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Do the biological characteristics of trout (*Salmo trutta*) smolts influence their spring migration timing and maiden marine sojourn duration?

Jonathan P. Gillson[1] | Robert E. Blackwell[1,2] | Stephen D. Gregory[3,4] | Jessica E. Marsh[3,4] | Tea Bašić[1] | Sophie A. M. Elliott[5,6] | R. Andrew King[7] | David L. Maxwell[1] | William D. Riley[1] | Jamie R. Stevens[7] | Alan M. Walker[1] | Rasmus B. Lauridsen[5,8]

[1]Centre for Environment, Fisheries and Aquaculture Science, Lowestoft, UK

[2]The Alan Turing Institute, British Library, London, UK

[3]Centre for Environment, Fisheries and Aquaculture Science, Weymouth, UK

[4]Centre for Conservation Ecology and Environmental Sciences, Faculty of Science and Technology, Bournemouth University, Talbot Campus, Poole, UK

[5]Salmon and Trout Research Centre, Game and Wildlife Conservation Trust, Dorset, UK

[6]The Missing Salmon Alliance, Hampshire, UK

[7]Department of Biosciences, Faculty of Health and Life Sciences, Hatherly Laboratories, University of Exeter, Exeter, UK

[8]Six Rivers Iceland, 691 Vopnafjordur, Iceland

Correspondence
Jonathan P. Gillson, Salmon and Freshwater (SAF) Team, Centre for Environment, Fisheries and Aquaculture Science, Lowestoft, NR33 0HT, UK.
Email: jonathan.gillson@cefas.gov.uk

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Abstract

Anadromous salmonids migrate seaward to exploit feeding and growth opportunities in marine habitats, yet how smolt biological characteristics influence their marine migratory behavior remains poorly understood. This study used 9 years of trout (*Salmo trutta*) population monitoring data from 15,595 tagged age-0+ parr, 1033 smolts detected migrating downstream in spring, and 99 adults detected returning from their first marine migration to the River Frome (Dorset, UK) to investigate the influence of smolt biological characteristics on their migration timing and maiden marine sojourn duration. Age-specific differences in the influence of smolt length on migration timing were found, with longer 1-year-old smolts emigrating later than their shorter counterparts within the same age class, but the opposite association existed for 2-year-old smolts. A bespoke integrated statistical model quantified the effects of smolt emigration day of year, age, sex, and length on the probability of first-time migrants returning to the river after one or more sea winters. Younger, later migrating smolts had a longer marine sojourn duration than their older, earlier migrating counterparts, and females remained at sea for longer periods than males. Although the statistical model was designed to maximize the use of information available in the data, it revealed only weak effects of smolt biological characteristics on the maiden marine sojourn duration. A complementary simulation study suggested that detecting more

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spring migrating smolts and analyzing longer time series of trout population monitoring data would increase the ability to detect statistically significant effects. Therefore, a strategic review of the trout population monitoring program, including more long-term biological data collection, is recommended. The modelling work presented here can provide guidance on the size of the required dataset and how to maximize the power of imperfect data.

KEYWORDS
body size, first-time migrant, fish tagging, marine returns, sea trout

1 | INTRODUCTION

Trout (*Salmo trutta* L.) is a socio-economically important salmonid species indigenous to Europe, North Africa, and western Asia (MacCrimmon et al., 1970). It is arguably one of the most diverse salmonids that exhibits considerable variation in morphologies, life histories, and migratory tactics (Klemetsen, 2013). Individuals adopt a continuum of life-history strategies ranging from freshwater resident (non-migratory) to potamodromous (freshwater migratory) and anadromous (marine migratory) forms (reviewed in Klemetsen et al., 2003). Resident and potamodromous *S. trutta* complete their life cycle in fresh water, while their anadromous counterparts stay up to 8 years in fresh water before migrating seaward to feed and grow, subsequently returning to reproduce (reviewed by Thorstad et al., 2016). As both resident and migratory individuals can coexist within *S. trutta* populations, their fitness is likely to be similar, otherwise one life-history strategy would disappear over time (Gross, 1984). Anadromous *S. trutta* undergo a complex physiological and morphological transformation from parr to smolts prior to seaward migration (Hoar, 1988). This developmental transformation, termed smoltification, is typically size-dependent, mediated through changes in photoperiod and temperature (McCormick, 2012). Smoltification is associated with increased salinity tolerance, which is an important seawater adaptation believed to optimize the performance and survival of anadromous *S. trutta* in the marine environment (Aarestrup et al., 2000; Nielsen et al., 2004). Anadromy confers a fitness advantage if the benefits of improved feeding and growth opportunities at sea lead to increased fecundity and outweigh the costs of higher energetic demands of smoltification, migration, and increased mortality (reviewed in Ferguson et al., 2019). The balance between these benefits and costs will likely depend on a range of biological characteristics and behaviors. For example, females are more likely to become anadromous than males because they typically gain more in terms of reproductive success from the acquisition of a larger body size potentially afforded by marine feeding (Berg & Berg, 1989; Cucherousset et al., 2005; Knutsen et al., 2004). However, a less well-understood aspect of the cost–benefit evolutionary trade-off of anadromy is the amount of time spent at sea, known as the marine sojourn duration (Jonsson & Jonsson, 2011).

The marine migratory behavior of *S. trutta*, including seaward migration timing and marine sojourn duration, is likely governed by trade-offs between mortality and growth potential in different habitats, and the most beneficial strategy might vary among individuals and populations (Thorstad et al., 2016). Interplay between environmental factors, genetics, and parental heritability has an important role in shaping their marine migratory behavior (Ferguson et al., 2019). Smolts typically migrate seaward for the first time in spring (Flaten et al., 2016; Jensen et al., 2012; Jonsson & Jonsson, 2002), but have also been reported leaving rivers at other times of the year, such as autumn (Aarestrup et al., 2018; Jonsson & Jonsson, 2009a; Winter et al., 2016). First-time migrants exhibit considerable variation in marine sojourn duration, with individuals spending 1 to 36 months at sea before returning to fresh water (reviewed by Nevoux et al., 2019). Previous studies have shown that their marine migratory behavior is influenced by a range of biotic and abiotic factors, such as body size, age, sex, food availability, river discharge, and water temperature (Berg & Berg, 1989; Jensen et al., 2012; Jonsson, 1985; Staveley et al., 2024). However, few studies have quantified the relative influence of biotic or abiotic factors on the marine migratory behavior of first-time migrants, which likely differ from veteran migrants in their response to drivers (Jensen et al., 2022). Indeed, most studies investigating the influence of smolt biological characteristics on marine migratory behavior have focused on explanatory variables independently without considering their interactions in northern latitudes (e.g., Davidsen et al., 2023; Jensen et al., 2012, 2020). In contrast, the relative influence of age, sex, and length on marine migratory behavior in more southerly latitudes has received relatively little attention.

Over the last four decades, *S. trutta* have suffered population declines in many regions due to human activities in freshwater and marine environments (ICES, 2013). Although the highest numbers of mortalities typically occur in fresh water (Smialek et al., 2021), increased marine mortality, due to stressors such as climate change, overexploitation, and sea lice from salmon mariculture (Jonsson & Jonsson, 2009b; Limburg & Waldman, 2009; Thorstad et al., 2015), is widely accepted to be an important contributory factor to recent population declines (Thorstad et al., 2016). Unfortunately, anadromous *S. trutta* are among the least studied salmonids in the marine environment (Drenner et al., 2012), and therefore knowledge about the marine phase of their life cycle is far from complete (reviewed in Birnie-Gauvin et al., 2019). Improved knowledge about their marine migratory behavior is essential to support decision-making processes involved in the development of management practices for conservation purposes. It has been recommended that management practices

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TABLE 1 A set of a priori explanatory variables expected to describe variation in the maiden marine sojourn duration of anadromous *Salmo trutta* chosen based on a review of the literature.

Explanatory variable	Description	Hypothesized effect	References
Smolt age	Age of the smolt (years)	Negative: Older smolts migrate to sea earlier and have a shorter marine sojourn duration than younger smolts	Eldøy et al. (2015); Jonsson (1985); Økland et al. (1993)
Sex	Male or female genetic sex determination	Females have a longer marine sojourn duration than males	Berg and Berg (1989); Eldøy et al. (2021); Wysujack et al. (2009)
Emigration day of year	The day of the year the emigrating smolt was detected migrating seaward	Positive: Later-migrating smolts have a longer marine sojourn duration than earlier-migrating smolts	Berg and Berg (1989); Davidsen et al. (2023); Eldøy et al. (2015)
Smolt length	Fork length of the smolt (mm)	Negative: Smolts attaining longer juvenile length in fresh water have a briefer marine sojourn duration than their shorter counterparts	Berg and Berg (1989); Eldøy et al. (2015); Eldøy et al. (2021)

target freshwater habitats to maximize the number of smolts entering the ocean in the best condition and minimize stressor impacts that compromise marine survival (reviewed by Thorstad et al., 2021; Gillson et al., 2022). Hence, a better understanding of how smolt biological characteristics influence the marine migratory behavior of *S. trutta* will aid the development of effective management practices that maximize their lifetime fecundity to help conserve wild populations, particularly in chalk streams that have received relatively little research attention. Accordingly, this study sought to evaluate the influence of smolt biological characteristics on the spring migration timing and maiden marine sojourn duration of *S. trutta* using fish tagging and trapping data collected as part of a salmonid population monitoring program on the River Frome (Dorset, UK). Although *S. trutta* exhibit a wide range of life histories, the focus of this study was on smolts during their maiden marine migration in spring because: (i) they represent an important *S. trutta* population component (Klemetsen et al., 2003) and (ii) their body length, age, and sex are biological characteristics thought to govern their marine migratory behavior (Berg & Berg, 1989; Jensen et al., 2012; Jonsson, 1985). Four hypotheses were tested according to the findings of previous studies (Table 1): (1) longer smolts will migrate earlier than shorter smolts, (2) the influence of smolt length on migration timing will be age- and sex-specific, (3) females will have a longer maiden marine sojourn duration than males, and (4) longer smolts will have a briefer maiden marine sojourn duration than shorter smolts.

Nine years (2015–2023) of data for *S. trutta* tagged between 2015 and 2019 were available for analysis of marine migratory behavior. The first step in the analysis was to explore patterns in the smolt data at the population-level, including age composition, sex ratio, migration timing, maiden marine sojourn duration, and marine return rates. In the second stage, the four hypotheses were tested. Hypotheses 1 and 2 were tested using linear regression models to quantify the influence of smolt length, age, and sex, and their interactions, on migration timing. To address hypotheses 3 and 4, a bespoke integrated statistical model was designed to quantify the strength of associations between maiden marine sojourn duration and a set of explanatory variables representing individual smolt biological characteristics. Although the statistical model was designed to maximize the use of information available from the data, the number of complete data cases that included smolt length measurements for individuals which could be tracked through the juvenile-to-adult life stages was limited. Therefore, a complementary post hoc exploration of uncertainty in the model-estimated effect sizes using simulation was undertaken to explore how plausible changes in sample size might have affected inferences from the model.

2 | MATERIALS AND METHODS

2.1 | Study area

Salmo trutta population monitoring data from the River Frome (Dorset, UK) were used for this study (Figure 1). The River Frome is a lowland, aquifer-fed chalk stream that rises at Evershot (50°50′24″N, 02°36′12″W), before flowing 70 km through highly braided but largely non-impounded channels to reach the tidal limit at Wareham (50°40′38″N, 02°7′3″W), prior to entering Poole Harbour estuary and then the English Channel.

2.2 | *Salmo trutta* population monitoring data

Monitoring data for the River Frome *S. trutta* population were collected in annual standardized surveys undertaken by the Game and Wildlife Conservation Trust (GWCT) and the Centre for Environment, Fisheries, and Aquaculture Science (Cefas) and tag detections between 2015 and 2023. Since 2015, approximately 3000 juvenile *S. trutta* have been captured each autumn (late-August to mid-September) at sites throughout the catchment using single or multiple pass electric fishing (pulsed DC with a square-wave waveform fished at 50 Hz, ~200 V, and 25%–30% duty cycle). Captured juveniles were anesthetized (2-phenoxy-ethanol), their fork length (nearest mm) and weight (g) measured, a scale sample taken, marked externally by the removal of their adipose fin, and then tagged with a passive integrated transponder (PIT) tag inserted into the coelomic cavity. Following recovery, all fish were returned to the river at their site of capture.

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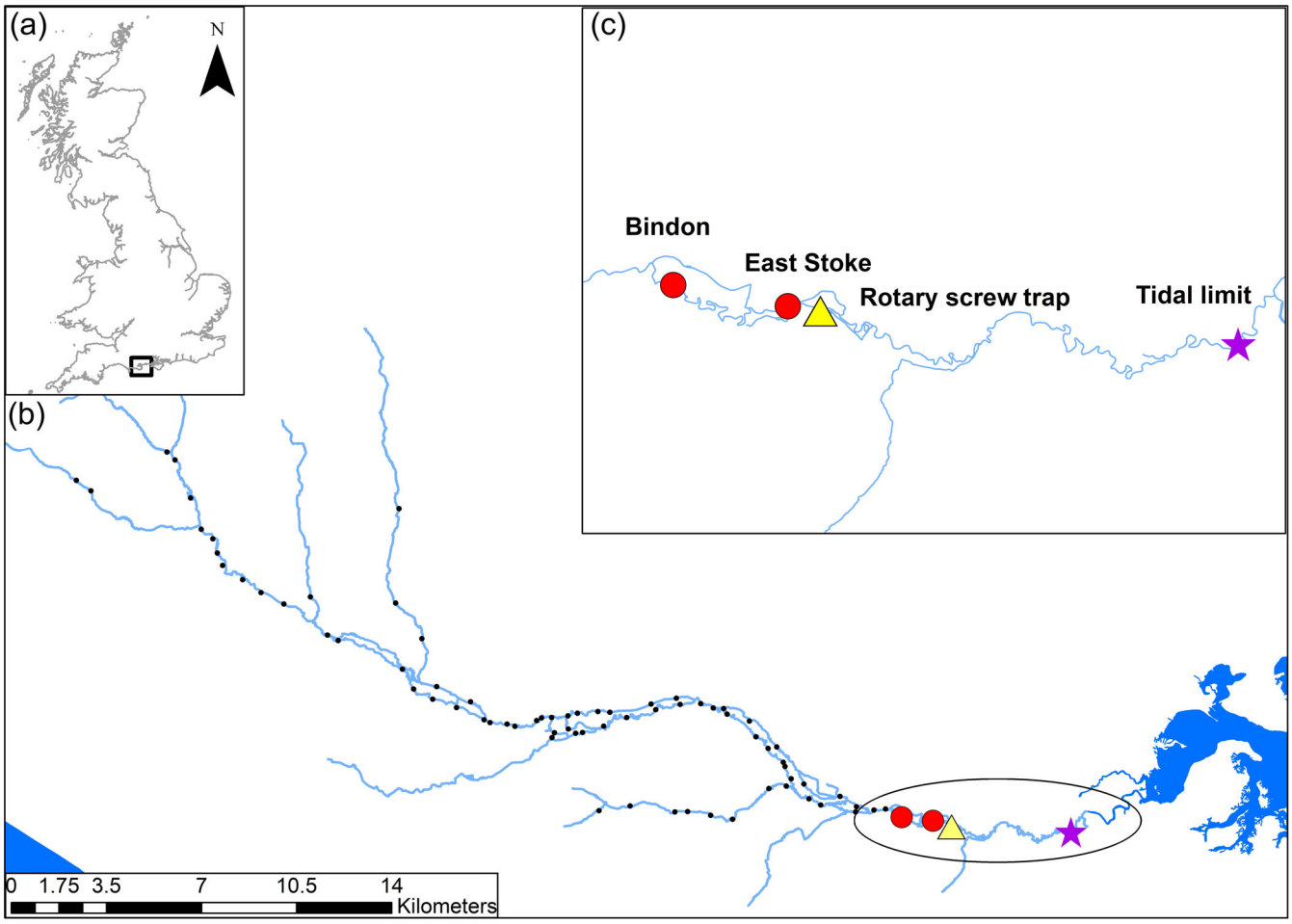


FIGURE 1 A map showing (a) the location of the River Frome in the UK, and the locations of the age-0+ parr tagging sites (black dots), passive integrated transponder (PIT) tag detection devices (red dots), rotary screw trap (yellow triangle), and tidal limit (purple star) (b) in the catchment and (c) on the river.

Animal handling and processing procedures were approved by the GWCT Animal Welfare and Ethical Review Body and carried out by licensed personnel under a UK Home Office ASPA licence (PPL 80/1480 and 30/3277). Age was determined from length–frequency histograms of juvenile fork length or, where this was ambiguous, by analysis of scales.

In the following springs (March to May), PIT-tagged juvenile *S. trutta* were detected moving downstream to the tidal reaches during their smolt migration. A proportion of these smolts were recaptured after being diverted into a small side channel of the lower river at East Stoke (50°40′47″N, 02°11′2″W) using a bioacoustic fish fence. These smolts were sampled following capture in a rotary screw trap (RST). Together, PIT tag detection and RST capture allowed the probability of recording and sampling migrating smolts to be maximized. It was felt reasonable to assume that PIT tag detections were from smolts because: (i) the nearest tagging site (1.75 km) upstream from the lower PIT antenna array exceeded the reported dispersal distance of age-0+ parr (Palm et al., 2023; Vøllestad et al., 2012), (ii) all fish caught in the RST had the morphological characteristics of smolts (i.e., size, silver coloration, and absence of parr-markings), and (iii) the proportion of fish detected moving downstream peaked in spring relative to other times of the year (Figure S1). The RST was operated to sample most of the smolt migration period in this river and the diurnal migration pattern, which amounted to >12 h per 24-h period for >35 days (of ≈50 days) of each annual smolt run. Across sampling years, the mean annual efficiencies of the bioacoustic fish fence and the RST at capturing *S. trutta* smolts were 35% (standard deviation [SD] = 11%) and 22% (SD = 5%), respectively. During operation, the RST was emptied every 30 min, and the captured fish were removed, anesthetized (2- phenoxy-ethanol), examined for a mark (PIT tag and adipose clip) that was recorded, a scale sample was collected, and their fork length (nearest mm) and weight (g) measured. Following recovery from anesthesia, all captured smolts were returned to the river 50 m downstream of the RST within 1 h of capture. Anadromous *S. trutta* that returned from the sea to the river before winter 2023 were detected on two continuously operating PIT antenna arrays. The first array is located at East Stoke 8 km upstream of the tidal limit, whilst the second array is positioned at Bindon 3.5 km further upstream.

Parr older than age-0+ were removed from the tagging data prior to analysis because only 28 of these individuals were tagged during

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TABLE 2 *Salmo trutta* population monitoring data sources and formats.

Variable	Source	Format	Sample size	Period
Parr age and length	Parr tagging records	Age (years) and fork length (mm) of the parr in fresh water	15,595 age-0+ tagged parr	August 2015–September 2019
Smolt age	Derived from parr tagging records and smolt PIT tag detections	Age (years) of the smolt	1033 tagged smolts (1536 detections)	March 2016–May 2021
Smolt length (observed)	Sub-sample of the seaward migrating smolts captured in the rotary screw trap	Fork length (mm) of the smolt	62 tagged smolts (a sub-sample of the 1033 detected tagged smolts)	March 2016–May 2021
Smolt length (modelled)	Predicted from a smolt length sub-model	Fork length (mm) estimate for a smolt detected leaving the river but not captured in the rotary screw trap	96 tagged smolts	March 2016–May 2021
Seaward migration timing	Smolt PIT tag detections	The timestamp (date and time) the smolt was detected migrating seaward	1033 tagged smolts (1536 detections)	March 2016–May 2021
Return migration timing	Sea trout PIT tag detections	The timestamp (date and time) the sea trout was detected returning for the first-time from the sea to the river	99 tagged sea trout (185 detections)	September 2016–December 2023
Sex	Genetic analysis of scale samples taken during fish tagging	Male or female genetic sex determination	813 detected tagged smolts	August 2015–September 2019

the study period. This resulted in a dataset of 15,595 age-0+ parr tagged between August 2015 and September 2019 (Table 2). Of these, 1033 were subsequently detected moving downstream past the two PIT antenna arrays at East Stoke and Bindon during the smolt migration window (1 March–31 May) in the springs of 2016 to 2021. Just 62 of these smolts were captured in the RST and measured. Subsequently, 99 tagged *S. trutta* were detected by the two PIT antenna arrays returning for their first time at sea to the river between 2016 and 2023. Of these, three individuals had been captured in the RST as smolts and measured.

The maiden marine sojourn duration expressed in days was estimated by subtracting the first return detection timestamp from the last smolt detection timestamp. First-time migrants that returned to the river before April 1 in the year following their migration as smolts were classified as zero-sea-winter (0SW) *S. trutta*, while those that returned after that date were classed as either one-sea-winter (1SW) or two-sea-winter (2SW) *S. trutta* after spending 1 or 2 years at sea, respectively. The date of April 1 was selected as the cut-off date for a sea-winter for three reasons: (i) all first-time migrants were detected returning to the river from June to December, (ii) 0SW *S. trutta* returned in the same calendar year as they smolted, and (iii) this date prevented potential misinterpretation of missed detections of fish returning in summer to winter that were subsequently detected leaving the river the following spring after spawning. The percentage marine return rates were calculated by dividing the number of *S. trutta* detected returning for the first time from the sea to the river by the total number of seaward-migrating smolts and multiplying the resulting value by 100, without accounting for the detection efficiency of monitoring devices.

2.3 | Sex determination

Genetic analysis of scale samples collected during fish tagging was undertaken to determine the sex of individual *S. trutta*. Genomic DNA was extracted from the scales, and molecular sexing was conducted by applying a duplex polymerase chain reaction approach to amplify a portion of the male-specific Y-chromosome master sex-determining (sdY) gene and the fatty acid-binding protein 6b (*fabp6b*) gene (amplification positive controls). A more detailed description of the molecular sexing procedure can be found in King and Stevens (2020), King et al. (2023), and Quéméré et al. (2014).

2.4 | Data analysis

A candidate set of linear regression models was designed to quantify the effects of smolt length, age, and sex, and their interactions, on emigration day of year to test the influence of smolt biological characteristics on migration timing. This analysis used smolts captured and measured in the RST ($n = 62$). The linear regression models took the form:

$$\text{doy}_i \sim \text{Normal}\left(\alpha + \beta X_i, \sigma^2\right) \quad (1)$$

where doy_i is smolt emigration day of year for individual *S. trutta* i, α is a constant intercept, β is a vector of K parameters relating $\beta = \beta 1, \beta 2, \ldots \beta k$ explanatory variables in matrix X_i to doy_i, and σ^2 is the variance term capturing the model error. For the saturated model, the explanatory variables were smolt length, age, and sex, and their

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interactions. Candidate models were compared by their goodness of fit using Akaike Information Criterion corrected for small sample sizes (AICc; Burnham & Anderson, 2002) implemented in function aictabCustom() of R package AICcmodavg (Mazerolle, 2020) to identify the "best-fitting" model. Diagnostic plots were used to check that the best-fitting model did not violate the assumptions of linear regression (Figure S2).

A bespoke integrated statistical model that quantified the effects of smolt biological characteristics and behaviors on marine sojourn duration was designed and parameterized to test the influence of smolt age, sex, emigration day of year, and length on the probability of first-time migrants returning to the river after one or more sea winters. The number of complete records of juveniles with length data available for analysis was maximized by predicting the lengths of seaward-migrating tagged smolts detected but not captured and measured in the RST ($n = 96$) and including them as covariates in the marine sojourn duration analysis. To do this, an integrated model was designed to predict the missing smolt lengths from covariates associated with observed smolt lengths, that is, those that were captured and measured in the RST ($n = 62$), while simultaneously associating those predicted smolt lengths (together with other covariates) to marine sojourn duration. This design was chosen to allow uncertainty in smolt length predictions to be properly accounted for in the marine sojourn duration analysis. The data used to predict the missing smolt lengths were broadly representative of the observed age-0+ parr length data (Figure S3). The model had two "sub-models", one for smolt length prediction and the other for marine sojourn duration. The smolt length sub-model took the form:

$$\mathrm{LF}_i \sim \mathrm{Normal}(\alpha + \beta X_i, \sigma^2) \quad (2)$$

where LF_i is the smolt fork length of individual *S. trutta i*, α is a constant intercept, β is a vector of K parameters relating $\beta = \beta 1, \beta 2, \ldots \beta k$ explanatory variables in matrix X_i to LF_i, and σ^2 is the variance term capturing the model error. For this model, the explanatory variables were age-0+ parr capture year, age-0+ parr length, and an interaction term between the number of days at liberty between age-0+ parr capture and smolt recapture/redetection and smolt age. The marine sojourn duration sub-model took the form:

$$\begin{aligned} y_i &\sim \mathrm{Bernoulli}(p_i) \\ p_i &= \mathrm{logit}^{-1}(\gamma + \zeta Z_i + \delta \lambda_i) \end{aligned} \quad (3)$$

where y_i is a binary measure of the maiden marine sojourn duration of individual *S. trutta i* in which 0 = 0SW represents a fish returning within 1 year of their seaward smolt migration and 1 = 1 + SW represents a fish returning after one or more years at sea. The 1 + SW return probability p_i is related to the explanatory variables through an inverse logit function, γ is a constant overall marine sojourn duration, ζ is a vector of M parameters relating $\zeta = \zeta 1, \zeta 2, \ldots \zeta m$ explanatory variables (given in Table 1) in matrix Z to y for individual i, and δ is a parameter relating the effect of observed and predicted missing smolt lengths λ_i to y_i.

All continuous explanatory variables were z-standardized by subtracting their mean and dividing by their standard deviation. Model parameters were estimated by Markov Chain Monte Carlo (MCMC) using JAGS (Just Another Gibbs Sampler; Plummer, 2003) fit using the R package rjags (Plummer, 2022). Four parallel MCMC chains were run for 100,000 iterations, and all parameter estimates were presented with their 95% Bayesian credible intervals. Convergence was assessed by visually examining MCMC trace plots and the Gelman–Rubin statistic (Brooks & Gelman, 1998), and was considered stable if the chains were mixing and non-convergent, that is the Gelman-Rubin test statistic <1.05 for all parameters. Weakly informative Normal$(\mu = 0, \tau = 1/1000)$ priors were given for constants and explanatory variable effects, and a Uniform$(\min = 0, \max = 10)$ prior was given to σ. The JAGS code for the integrated model is provided in Supporting Information Data S1. Estimated effect sizes from the integrated model were compared against those estimated from non-integrated separate models to explore the effect of uncertainty propagation on the integrated model estimates (see Supporting Information Data S1). Model performance was assessed by calculating the area under the receiver operator characteristic curve (AUC) using the R package Metrics (Hamner & Frasco, 2018). Using the AUC is a common practice to evaluate the performance of models that include a binary response variable (e.g., Hernandez et al., 2006; McCune, 2016). Calculating the AUC generates a value between 0.0 and 1.0, with values of 1.0 indicating perfect discrimination, 0.7 denoting a "useful" model, and 0.5 signifying that the model performs no better than random.

Although the statistical model was designed to maximize the use of information available from the data, a complementary *post hoc* exploration of uncertainty in the model-estimated effect sizes was undertaken to evaluate how plausible changes to data collection might affect inferences from the model. Specifically, a simulation study tested whether the variance and significance of effect sizes (using coefficients estimated from the data and applying a $p < 0.05$ threshold) were influenced by increases in sample size due to changes at the following data collection stages: the percentage of age-0+ parr tagged, the percentage of spring migrating smolts detected, and the percentage of smolts measured for fork length. Three scenarios for each data collection stage were tested (Table 3). These values were selected because they were judged by experts to result in plausible increases in sample sizes given the effort and cost of data collection. In addition, the duration of the tagging time series data ($n = 5$) was increased by 1, 3, and 5 years to test whether a short, medium, or long-term increase in data collection influenced the results. For each scenario, the data were bootstrapped to create a dataset with the desired characteristics. The response variable was created using the coefficients estimated from the bootstrapped dataset, to which a binomial generalized linear model was fitted, and the estimated effect size variances and significances were extracted. This was repeated for 10,000 fits for each scenario.

3 | RESULTS

3.1 | Smolt population-level patterns

In total, 6.6% of the tagged juveniles were detected moving downstream to the tidal reaches in spring over the 3-month period, with a

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TABLE 3 Scenarios used to explore the sensitivity of the statistical model to different sample sizes resulting from plausible changes to the data collection protocol.

Data collection stage	Scenario	Number of years in time series	Total number of age-0+ parr tagged	Total number of smolts detected	Mean number of adults with smolt fork length measurements	Mean number of adults without smolt fork length measurements	Total number of smolts detected as adults
Age-0+ parr tagged (15,595)	+10%	5	17,160	1133	3.44	105.68	109
	+20%	5	18,720	1236	3.73	115.37	119
	+30%	5	20,280	1339	4.00	125.06	129
Smolts detected (6.6%)	+1%	5	15,600	1186	3.59	110.51	114
	+3%	5	15,600	1498	4.48	139.57	144
	+5%	5	15,600	1810	5.35	168.67	174
Smolts measured (6.0%)	= 10%	5	15,600	1030	10.00	88.00	99
	= 20%	5	15,600	1030	20.00	78.00	99
	= 30%	5	15,600	1030	30.00	68.00	99
Time series (5 years)	+1 year	6	18,720	1236	3.73	115.35	119
	+3 years	8	24,960	1648	4.89	154.15	159
	+5 years	10	31,200	2060	6.09	191.92	198

Note: These data are illustrative of a stochastic process in which the numbers of returning adult *Salmo trutta* with and without smolt fork length measurements per year are randomly drawn each iteration with the scenario-specific probability. The original number of age-0+ parr tagged, percentage of smolts detected and measured, and number of years in the time series are shown in parenthesis.

median emigration date of April 4 (range = 1 March–28 May). All smolts from the 2015 to 2019 year classes were aged S1 or S2 (Figure S4). Differences in smolt age composition were evident, with a significantly larger percentage of smolts aged S2 (59%) than S1 (41%) across years (Exact binomial test: $n = 1025$, $p = <0.001$, 95% CI = 0.38–0.44). Distinct sex ratios were also identified. Overall, the percentage of females (59%) was significantly greater than males (41%) across years (exact binomial test: $n = 812$, $p = <0.001$, 95% CI = 0.56–0.63).

3.2 | Influence of smolt length, age, and sex on migration timing

Emigration day of year was significantly later for smolts aged S1 than S2 (One-way analysis of variance: $F[1, 60] = 22.28$, df = 1, $p < 0.0001$). The model that best described smolt emigration day of year included an interaction between length and age and explained 29% of the variance in the response variable (Table 4). Divergent associations between smolt length and emigration day of year existed by age class, with length positively and negatively associated with emigration day for smolts aged S1 and S2, respectively (Figure 2). Sex was not an important explanatory variable included in the best-fitting model. Differences in smolt length by age class for early and late season migrants existed, with longer smolts aged S1 emigrating later in the year than similar-sized smolts aged S2.

3.3 | Maiden marine sojourn patterns

Large inter-annual variation in the marine sojourn duration of first-time migrants existed (Figure 3). The mean maiden marine sojourn duration was 387 (SD = 265, range = 75–961) and 302 (SD = 213, range = 94–960) days for smolts aged S1 and S2, respectively. First-time migrants were detected returning from their marine sojourn to the river between June 18 and December 12, with a median return date of October 23. Most first-time migrants that returned to the river after zero or one winter at sea were smolts aged S2, whereas smolts aged S1 provided a greater contribution to the percentage of first-time migrants returning after two sea winters (Figure 4). No major differences in the number of winters that males and females spent at sea were evident. Slightly more females (55%) spent zero or one winter at sea than males (45%) and it appeared that more males (80%) than females (20%) spent two winters at sea, but this observation was constrained by small sample size (four males vs. one female).

Annual marine return rates were highly variable across smolt years (Figure S5). Across years, annual marine return rates were highest and lowest in the 2018 (21%) and 2021 (7%) smolt years, respectively. No significant differences in annual marine return rates by smolt age (Pearson's chi-squared test: $X^2[1, n = 812] = 2.17$, $p = 0.14$) or sex (Pearson's chi-squared test: $X^2[1, n = 812] = 1.98$, $p = 0.16$) were identified (Figure S6). In contrast, a significantly higher proportion of detected returners spent zero (63%) rather than one (32%) or two (5%) winters at sea (Pearson's chi-squared test: $X^2[2, n = 99] = 49.86$, $p = <0.001$; Figure S7).

3.4 | Associations between smolt biological characteristics and maiden marine sojourn duration

All parameter estimates for the integrated model converged without issue and all Gelman–Rubin R statistics were <1.05 indicating good mixing of the chains (Figure S8).

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TABLE 4 Statistics comparing fits for smolt migration timing models with different combinations of individual biological characteristics using Akaike Information Criterion corrected for small sample sizes (AICc).

Model	Model terms	*K*	AICc	Δ AICc	L	AICcWt	L-L	CW	Adj.r^2	*p* value
2	Length, age	5	491.24	0.00	1.00	0.93	−240.08	0.93	0.291	0.00004
4	Length, age, sex	9	496.42	5.18	0.08	0.07	−237.48	1.00	0.300	0.00033
1	Length	3	504.84	13.59	0.00	0.00	−249.21	1.00	0.080	0.01450
3	Length, sex	5	506.95	15.71	0.00	0.00	−247.94	1.00	0.087	0.04068

Note: Model terms include smolt length (length, mm), age (age, S1 or S2) and sex (sex, male or female). Also given are the number of parameters (*K*), the Akaike Information Criterion score (AICc), the difference in the information score between the top-ranked model and the model being compared (Δ AICc), the model likelihood (L), the AICc weight (AICcWt), the log-likelihood (L-L), the sum of the AICc weights (Cum.Weight), adjusted R^2 (Adj.r^2), and the *p* value (*p* value).

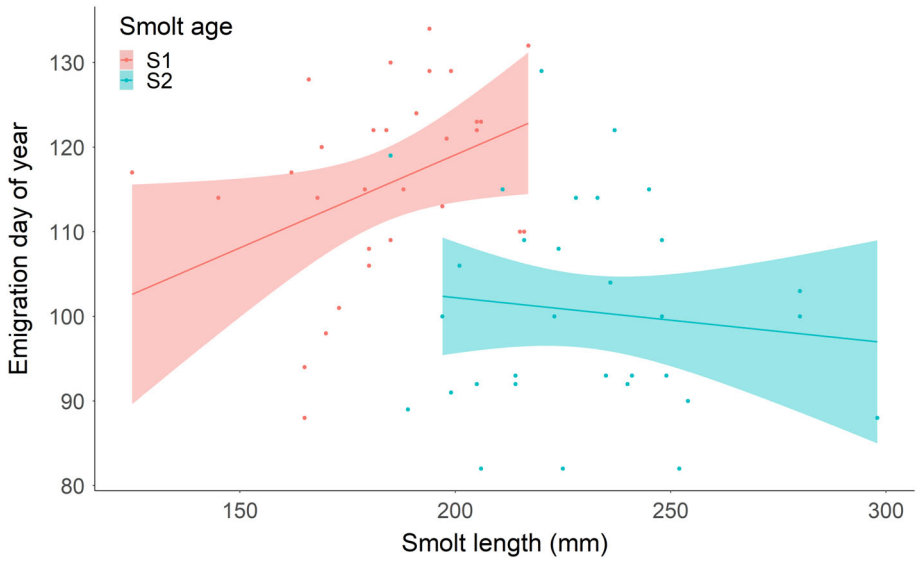


FIGURE 2 A scatter plot showing the association between smolt emigration day of year and length-by-age for the best-fitting migration timing model. Points are the data, solid lines show the linear regression fit to the data, and the shaded areas display the 95% confidence intervals.

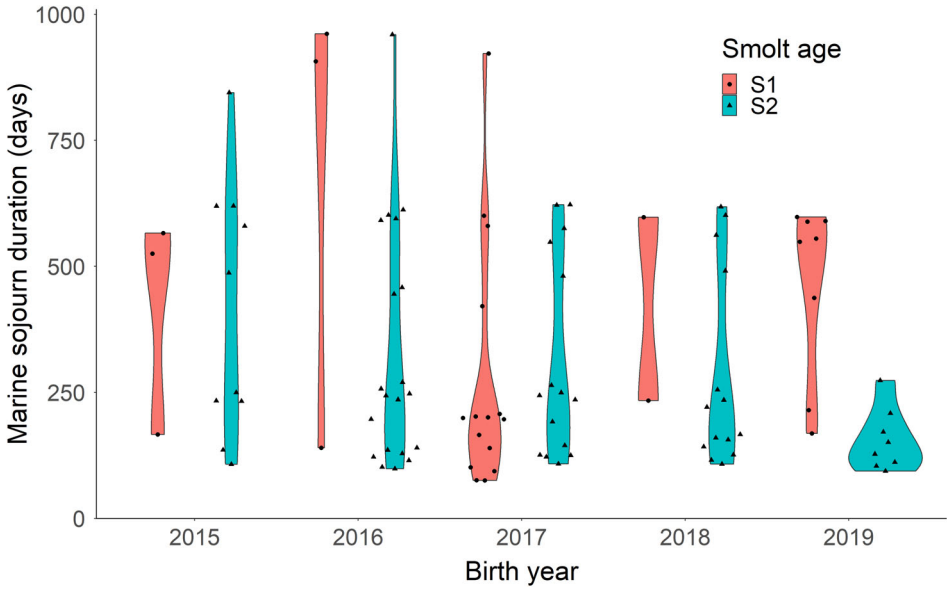


FIGURE 3 A violin plot of maiden marine sojourn duration (days) by smolt age for the River Frome age-0+ *Salmo trutta* population between the 2015 and 2019 year classes. Points are jittered on the *x* axis to show the maiden marine sojourn duration for individually tagged smolts.

Age-0+ parr length, the number of days at liberty for smolts aged S1, and the variance in the smolt length sub-model were significant predictors of smolt length, with 95% credible intervals that did not intercept zero but high uncertainty existed around most of their estimates (Figures 5 and 6). Age-0+ parr length and the number of days at liberty for smolts aged S1 had significant positive effects on smolt

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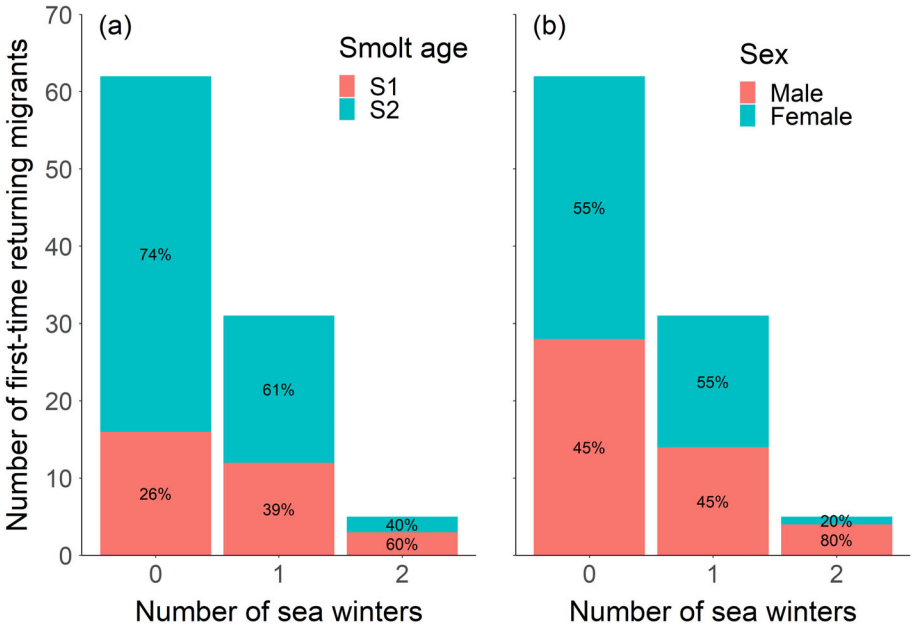


FIGURE 4 Bar charts of the number of first-time returning migrants spending zero, one, or two winters at sea by smolt age (a) and sex (b) for the River Frome age-0+ *Salmo trutta* population. The percentages on the bars indicate the number of smolts per age group or sex class relative to the total number of first-time returning migrants in each sea winter class.

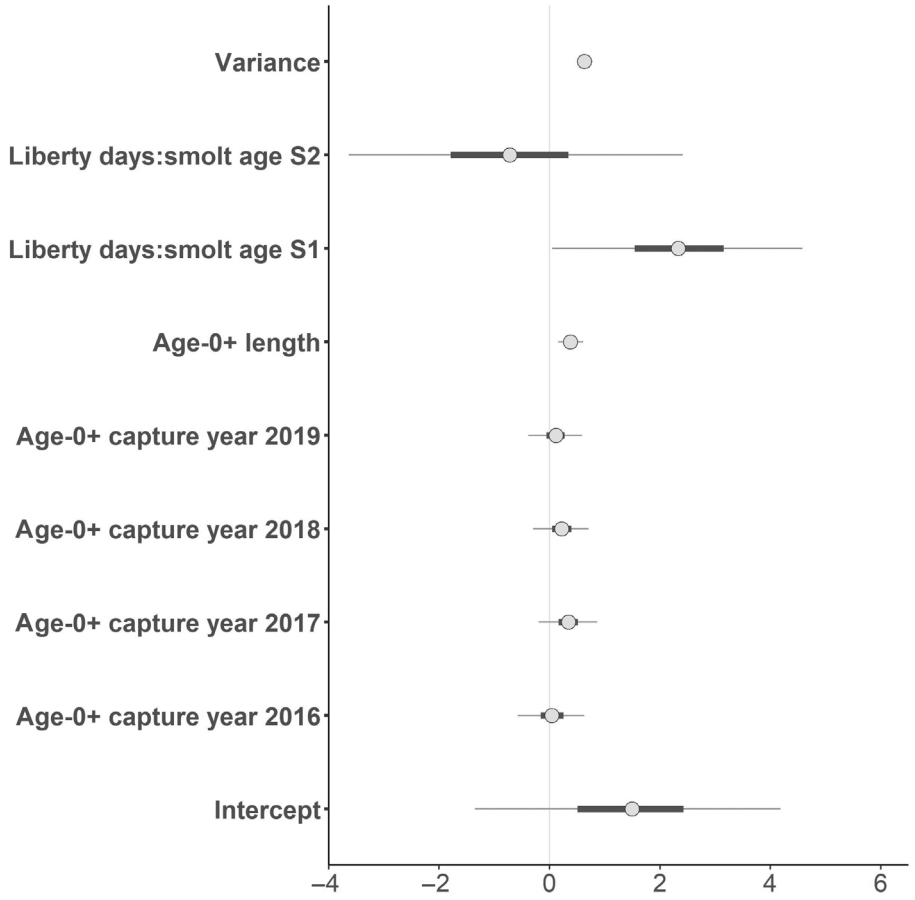


FIGURE 5 A caterpillar plot showing estimates of the population-level effects for River Frome smolt length sub-model. The solid vertical line indicates zero on the *x* axis. Points are the estimates, and the thick and thin lines show the 50% and 95% Bayesian credible intervals, respectively.

length. Predictions of missing smolt lengths were within the observed range of values for measured smolts (Figure S9).

All the explanatory variables in the marine sojourn duration sub-model had weak effects on the probability of first-time migrants returning to the river after one or more sea winters (1 + SW), with wide 95% credible intervals that overlapped zero (Figures 7 and 8). Smolt emigration day of year had a positive effect on the 1 + SW return probability. Differences in the 1 + SW return probability by smolt age and sex were identified, with the 1 + SW return probability higher for female smolts aged S1 than S2 and vice versa for male

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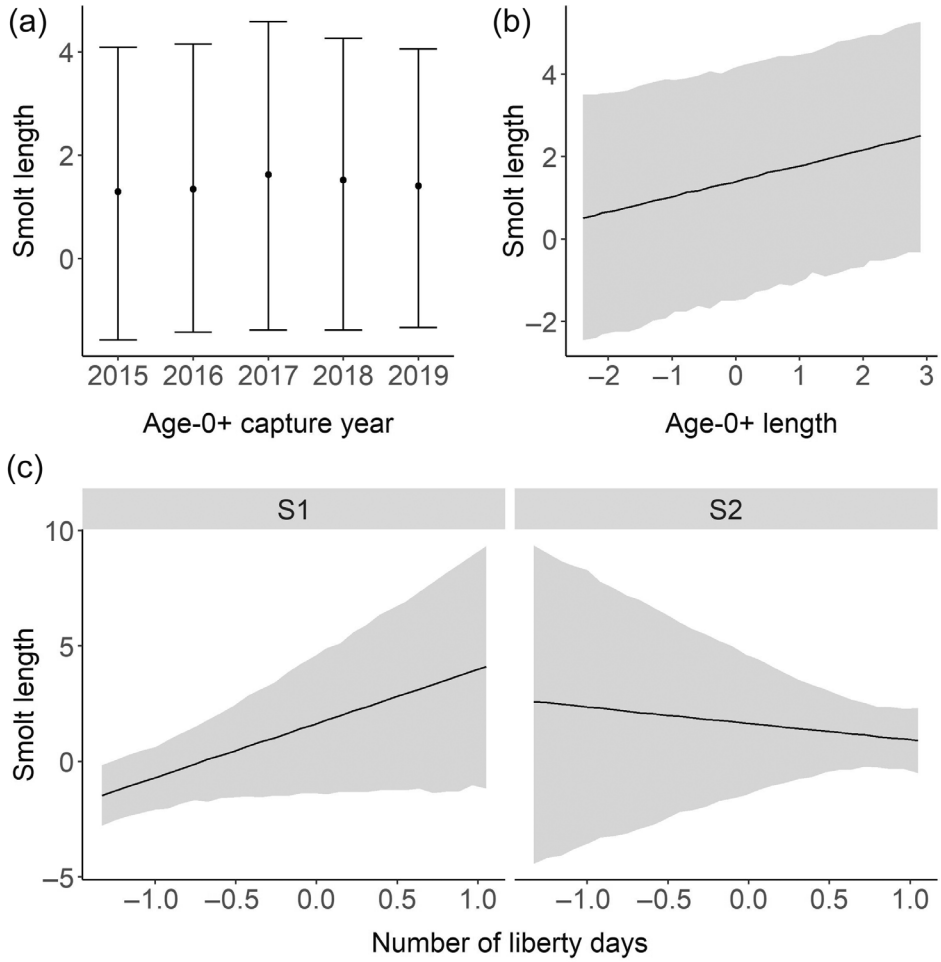


FIGURE 6 Marginal effect of standardized age-0+ parr capture year (a), age-0+ parr length (b), and the number of days at liberty between age-0+ parr capture and smolt recapture/redetection (c) on smolt length. See Methods for a description of the standardization. The bar and the shaded grey area represent the 95% Bayesian credible intervals.

smolts. Smolt length had a negligible effect on the 1 + SW return probability. The AUC was calculated to be 0.68 (±0.68–0.69 based on 95% credible intervals) suggesting satisfactory model performance. Comparison of the effect sizes against those from non-integrated separate models revealed qualitatively similar results, suggesting that the uncertainty propagation permitted by the bespoke integrated model did not affect inferences (Table S1 and Figure S10).

3.5 | Model sensitivity scenarios

The simulation study indicated that increasing sample sizes at most data collection stages reduced uncertainty around the effect sizes of explanatory variables in the marine sojourn duration sub-model (Figure 9). Increasing the percentage of smolts detected emigrating from 6.6% to 11.6%, or including five additional years of time series data, was projected to result in the interaction between sex and smolt age having a more statistically detectable effect on marine sojourn duration. No other simulated increases in sample size were projected to improve the significance of the results below the $p = 0.05$ threshold.

4 | DISCUSSION

This study revealed new insights into the smolt biological characteristics that influence the spring migration timing of *S. trutta* using a 9-year capture-mark-recapture dataset of individually tagged *S. trutta* on the River Frome (Dorset, UK). Specifically, the existence of age-specific differences in the influence of smolt length on spring migration timing was demonstrated for the first time. As expected, longer smolts migrated seaward earlier in the year than shorter smolts, supporting hypothesis 1 and the findings of previous studies (Bohlin et al., 1996; Jensen et al., 2012; Jonsson & Jonsson, 2009a). However, the importance of factoring age into the association between smolt emigration day of year and length was highlighted by the finding that longer 1-year-old smolts migrated seaward later than their shorter counterparts within the same age class, but the opposite association was observed for 2-year-old smolts. Smolt age and length, but not sex, were important biological characteristics that influenced migration timing, partially verifying hypothesis 2. These are novel findings about age-specific differences in the influence of smolt length on migration timing that have not been reported in the literature before. Overall, there was weak evidence with regards to the effects of smolt biological characteristics on the maiden marine sojourn duration.

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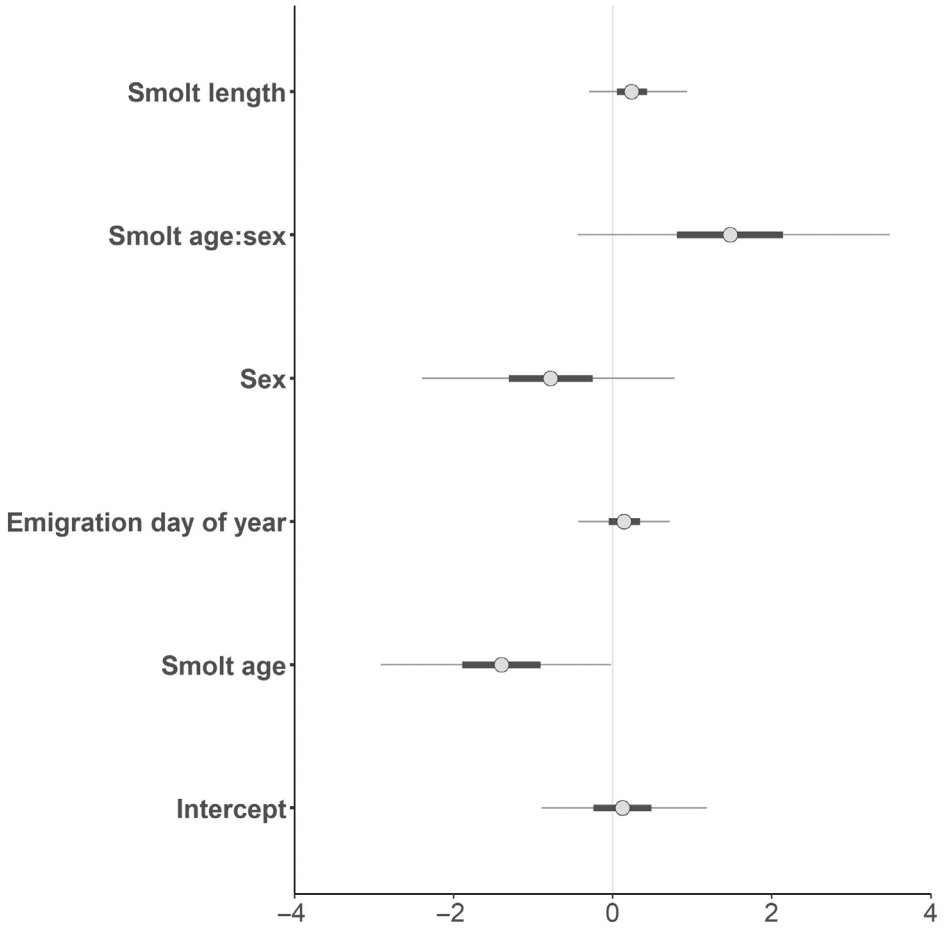


FIGURE 7 A caterpillar plot showing estimates of the population-level effects for the River Frome marine sojourn duration sub-model. The solid vertical line indicates zero on the *x* axis. Points are the estimates, and the thick and thin lines show the 50% and 95% Bayesian credible intervals, respectively.

Females had a longer maiden marine sojourn duration than males, confirming hypothesis 3 and previously observed for other *S. trutta* populations (Berg & Berg, 1989; Berg & Jonsson, 1990; Cucherousset et al., 2005). In contrast, smolt length had a negligible effect on maiden marine sojourn duration, and thus hypothesis 4 could not be confirmed. Although the analysis was designed to maximize the use of information in the available data, uncertainties in the quantified effects rendered most marine sojourn duration results equivocal. A complementary simulation study showed that boosting sample size at different data collection stages could improve the detection of ecologically important results.

4.1 | Smolt migration timing

Previous studies have shown that longer smolts migrate seaward earlier in the year than shorter smolts due to their greater energy reserves, higher osmoregulatory capacity, faster swimming speeds, and reduced vulnerability to predation decreasing mortality risk (Bohlin et al., 1996; Jensen et al., 2012; Jonsson & Jonsson, 2009a). The present study confirmed the existence of length-specific differences in smolt migration timing and benefited from access to age and sex data that were used to refine the association between emigration day of year and length. This refinement that adjusted for smolt age changed the direction of the association. Longer 1-year-old smolts were found to migrate seaward later than their shorter counterparts within the same age class, but the opposite association existed for 2-year-old smolts. Prior to seaward migration, the longer 1-year-old smolts that migrated later had higher in-river growth rates and a more prolonged growth period than their shorter, earlier migrating counterparts. Although the mechanism(s) underlying this finding require further investigation, plausible hypotheses could include age- and length-specific differences in metabolic rates and the onset of energetic constraints due to food limitation (Forseth et al., 1999), the effects of environmental conditions on swimming capability, and the propensity for diurnal migration (Ibbotson et al., 2011) and to adopt shoaling behavior to avoid predators (Riley et al., 2014). These results indicate that studies failing to factor age into the association between smolt migration timing and length run the risk of falling foul of Simpson's paradox (Simpson, 1951), where an association between two variables appears in different groups of data but disappears or reverses when they are combined.

Our results corroborate the findings of previous studies that demonstrated an age- and size-dependent smolt migration strategy (Jensen et al., 2012; Jonsson, 1985; Økland et al., 1993). The observed differences in smolt length by age class for early and late season migrants might be explained by variation in juvenile growth rates prior to smoltification. Faster-growing juveniles smolt younger at a smaller body size

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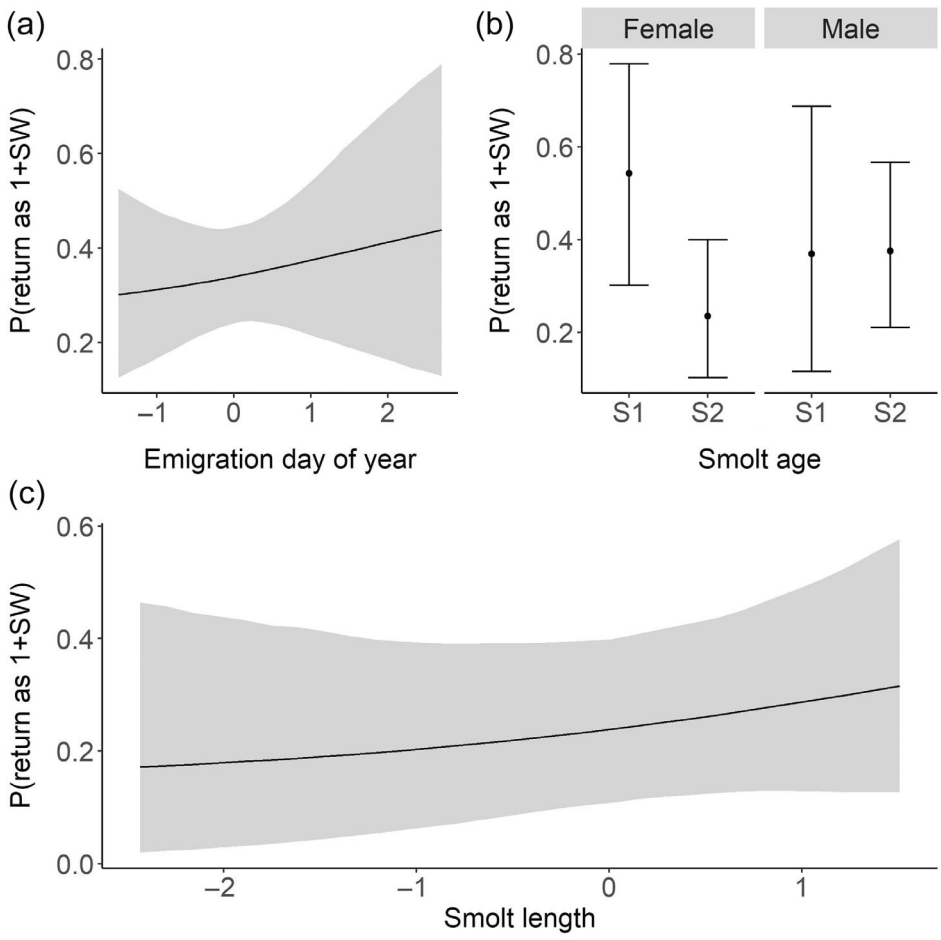


FIGURE 8 Marginal effect of the standardized smolt emigration day of year (a), interaction between smolt age and sex (b), and smolt length (c) on the relative probability (*p*) of *Salmo trutta* returning to the River Frome after one or more sea winters (1 + SW). See Methods for a description of the standardization. The bar and shaded grey area represent the 95% Bayesian credible intervals.

and migrate earlier than slower-growing individuals (Forseth et al., 1999; Økland et al., 1993). Perhaps the longer, later migrating 1-year-old smolts that remained in fresh water for a more prolonged period underwent compensatory growth before reaching the smolt size threshold. In contrast, the later migrating 2-year-old smolts with a similar length might have failed to reach the smolt size threshold in the previous spring and delayed their seaward migration until the following year, when they attained a sufficient body size to maximize survival. Growing to a larger body size and migrating later might constitute more of an adaptive advantage for 1- than 2-year-old smolts because this strategy better enhances their physiological state to reduce vulnerability to cold temperatures, osmoregulatory problems, and predation. Hence, the benefits of growing to a larger body size might exceed the costs of late migration to a greater extent for younger than older smolts.

4.2 | Maiden marine sojourn duration

First-time migrants from the River Frome exhibited large variation in their marine sojourn duration (326 ± 231 days; range = 75–961), within the range (30–1096 days) observed by previous studies (reviewed in Nevoux et al., 2019). They were detected returning from their marine sojourn to the river between summer and early winter, with a median return date of October 23 (range = 18 June–12 December). Anadromous *S. trutta* migrate seaward to exploit improved feeding and growth opportunities because the productivity of marine habitats is typically greater than freshwater habitats in temperate latitudes (Gross et al., 1988). Their marine sojourn duration is governed by trade-offs between growth and survival, whereby individuals that stay longer at sea can potentially acquire larger body sizes, but at the expense of a higher mortality risk and an increased likelihood of straying into other rivers (Berg & Jonsson, 1990; Davidsen et al., 2023; Eldøy et al., 2015).

Annual marine return rates for first-time migrants in the present study (7%–21%) corresponded with previous findings (7%–34%) for other *S. trutta* populations (Gargan et al., 2006; Jensen et al., 2019; Jonsson & Jonsson, 2009a). A significant difference in annual marine return rates by the number of sea winters was identified. First-time migrants that spent one or more winters at sea had lower annual marine return rates than individuals remaining in the marine environment for zero sea winters, perhaps because their comparatively longer marine sojourn duration exposes them to higher mortality that is associated with lower survival at sea (Berg & Berg, 1989; Berg & Jonsson, 1990).

The current analysis supported the expectation that smolt migration timing, age, and sex were associated with the maiden marine sojourn duration of the River Frome *S. trutta* population, although the

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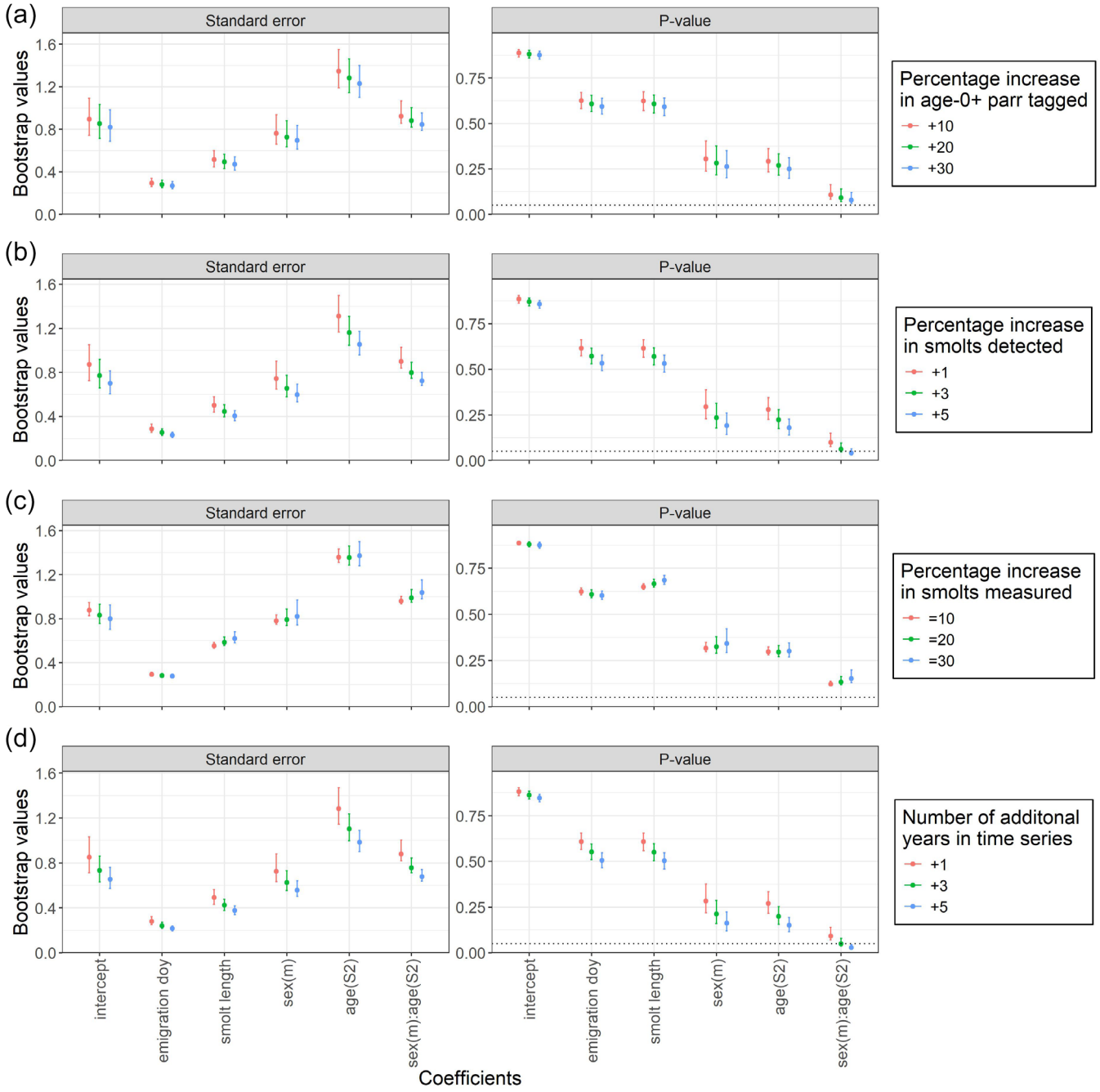


FIGURE 9 Results of the simulation study exploring the influence of different sample sizes resulting from the following plausible changes to the data collection protocol: (a) percentage increase in the numbers of age-0+ parr tagged, (b) percentage increase in the numbers of smolts detected emigrating, (c) percentage increase in the numbers of smolts measured for fork length, and (d) the temporal span of the study. The *y*-axis values are labelled as bootstrap values because they are derived from a bootstrap procedure on the original dataset. Points and error bars show the mean estimate and 95% confidence intervals based on 10,000 simulations, respectively. The horizontal dashed lines on the plots on the right-hand panel denote the $p = 0.05$ threshold level for assessing statistical significance.

estimated effects were weak. These results add to the growing body of evidence suggesting that smolt biological characteristics and behaviors affect the marine sojourn duration of *S. trutta* (Berg & Berg, 1989; Berg & Jonsson, 1990; Jonsson, 1985; Jonsson & Jonsson, 2009a), but also highlight the need for further study. Smolt emigration day of year positively affected the maiden marine sojourn duration. Younger smolts that migrated seaward later in the year remained in the marine environment for longer than older smolts migrating earlier in the season, consistent with the findings of previous studies (Eldøy et al., 2015; Jonsson, 1985; Økland et al., 1993). These younger, later migrating smolts might remain in the marine environment for longer than their older, earlier migrating counterparts because they require more time to exploit feeding opportunities to acquire energy to maximize growth and reproductive capacity. Females were found to have

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a longer maiden marine sojourn duration than males. The observed differences in maiden marine sojourn duration by sex might be related to variation in the energetic requirements of males and females. Females remain at sea for longer periods than males because the acquisition of a larger body size is more strongly associated with reproductive success for females than males (Berg & Berg, 1989; Berg & Jonsson, 1990; Cucherousset et al., 2005). Of course, this assumes that all females returning to the river for the first time spawn successfully, and the percentage of successful spawners requires verification, particularly for 0SW *S. trutta* that return in the same year as they smolt. Sex-specific differences in the mass required to optimize reproductive capacity and reach a maturity threshold are important biological characteristics that influence the marine sojourn duration (reviewed in Jonsson & Jonsson, 1993). Smolt length had a negligible effect on the maiden marine sojourn duration. Previous studies have shown that longer smolts have a briefer marine sojourn duration than shorter smolts because they spend less time feeding and growing at sea before reaching maturity and returning as adults to their river of origin to spawn (Eldøy et al., 2015, 2021; Paterson et al., 2021). An analysis of the same data using non-integrated separate models suggested that the uncertainty propagation permitted by the bespoke integrated model did not change these findings qualitatively. Furthermore, the simulation study indicated that the negligible effect of smolt length identified in this study was unlikely due to small sample size because increasing sample sizes still resulted in smolt length having a negligible effect on the maiden marine sojourn duration.

4.3 | Simulated influence of data collection changes on effect detection

Limited support for the effects of smolt biological characteristics on the maiden marine sojourn duration of *S. trutta* was provided by the present study. Although the statistical model was designed to maximize the use of information in the available data, there were only a few complete data cases from which to draw inferences. The simulation study indicated that an increase from 6.6% to 11.6% in the number of spring migrating smolts detected or adding 5 more years of time series data would result in the identification of statistically significant effects for the interaction between sex and smolt age on marine sojourn duration. These results highlight the importance of long-term monitoring programs or large sample sizes to describe the biological drivers of marine migratory behavior. Detections of spring migrating smolts could potentially be increased by operating the bioacoustic fish fence earlier in the year and increasing its impenetrability to divert more fish into the side channel, installing an additional PIT antenna array closer to the tidal limit, and improving the capture efficiency of the fish trap. Of course, there are other reasons why the effects detected were only weak. For example, the biological characteristics and behaviors considered might only have a limited effect on the marine sojourn duration in *S. trutta* populations. Or perhaps the variables considered interacted with factors not explored in this analysis, such as genetic heritability of migratory behaviors (Ferguson et al., 2019), energetic state (Forseth et al., 1999), body condition (Bordeleau et al., 2018), habitat and food availability (Wysujack et al., 2009), competition (Eldøy et al., 2015), predation risk (del Villar-Guerra et al., 2019), water temperature (Berg & Berg, 1989), river discharge (Jensen et al., 2012), and marine productivity (Gross et al., 1988), for which comparable data were incomplete or unavailable.

4.4 | Caveats

As the lower PIT antenna array at East Stoke is located 8 km upstream of the tidal limit, it cannot be guaranteed that all tagged juveniles detected migrating downstream in spring entered the sea. Considering other life stages migrating at different times of the year might have provided better insight into the underlying mechanisms. Spring migrants were the focus of this analysis because they provided a far greater percentage contribution (92%) to the number of juveniles detected moving downstream to the tidal reaches than autumn migrants (8%). Intriguingly, one tagged age-0+ parr was detected moving downstream to the tidal reaches in autumn, but whether this observation was indicative of early migration of young-of-the-year *S. trutta* or a predation event remains unclear. Previous studies have reported precocious age-0+ parr migration, particularly into the low salinity waters of the Baltic Sea (Andersson et al., 2024; Landergren, 2004; Limburg et al., 2001). In future, it would be interesting to evaluate how the biological characteristics and behaviors of spring and autumn migrants influence the maiden marine sojourn of *S. trutta*. The annual marine return rates of first-time migrants did not account for the potentially confounding effects of imperfect detection resulting from inefficiency in monitoring devices and straying into other rivers (Källo et al., 2023). Partitioning annual marine return rates into specific environments (e.g., estuarine, nearshore, or offshore waters) was not possible, but this would have provided insight into survival differentials among habitats. In addition, the limited number of complete data cases available from the 9 years of *S. trutta* population monitoring data constrained the type of analysis that was possible. Despite these caveats, this analysis identified important new smolt biological characteristics that influence the spring migration timing and marine sojourn duration of *S. trutta*, in addition to the characteristics consistent with previous studies (e.g., Berg & Berg, 1989; Jonsson, 1985; Jonsson & Jonsson, 2009a), and thereby contributing to the development of a conceptual model of *S. trutta* migratory behavior.

5 | CONCLUSIONS

This study revealed new insights into the smolt biological characteristics that influence the spring migration timing of *S. trutta*. Specifically, it demonstrated for the first time the existence of age-specific differences in the influence of smolt length on spring migration timing, with longer 1-year-old smolts emigrating later than their shorter counterparts within the same age class, but the opposite association existed

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for 2-year-old smolts. In terms of the adaptive significance of this finding, the benefits of growing to a larger body size to enhance physiological state might outweigh the costs of late migration to a greater extent for younger than older smolts. Overall, only equivocal evidence was found with regards to which smolt biological characteristics are associated with their maiden marine sojourn duration. There was some empirical support that smolt migration timing, age, and sex affect the maiden marine sojourn duration. Mechanisms underlying the associations between smolt biological characteristics and the maiden marine sojourn duration could not be elucidated. Further studies using a more comprehensive dataset consisting of additional smolt detections and captures are required to validate these findings, and the modelling work presented here provides guidance on the size of the required dataset and how to maximize the power of imperfect data.

Although the percentage of tagged juveniles detected as spring migrating smolts was small (6.6%), this study cannot make inferences about the extent of anadromy because mortality estimates were not available to evaluate the proportion of freshwater residents. Other studies have demonstrated that anadromy is an important life-history tactic for the River Frome *S. trutta* population, which contributes disproportionally to recruitment throughout the catchment (Goodwin et al., 2016; Jones et al., 2024). Future research should address knowledge gaps concerning: (i) spatio-temporal variation in life-history strategies; (ii) how factors in the juvenile freshwater stages influence life-history outcomes and the implications for growth, migratory behavior, and survival; and (iii) the maturation state of 0SW *S. trutta* and the effect of sex on their maiden marine sojourn duration and return timing. General findings on the ecology of *S. trutta* are emerging, but more detailed analyses using better population monitoring data are necessary. Given the large variation in *S. trutta* life histories and finding only weak associations between smolt biological characteristics and the maiden marine sojourn duration suggests that developing stock-recruitment models including the biological drivers of marine recruitment from datasets, such as those analyzed here, might prove challenging. More extensive and strategic monitoring of the biological characteristics of *S. trutta* along important salmonid rivers will aid future analyses. Undertaking a strategic review of the River Frome *S. trutta* population monitoring program guided by a conceptual life-history model to improve the efficacy and consistency of long-term biological data collection is recommended. Evidence from the simulation study indicated that efforts to improve the *S. trutta* population monitoring program should focus on detecting more spring migrating smolts, and persisting with monitoring over a long time series, rather than expending extra effort tagging additional fish each year. Since the completion of this study, the River Frome *S. trutta* population monitoring program has been modified to increase detections and captures of spring migrating smolts.

AUTHOR CONTRIBUTIONS

All 12 authors have been involved in the project and contributed significantly to the writing. Conceived and designed the investigation: J.G., R.L., S.G., and W.R. Data generation: J.G., R.B., R.L., S.G., S.E., W.R., J.M., R.A.K., and J.S. Data analysis and interpretation: J.G., R.B., S.G., J.M., S.E., and D.M. Manuscript preparation: J.G., S.G., J.M., A.W., R.B., T.B., S.E., R.A.K., D.M., W.R., J.S., and R.L. Funding: J.G. and R.L.

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ORCID

Jonathan P. Gillson https://orcid.org/0000-0001-7286-3946

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