons. First, it makes the different methods for estimating body size directly comparable. Second, on the natural log scale, the parameter estimate for the explanatory variable describes proportional change in the response variable.

Results

The allometry of scale radius on body length

Individual scale radius—body length allometries of the Orkla salmon (shown in Fig. 2*a*)—was close to isometry, with the average allometric slope estimated at 0.997 ± 0.002. We observed less support for the more complex regression model that considered the effects of fish origin and capture location on individual scale radius—body length allometries (AIC values of the more complex and simpler models, respectively: −1765.7 vs. −1769.8, Table 2). The simpler regression model indicated that there was little detectable relationship between allometric slope and sea age in this population (Fig. 2*b*, Table 2), whereas the more complex model indicated relatively minor effects of fish origin and recapture location on individual scale radius allometries (Table 2). Together, these results imply that (i) individual allometric slopes were not influenced by the origin of the fish nor their recapture location and (ii) once an individual smolts and emigrates from freshwater, scale radius and body length grow along the same allometric trajectory regardless of age. We also observed that the ontogenetic allometric slopes of the Orkla salmon were slightly steeper than those observed by Heidarsson et al. (2006), where the average individual allometric slope of the Elliðaár and Vesturdalsá salmon was estimated at 0.950 ± 0.01 and 0.974 ± 0.02, respectively (Fig. 2*c*). Note that measurements of fork length were used in the Icelandic data, whereas measurements of total length were used in the river Orkla dataset.

Table 2. Summary of the two linear models used to address Question 2, “Do scale size allometric slopes differ among salmon life history variants?”.

	Sea age only		*Sea age + fish origin + recapture location*	
Predictor	Estimate	95% CI	estimate	95% CI
Intercept	0.996	0.988–1.003	0.991	0.976–1.007
Sea age	0.001	−0.004–0.006	0.001	− 0.005–0.006
Fish origin (wild)			− 0.007	− 0.020–0.006
Recapture location (river)			0.007	− 0.007–0.021
Recapture location (sea)			0.004	− 0.009–0.017
n observations	431		431	
R^2	0.001		0.005	
AIC	−1769.83		−1765.71	

Note: One model considered only the relationship between scale radius allometric slope and fish sea age. The other more complex model, considered the additional influence of fish origin (wild or hatchery) and recapture location (Norwegian river, Norwegian coastal fishery, or Faroe Islands coastal fishery) on the same relationship. In the more complex model, the intercept represents fish of hatchery origin that were recaptured in the Faroe Islands. A parameter estimate significantly different from zero is indicated by 95% confidence intervals that do not overlap zero.

Relationship between scale radius and genetic predisposition for age at maturity

When controlling for log-transformed total fish length (parameter estimate ± SE, 0.94 ± 0.02, $p < 0.0001$), we observed a negative effect of genetic sea age on scale size at capture (Fig. 3, parameter estimate ± SE, −0.03 ± 0.01, $p < 0.01$). The parameter estimate for the effect of genetic sea age on scale radius indicates that a 1-year increase in genetic sea age was associated with scales that were approximately 3% smaller on average for a given body size.

How does method of body length estimation affect the statistical relationship between age at maturity and growth?

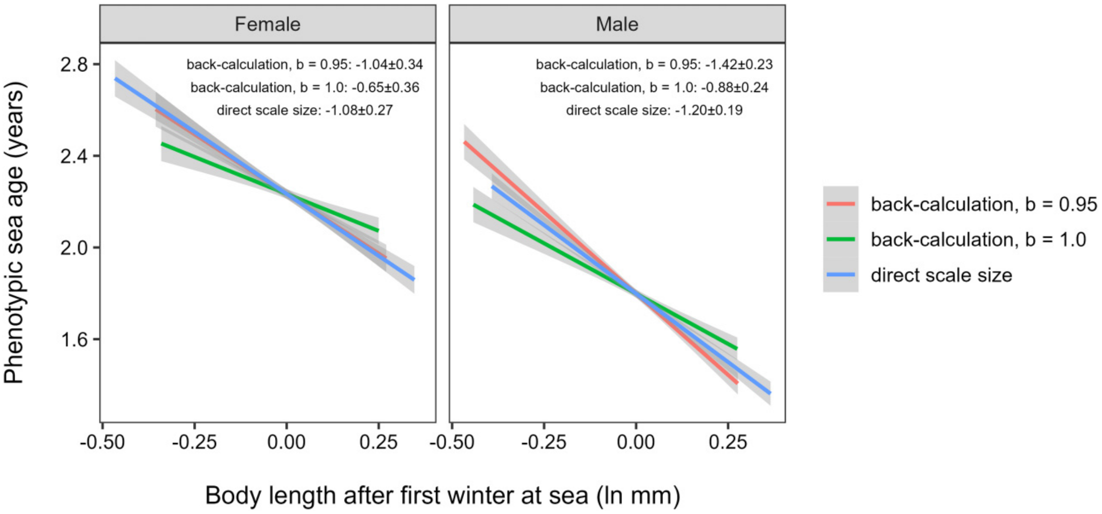
Both back-calculation methods and the direct scale-size approach indicated that realization of a larger body length after the first winter spent at sea was associated with earlier maturation. However, dependent on the method employed for estimating body length, we observed differences in the strength of this relationship. In both females and males, similarly steep relationships between phenotypic sea age and body length were observed when using the direct scale-size approach and back-calculation assuming negative allometry. Back-calculation assuming isometry resulted in the most shallow relationship between sea age and body length in both genders (Fig. 4). The raw data underpinning these relationships are shown in Supplementary Fig. S1, indicating the presence of a potential outlier—a single female that spent 5 years at sea before returning to spawn in freshwater. However, exclusion of this individual from the analysis resulted in only minor quantitative change in the parameter estimates describing the relationships between phenotypic sea age and body length for female salmon that were yielded by the respective methods for retrospective estimation of body length from scale samples (Supplementary Fig. S2).

Discussion

We show that Atlantic salmon with a genetic predisposition to delay maturation have smaller scales for their size. This implies that age at maturity and the relative size or number of scales on the body are pleiotropically related in this species. That is, they are influenced by the same set of genes. Hence, in Atlantic salmon, which is rapidly becoming a model organism for ecological and evolutionary studies of maturation (Mobley et al. 2021), it may be problematic to use scale radius as a direct proxy for body length and growth at earlier life stages when investigating patterns in age at maturity. Several alternative approaches for such investigations exist. Our analysis indicated that the allometric relationship between scale radius and body length in Atlantic salmon from the time of smolting until maturation is close to isometry, and similar among individuals that mature at different ages. Thus, one alternative is to employ some sort of back-calculation model with an assumed allometry. From the empirical data at hand, it seems reasonable to assume that the ontogenetic allometric scaling coefficient describing the relationship between scale radius and body length falls between 0.95 and 1.00 from the smolt stage to maturation. Another alternative may be to use relative rather than absolute scale size as an explanatory variable in statistical analyses of maturation age. Here, the radius of the scale at the developmental stage of interest (e.g., at the end of the first winter spent at sea) would be divided by the radius of the scale at an earlier developmental stage, such as the termination of freshwater residence (i.e., smolting). A downside of this approach is that it may be difficult to express the size of the scale during freshwater residence in relative terms, thus precluding it from being considered as an explanatory variable in such analyses.

Our analysis underscores that using scale-derived estimates of body size in analyses of fish life-history variation can be complicated and potentially prone to pitfalls. A prime example of a potentially problematic situation is when quantify-

Fig. 4. Ordinary least squares regression relationships between phenotypic sea age and the interaction between gender and body length after the first winter spent at sea among 1244 adult Atlantic salmon captured by recreational anglers in the river Surna, Norway. Individual body length values after the first sea winter were estimated retrospectively from scale samples and measurements of body length at capture reported by the anglers. These body length values were estimated using three different methods (i) the direct scale-size approach, (ii) back-calculation assuming isometry ($b = 1.0$), and (iii) back-calculation assuming negative allometry ($b = 0.95$). The body length values estimated by each method were natural log transformed and centered on capture year mean values prior to analysis. A separate regression model was fitted to the data associated with each body length estimation method. Parameter estimates for the interaction between gender and body length yielded by each estimation method are decomposed by gender in the figure. Grey-shaded ribbons indicate ±1 standard error.



ing the maturation vs. growth reaction norm (Heino et al. 2002). This concept has been of critical importance in furthering our understanding of temporal changes in fish life-history scheduling and population abundance (e.g., Olsen et al. 2004; Heino and Dieckmann 2008; Kokkonen et al. 2015). However, if other species exhibit systematic among-individual variation in scale size, then care must be exercised when delineating the growth variable in this reaction norm and other similar analyses as spurious patterns may otherwise result. Yet, there are also many situations where we do not expect that the choice of a given method for back-calculation or the direct-scale approach will matter much. For example, in situations where biological variation is compared *within* life-history variants. Further, there are also situations where biological variation is compared *among* life-history variants where the choice of method for retrospective estimation of body size may have negligible effect. For example, Vollset et al. (2022) used isometric back-calculation to investigate temporal changes in the marine growth of salmon. In their analysis, each estimate of yearly mean growth was based on individuals from different life-history groups and with a large range of adult body lengths. Hence any effect of methodological error would likely be swamped by among-year differences in marine growth, meaning that the overall results would likely have been similar if the authors had employed a different back-calculation method or used the direct scale-size approach.

Methodological issues aside, a novel result stemming from the current analysis is why individuals genetically predisposed to mature later and at a larger size have relatively small, and thus more numerous scales? Understanding the origins of this variation in scale size is a daunting but exciting task that might be best approached by considering the functional role of fish scales. The most obvious function of the fish scale is protection against wounding and subsequent infection. In Atlantic salmon, physical wounds might be inflicted by predators in freshwater or at sea. However, wounding could also result from fighting with conspecifics during spawning or the migration up- and down often turbulent rock and waterfall-strewn rivers. However, such challenges likely apply equally to all salmon. Less obvious though is the role played by fish scales in locomotion. Atlantic salmon cover vast distances during their migrations (Gilbey et al. 2021; Rikardsen et al. 2021). Individuals that spend an additional year or more at sea may swim considerably longer distances than individuals that return to freshwater after spending only 1 year at sea. It would seem likely then that such individuals may stand to benefit from more efficient mobility. Efficient swimming in fish requires a certain degree of body stiffness (Liao 2022). While the muscles can provide active stiffening, the skeleton, skin, and scales together contribute passive stiffening and help “tune” the stiffness of the body to optimize swimming efficiency. However, swimming efficiency can also be influenced by “springiness.” Fish scales and the integument that binds them together also act as a mechanical spring that passively recycles movement energy (Liao 2022). Precisely how relative scale size might affect either of these roles is unclear at present, but it is not implausible that the systematic differences in relative scale size observed here represent different optimal solutions to challenges associated with protection or mobility that change with age and thus body size.

Conclusion

When using scale material to study the relationship between growth and maturation in salmon, we recommend back-calculation of individual body lengths using an assumed allometric scaling coefficient. We also urge caution in similar analyses of life-history variation in other fish species, as it seems unlikely that the correlation between life-history scheduling and scale size observed here is restricted to a single species.

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Data availability

The data analyzed in this study are available from the corresponding author upon reasonable request.

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Competing interests

The authors declare that there are no competing interests.

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Supplementary material

Supplementary data are available with the article at https://doi.org/10.1139/cjfas-2023-0154.

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