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Understanding immediate and carry-over effects to prioritise habitat protection and restoration: a case study of threatened Atlantic salmon

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ABSTRACT

As habitat degradation threatens global biodiversity and conservation efforts are resource limited, maximising the effectiveness of habitat protection and thus restoration of wild populations is essential. For animals that occupy multiple habitats throughout their lifetime, understanding how the immediate (i.e., affecting a given life stage) and carry-over (i.e., affecting a subsequent life stage) effects of habitat quality impact their population dynamics could help prioritise effective habitat protection. Here, we use a bespoke integrated path analysis model that simultaneously accounts for effects of habitat characteristics, density-dependent regulation, and random effect structures, to draw inference from a case study dataset for the threatened diadromous fish, Atlantic salmon (*Salmo salar*). We show that higher quality growing habitat promotes greater young-of-year (YOY) body length by the end of the growing season that results in a subsequent higher probability of them surviving to be detected as seaward migrating juveniles. Further, these growing habitat characteristics, along with instream macrophyte cover, promote higher YOY abundance at the end of the growing season. Higher YOY abundance is associated with, on average, shorter YOY and a lower probability of subsequent survival, suggesting density-dependent processes are evident throughout these juvenile life stages. Our study demonstrates that detailed population and habitat monitoring data can be used to disentangle and quantify immediate and carry-over effects from myriad other regulatory processes. We postulate that such findings are useful to prioritise effective habitat management that maximises its beneficial (or minimises its detrimental) immediate and carry-over effects to different life stages of the target population.

1. Introduction

An organism's habitat provides abiotic and biotic resources and conditions essential for an individual to persist (i.e., survive and reproduce; Hall et al., 1997). Accordingly, the degradation and loss of habitat is one of the most urgent threats to global biodiversity, with population declines across terrestrial and aquatic ecosystems in part attributed to a reduction in habitat suitable to support the functioning of wild populations (Arthington et al., 2016; Powers and Jetz, 2019; Hogue and Breon, 2022). Strategies to mitigate habitat loss and remediate human impacts on ecosystems are therefore prevalent in conservation (Bond and Lake, 2003; Geist and Hawkins, 2016). Identifying habitats in which to invest restoration efforts can be challenging, particularly for species that exhibit ontogenetic shifts or migration and thereby inhabit multiple, sometimes inaccessible or unknown, environments (Pretty et al., 2003; Palmer et al., 2005). In these cases, management actions tend to target accessible habitats associated with critical life history stages or major stressors for restoration (e.g., Rogosch et al., 2024). Correspondingly, a growing literature is using population monitoring data to evaluate the effectiveness of those restorations (e.g., Belder et al., 2018, 2021; Noe et al., 2022). Rather than use population monitoring data to measure the effectiveness of habitat management a posteriori, however, we postulate that these data could be used to prioritise habitat protection or restoration a priori.

To be successful, habitat management must be based on an understanding of what constitutes high quality habitat and how this affects

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population processes. Effects of habitat conditions associated with a life stage can affect individual performance and population demographic rates during that life stage (here, *immediately*), but also in subsequent life stages, referred to as carry-over effects (e.g., Harrison et al., 2011). Carry-over effects have been documented in a wide range of species with complex life histories, including birds (Norris and Taylor, 2006), amphibians (Chelgren et al., 2006), mammals (Beltran et al., 2019), and fish (Dingeldein and White, 2016). For example, a study of the pond-breeding frog, *Rana aurora aurora*, found that favourable aquatic habitat conditions were associated with larger body size at metamorphosis and attendant improved survival and earlier emigration from ponds to terrestrial habitats (Chelgren et al., 2006). Neglecting to consider carry-over effects could, therefore, underestimate the influence of habitat quality on a population. Furthermore, identifying habitat conditions with both beneficial immediate and carry-over effects would allow for prioritising intervention where advantages are most likely to propagate through the population. Detecting and quantifying carry-over effects between subsequent life stages can, however, be difficult due to their possible interaction with myriad other processes regulating population functioning, such as density-dependent competition (Norris and Taylor, 2006; Harrison et al., 2011). This emphasises the need for sufficient data and understanding to disentangle these effects on wild populations under study.

Atlantic salmon (*Salmo salar*; hereafter salmon) are a diadromous fish species that spends between one and eight years in freshwater before migrating to sea to feed and grow prior to returning to rivers as adults to reproduce (Hansen and Quinn, 1998; Klemetsen et al., 2003). Within freshwater, salmon undergo ontogenetic shifts in habitat use from development in riverbed gravels through to rapid growth in summer juvenile growing habitat (Armstrong et al., 2003). Despite a good understanding of salmon life histories and considerable conservation efforts, they have suffered widespread population declines around the North Atlantic over the last five decades (Gillson et al., 2022; ICES, 2024) and were recently listed as 'near threatened' globally, and 'vulnerable' in Europe, by the International Union for the Conservation of Nature (IUCN) Red List Assessment (Darwall, 2023; Sayer, 2024).

An important factor contributing to the observed population declines is higher mortality of early salmon life stages as river conditions and freshwater habitats have deteriorated due to, for example, agricultural inputs, pollutants, channel modifications, and impoundments (Dudgeon et al., 2006). An additional – somewhat overlooked – consideration could be that any beneficial carry-over effects of freshwater habitats on subsequent life stages, such as the positive effect of increased body size on subsequent survival at sea (Gregory et al., 2019; Gosselin et al., 2021), are diminished when freshwater habitat is sub-optimal (e.g., Burnett et al., 2017). Although considerable restoration has targeted freshwater habitats to assist salmon population recoveries, success of these strategies appears limited, or unmeasurable due to insufficient monitoring (Lennox et al., 2021). Effective strategies often target habitat quality (Lennox et al., 2021), for example, restoring habitat complexity through the addition of instream structures (van Zyll de Jong and Cowx, 2016).

After emerging from spawning gravels in spring, young-of-year (YOY) salmon generally exhibit limited dispersal to establish feeding territories, which they will hold throughout the growing season, irrespective of how the quality of habitat in those territories might change (Crisp, 1995; Armstrong et al., 1994; Beall et al., 1994; Armstrong et al., 2003). In lowland rivers, the quality of this "juvenile growing habitat" is characterised by the amount of instream macrophyte cover, such as *Ranunculus* spp., and sufficient water velocity to sustain adequate drift feeding opportunities (Riley et al., 2009; Marsh et al., 2021). The benefits of high-quality juvenile growing habitat include increased YOY abundance and length at the end of the growing season (Marsh et al., 2021). Although habitat use by YOY salmon has received considerable research attention (Armstrong et al., 2003; Crozier and Siegel, 2023), the extent to which the immediate benefits of high-quality YOY growing habitat carry-over to their subsequent seaward migrant life stage has been largely neglected (Crozier and Siegel, 2023).

The aim of this study was to explore whether, with detailed data and understanding, we could detect and quantify both the immediate and carry-over effects of habitat quality on population processes of a threatened migratory species. To do this, we used a rich ten-year dataset of juvenile salmon population monitoring data, including individual telemetry, together with site-specific juvenile growing habitat monitoring data. These data were collected on a population inhabiting a river of deteriorating habitat quality, in part due to long-term intensification of agricultural practices (Grabowski and Gurnell, 2016; Cowley, 2022). We developed an integrated path analysis model to test two research questions: i) does the quality of juvenile growing habitat immediately affect YOY abundance and mean length? and ii) do the effects of juvenile growing habitat carry-over to influence the subsequent probability of YOY surviving to be detected as a seaward-migrating juvenile in the following spring? We expected that higher juvenile growing habitat quality would be associated with higher YOY abundance and mean body length (Table 1). Moreover, we hypothesised that longer YOY would have a higher subsequent probability to survive and be detected as seaward migrating juveniles, despite stronger regulatory negative density-dependence, operating through resource competition, at sites with higher YOY abundance.

2. Materials and methods

2.1. Data

2.1.1. YOY salmon sampling

Sampling of YOY salmon was undertaken on the River Frome, a lowland, aquifer-fed chalk stream located in Dorset, Southern England (Fig. 1), which is one of five monitored "index" rivers in the UK that collect and submit adult salmon abundance and biological data annually to the International Council for the Exploration of the Sea (ICES, 2024). YOY salmon abundance and length data were collected during annual juvenile salmonid surveys across the River Frome catchment in late-August to mid-September from 2015 to 2024. Multiple (k) pass depletion electro-fishing surveys (description of electro-fishing settings used in Marsh et al., 2020) were carried out at 17 to 21 sampling sites (ranging in length between 55 and 170 m; Fig. 1, Table S1). At the end of each pass, captured YOY salmon were lightly sedated (2-phenoxyethanol: 0.2 ml/l), measured to the nearest mm (fork length), marked with a uniquely identifiable Passive Integrated Transponder (PIT) tag (12.5 mm length, 2.12 mm diameter; Biomark, Idaho, USA) inserted into the body cavity, and adipose fin clipped to provide an external indication of capture. To avoid possible effects of tag burden, fish smaller than 60 mm (2015 to 2023, $<$ 0.5% of sampled fish in each year, Table S2) and 70 mm in length (2024, $<$ 3.5% of sampled fish, Table S2) were not tagged (Richard et al., 2013; Vollset et al., 2020). Post-processing, fish were placed in holding bins with aerated water until all fishing passes were completed and they recovered normal behaviour, after which they were returned to their site of capture. All procedures were completed by licensed personnel under a UK Home Office A(*SP*)A License (PPL 30/3277 and PP9506723). The total catch of YOY salmon at a sampling site ranged from 3 to 484 between 2015 and 2024, with 14,480 individuals sampled in total.

In the River Frome, the majority of YOY salmon undergo a physiological transformation to adapt to saltwater (known as smoltification) and begin their seaward migration at age 1 year (Ibbotson et al., 2013). Every spring following the juvenile salmonid surveys, populations of seaward migrating juveniles have been monitored using PIT telemetry and trapping at East Stoke, which is located downstream of all sampled sites and 8 km upstream of the tidal limit (Fig. 1). In this study, we limited our analyses to age 1 seaward migrants detected from February to May ($n = 1340$) because: i) these fish constitute the large majority of the seaward migrating juvenile population (e.g., approximately 75%;

Table 1
Model terms considered for each sub-model in the integrated path analysis model (YOY = young-of-year salmon).

Sub-model	Explanatory variable	Terms tested	Hypothesis
YOY abundance	*Ranunculus* cover	Linear, quadratic	YOY salmon abundance is highest in sites with intermediate *Ranunculus* cover (Marsh et al., 2021)
	Depth	Linear, quadratic	YOY salmon abundance is highest in sites with intermediate depths (Armstrong et al., 2003)
	Fast velocity	Linear, quadratic	YOY salmon abundance is highest in sites with heterogenous water velocity (Heggenes et al., 1999)
	Distance from tidal limit	Linear, quadratic	YOY salmon abundance is highest in the middle of the catchment (Parry et al., 2018)
	Coarse sediment	Linear	YOY salmon abundance is highest in sites with more coarse sediment (Armstrong et al., 2003; Suttle et al., 2004)
YOY length	Salmon abundance	Linear	YOY salmon length is lower in sites with greater YOY salmon abundance due to density-dependent competition, even at low abundances (Achord et al., 2003; Gregory et al., 2017)
	Ranunculus cover	Linear	YOY salmon length is greater in sites with higher *Ranunculus* cover (Marsh et al., 2021, 2022)
	Coarse sediment	Linear	YOY salmon length is highest in sites with more coarse sediment (Suttle et al., 2004)
	Fast velocity	Linear	YOY salmon length is greater in sites with faster water velocities (Marsh et al., 2022)
Seaward migrant	Salmon abundance	Linear	The probability of YOY salmon surviving to be detected as a seaward migrant is higher in sites with higher YOY salmon abundance due to advantages of schooling and predator avoidance (Courchamp et al., 2008; Riley et al., 2018)
	Salmon length	Linear	The probability of YOY salmon surviving to be detected as a seaward migrant is higher in sites with higher mean YOY length as larger individuals have a higher probability of surviving to be detected the following spring (Zabel and Achord, 2004)

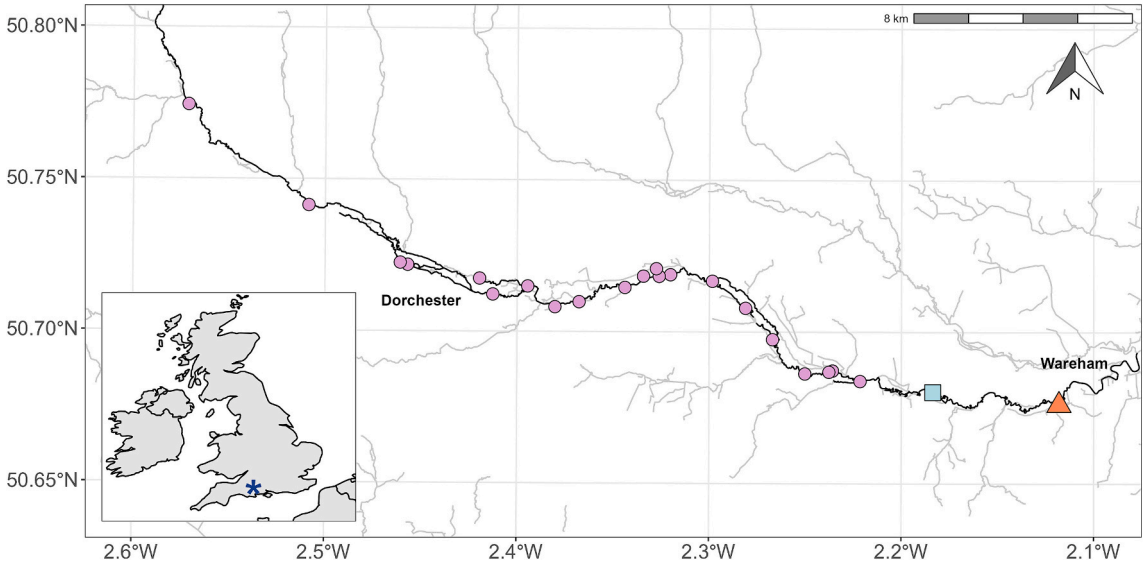


Fig. 1. Location of the sites surveyed annually for young-of-year (YOY) salmon (purple circles), the location of the passive integrated transponder (PIT) antennas used to detect tagged seaward migrating juvenile salmon at East Stoke (blue square), and the tidal limit (orange triangle) of the River Frome (black line) within the wider river network (grey lines), with the location of the River Frome in Dorset, southern England (inset map). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Ibbotson et al., 2013), and ii) any carry-over effects of summer growing habitat were expected to be more detectable among these juveniles compared to the minority of juveniles that followed alternative life strategies involving more time in the river before migrating to sea. Although the PIT antennas were not 100% efficient at detecting seaward migrants, we assumed that their efficiencies did not differ by fish size and so could be neglected without biasing our inferences.

From these juvenile monitoring data, we generated annual site-specific YOY salmon catches and mean YOY salmon lengths between 2015 and 2024, and annual numbers of spring seaward migrants originating from each of those sites between 2016 and 2025. This resulted in a dataset containing $n = 179$ site- and year- specific observations.

2.1.2. Habitat surveys

At each site in each year, habitat surveys were completed prior to salmonid sampling during the same survey period. To survey the habitat, we recorded the site length (m) and habitat characteristics at five quadrats (0.5 m × 0.5 m) evenly spaced across the river channel width along ten transects evenly spaced through the length of the site ($n = 50$ quadrats). At each transect, we recorded wetted channel width (m). At each quadrat, we recorded water depth (cm) in the centre of the quadrat, and estimated the percentage vertical view of the riverbed substrate composed of gravel and cobble (grain size > 2 mm; Wentworth, 1922, hereafter referred to as coarse sediment), the percentage vertical view of *Ranunculus* spp. (water crowfoot, the dominant macrophyte), and a classification of surface water velocity (velocities < and ≥ 50 cm/s were classified as slow and fast velocity, respectively). For each year, the product of the site length and mean wetted channel width described the site area (m^2) and site-level habitat characteristics were derived by taking a mean of the quadrat measures of water depth, *Ranunculus* cover, and coarse sediment (Figs. S1-S2). To describe water velocity at the site-level, we calculated the proportion of quadrats classified as fast velocity (Fig. S2). Lastly, to describe the position of a site within the catchment, we calculated the shortest river distance between the downstream start of each site and the tidal limit (Table 1)

using R packages *sf* (Pebesma, 2018) and *riverdist* (Tyers, 2024). These variables were selected based on hypothesised a priori expectations of their influence on YOY salmon abundance and growth opportunities (Table 1).

2.2. Statistical analysis

2.2.1. Integrated path analysis model

To test the hypothesised immediate effects of annual site-specific YOY growing habitat variables on YOY abundance, mean length, and their carry-over effects to the subsequent likelihood of YOY salmon surviving to be detected as a seaward migrant, we developed an integrated path analysis model (Gimenez et al., 2012; Fig. 2).

The electro-fishing depletion method that sampled the YOY salmon can be used to estimate abundance from successive catches by accounting for capture probability (Parent and Rivot, 2013). The annual (y) site-specific (s) abundance of YOY salmon ($YOY_{y,s}$) was a latent variable estimated by:

$$C_{1,y,s}|P_{y,s}, YOY_{y,s} \sim Binomial\left(YOY_{y,s}, P_{y,s}\right)$$

$$C_{2,y,s}|P_{y,s}, YOY_{y,s} - C_{1,y,s} \sim Binomial\left(YOY_{y,s} - C_{1,y,s}, P_{y,s}\right)$$

$$C_{3,y,s}|P_{y,s}, YOY_{y,s} - C_{1,y,s} - C_{2,y,s} \sim Binomial\left(YOY_{y,s} - C_{1,y,s} - C_{2,y,s}, P_{y,s}\right)$$

$$C_{4,y,s}|P_{y,s}, YOY_{y,s} - C_{1,y,s} - C_{2,y,s} - C_{3,y,s} \sim Binomial\left(YOY_{y,s} - C_{1,y,s} - C_{2,y,s} - C_{3,y,s}, P_{y,s.}\right)$$

where $C_{1,ys}$ is the first YOY salmon catch from $YOY_{y,s}$, $C_{2,y,s}, \ldots, C_{K,y,s}$ are successive YOY salmon catches in each of the remaining $K = 4$ passes from $YOY_{y,s}$ less the sum of the previous catches, and $P_{y,s}$ is the year- and site-specific capture probability that was specified as an inverse logit function of an intercept (α), site (β_s) and mean annual site-specific water depths (β) (Glover et al., 2018). The effects of hypothesised explanatory variables on the latent variable $YOY_{y,s}$ were then estimated by:

$$YOY_{y,s}|\lambda 0_{y,s} \sim Poisson\left(\lambda 0_{y,s}\right)$$

$$log\left(\lambda 0_{y,s}\right) = \alpha 0 + \theta 0 \chi 0_{y,s} + \nu_{y,s} + log(area)$$

where $\lambda 0_{y,s}$ is the expected year- and site-specific YOY salmon abundance, $\alpha 0$ is an intercept representing an overall mean YOY salmon abundance, the vector of coefficients $\theta 0 = \beta 0_1, \beta 0_2, \ldots, \beta 0_M$ describes the effects of M explanatory variables characterising habitat quality $\chi 0_{y,s} = \chi 0_{y,s,1}, \chi 0_{y,s,2}, \ldots, \chi 0_{y,s,M}$ on estimated YOY salmon abundance, $log(area)$ represents an offset term accounting for the variation in fishing area between years and sites, and $\nu_{y,s}$ represents a year within site random effect which was specified as $Normal(0, \sigma 0)$. We included a random effect to account for any unmeasured site-specific effects on YOY salmon abundance, which could vary inter-annually due to changes in fishing operator, as well as site proximity to spawning locations in the river.

Annual mean site-specific YOY salmon length ($Length_{y,s}$) was estimated as a function of habitat variables, as well as the latent YOY salmon abundance ($YOY_{y,s}$), following

$$Length_{y,s}|\mu_{y,s}, \sigma \sim Normal\left(\mu_{y,s}, \sigma\right)$$

$$\mu_{y,s} = \alpha 1 + \beta 1_a ln\left(YOY_{y,s}\right) + \theta 1 \chi 1_{y,s} + \eta_s$$

where $\mu_{y,s}$ is the expected year- and site-specific mean YOY salmon length, $\alpha 1$ is an intercept representing an overall mean length, $\beta 1_a$describes the effect of natural log-transformed YOY salmon abundance estimate on mean YOY salmon length within each site in each year, the vector of coefficients $\theta 1 = \beta 1_1, \beta 1_2, \ldots, \beta 1_N$ describes the effects of N explanatory variables characterising habitat $\chi 1_{y,s} = \chi 1_{y,s,1}, \chi 1_{y,s,2}, \ldots, \chi 1_{y,s,N}$ on mean YOY salmon length, η_s represents a random effect of site which was specified as $Normal(0, \sigma 1)$, and σ is a model error term.

From among the YOY salmon tagged at each site in each year ($YOY'_{y,s}$), the number of seaward migrants detected ($Migrant_{y,s}$) was estimated by

$$Migrant_{y,s}|P2_{y,s}, YOY'_{y,s} \sim Binomial\left(YOY'_{y,s}, P2_{y,s}\right)$$

$$logit\left(P2_{y,s}\right) = \alpha 2 + \beta 2_a ln\left(YOY_{y,s}\right) + \beta 2_l Length_{y,s}$$

where $P2_{y,s}$ is the probability of a tagged YOY salmon from year y and site s to survive and be detected as a seaward migrant (i.e., true survival confounded with detection efficiency), $\alpha 2$ is an intercept representing an

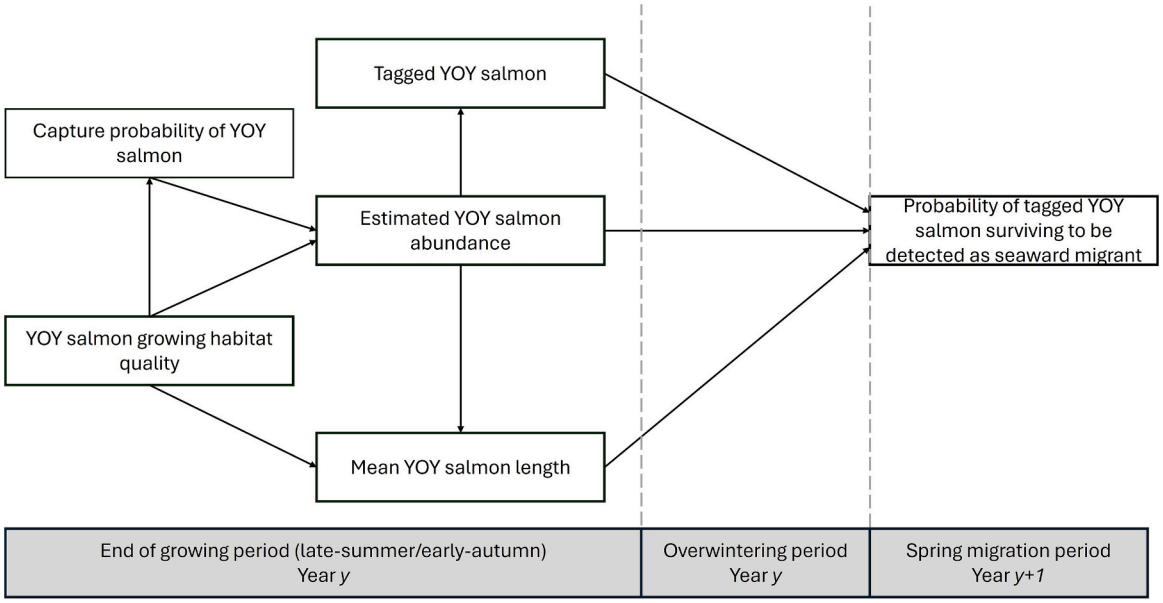


Fig. 2. Schematic of the integrated path analysis model to test for the hypothesised effects of juvenile salmon growing habitat quality on young-of-year (YOY) abundance and mean length, and their subsequent carry-over effects on the likelihood of YOY salmon surviving and being detected as seaward migrants in the following spring.

overall survival and detection probability, $\beta 2_a$ describes the effect of the natural log-transformed YOY salmon abundance estimate, and $\beta 2_l$ the effect of mean YOY salmon length, on the year- and site-specific probabilities.

2.2.2. Model fitting

To assess the validity and performance of our model, we used simulation testing to assess its ability to recover known parameter values from a simulated dataset (ten years, twenty sites, four fishing passes). The simulated dataset included year- and site-specific effects of an environmental covariate on YOY abundance and mean length, and year- and site-specific effects of abundance and mean length on the probability of YOY to survive and be detected as seaward migrants. We ran this test for multiple simulated datasets and for each we found the model to produce converged parameter estimates incorporating their known values (see Figs. S3-S9 for an example simulation result).

After reassuring simulation results, we fit the model to the observed data to test our hypothesised explanatory variable effects. We first explored collinearity among pairs of explanatory variables and found no pairs were highly correlated (Pearson's correlation coefficient $r \geq |0.6|$; Dormann et al., 2013) (Fig. S10). To promote a stable and robust model fit, and facilitate inference, explanatory variables were then z-standardised by subtracting their mean and dividing by their standard deviation. To test the influence of the a priori hypothesised important explanatory variables (Table 1), we first fit a saturated model with all variables included, before iteratively removing variables for which the credible intervals of the coefficient estimate overlapped zero (suggesting a weak effect) and refit the model until all weak influences were removed.

We assigned all parameters weakly informative priors (Table 2) and estimated their values using Just Another Gibbs Sampler (JAGS; Plummer, 2003) called by R (R Core Team, 2025) via the package rjags (Plummer, 2023). Parameter values were estimated from four parallel Monte Carlo Markov Chains (MCMC) run for 100,000 iterations thinned by 1000, after an adaptation and burn-in of 40,000 and 20,000 iterations, respectively. To assess MCMC convergence, we inspected MCMC trace plots visually and calculated the $\widehat{R}$ convergence diagnostic (Vehtari et al., 2021) using package *posterior* (Bürkner et al., 2023); convergence was achieved if the chains were mixing and $\widehat{R}$ was <1.01 for all parameters. To ensure that the model was well specified for our data, we compared observed data to simulated data from the posterior predictive distribution using package *bayesplot* (Gabry and Mahr, 2024).

Table 2
Prior distributions for unknown parameters estimated in the integrated path analysis model (YOY = young-of-year salmon).

Model component	Parameter	Prior
Ecological process		
YOY abundance	$\alpha 0$	$\sim Uniform(-20, 20)$
	$\beta 0_1, \ldots, \beta 0_M$	$\sim Uniform(-20, 20)$
	$\sigma 0$	$\sim 1/Gamma(0.01, 0.01)$
YOY length	$\alpha 1$	$\sim Normal(0, 100)$
	$\beta 1_a$	$\sim Normal(0, 100)$
	$\beta 1_1, \ldots \beta 1_N$	$\sim Normal(0, 100)$
	σ	$\sim 1/Gamma(0.01, 0.01)$
	$\sigma 1$	$\sim 1/Gamma(0.01, 0.01)$
Seaward migrant	$\alpha 2$	$\sim Logistic(0, 1)$
	$\beta 2_a$	$\sim Uniform(-20, 20)$
	$\beta 2_l$	$\sim Uniform(-20, 20)$
Observation process		
YOY capture probability	α	$\sim Logistic(0, 1)$
	β	$\sim Uniform(-20, 20)$
	β_s	$\sim Uniform(-20, 20)$

3. Results

Five iterative steps removed explanatory variables with weak influence. Visual assessment of the MCMC chains and $\widehat{R}$ convergence diagnostic (all <1.01, with the exception of six parameters <1.02) suggested that the MCMC chains were stationary and well-mixed (Table S3, Figs. S11 - S12). For non-latent variables, posterior predictive checks indicated that the model was consistent with the data (Figs. S13 and S14).

Mean YOY abundance across sites was estimated to fluctuate markedly over time, ranging from 39 [95% credible intervals: 36, 44] in 2016 to 123 [118, 130] in 2021, but was, on average, lower in the second half of the time-series relative to the first half (2015–2019: 96 [91, 102]; 2020–2024: 80 [76, 86]; Fig. 3a). In contrast, mean YOY length across sites remained similar throughout the time-series, ranging from 9.09 [8.75, 9.42] to 9.38 [9.01, 9.74] cm (Fig. 3b). The probability of a tagged YOY salmon surviving to be detected as a seaward migrant ranged between 0.08 [0.08, 0.09] and 0.12 [0.11, 0.14], with peaks in probability in 2016 and 2024 corresponding to the lowest estimates of YOY abundance (Fig. 3a and c). The mean capture probability of YOY salmon was estimated to range between 0.57 [0.52, 0.62] and 0.61 [0.55, 0.66] throughout the time-series and was positively influenced by water depth (0.11 [0.03, 0.18]) (Figs. S15 and S16). While site-level variation in capture probability, YOY abundance and to a lesser extent, YOY length was evident, there was no clear spatial pattern

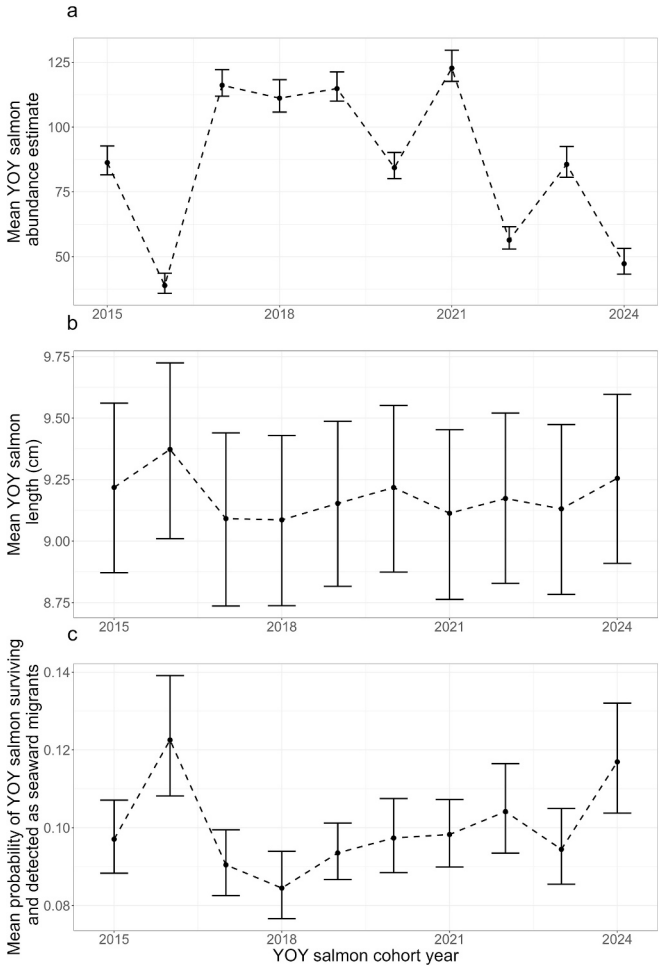


Fig. 3. Estimated mean a) young-of-year (YOY) salmon abundance, b) YOY salmon length, and c) probability of YOY salmon surviving to be detected as a seaward migrant across the study sites between 2015 and 2024. Points show the mean estimate and error bars denote the 95% credible intervals.

(Figs. S16 and S17).

The final model retained the positive influences of *Ranunculus* cover (posterior mean estimate: 0.26 [95% credible intervals: 0.13, 0.39]) and coarse sediment (0.25 [0.12, 0.38]), and the negative influence of distance from tidal limit (−0.25 [−0.38, −0.14]), on estimated YOY salmon abundance, respectively (Figs. 4 and 5a). The proportion of fast velocity was found to positively influence estimated YOY abundance until the proportion reached approximately 0.44, after which it had a negative influence (Figs. 4 and 5a). Mean YOY length was shown to be negatively influenced by estimated YOY abundance (−0.17 [−0.25, −0.07]) and positively influenced by coarse sediment (0.16 [0.07, 0.24]) and the proportion of fast velocity (0.13 [0.03, 0.24]) (Figs. 4 and 5b). Lastly, the probability of YOY salmon to survive and be detected as seaward migrants was negatively influenced by estimated YOY abundance (−0.11 [−0.18, −0.03]) and positively influenced by mean YOY length (0.28 [0.19, 0.37]), with the probability increasing nearly three-fold from 0.06 to 0.15 with an increase in length from 7.7 to 11.0 cm (Figs. 4 and 5c). The indirect and overall effects of habitat variables on the probability of YOY salmon to survive and be detected as seaward migrants were relatively weak, whereas there was a larger overall negative effect of YOY abundance on the probability of YOY salmon to survive and be detected (Table 3).

4. Discussion

Population monitoring data is used to assess the efficacy of habitat protection or restoration a posteriori (e.g., Noe et al., 2022). We postulate that similar data, together with habitat monitoring data, could be used to help prioritise habitat protection or restoration a priori, particularly when both immediate and carry-over effects of habitat quality are considered. For salmon, we have shown that high-quality juvenile growing habitat promoted longer body length by the end of the growing season that – in turn – resulted in a higher probability of YOY salmon surviving to be detected as seaward migrating juveniles. We were able to quantify these effects in the presence of negative influences of YOY abundance on their length and (to a lesser extent) subsequent survival to be detected as a migrating juvenile, presumably due to competition for limited resources in the River Frome. At least for this river, it seems that ensuring high-quality freshwater juvenile growing habitat should result in benefits that carry-over to promote higher numbers of juveniles migrating to sea. Maximising the quantity of seaward migrating juveniles has the potential to improve salmon population resilience to environmental change (Thorstad et al., 2021; Gillson et al., 2022). Our findings therefore highlight that juvenile growing habitat is a priority target for protection and restoration of salmon populations. In particular, the River Frome, which has been judged to be in unfavourable condition based on habitat and water quality metrics (Grabowski and Gurnell, 2016; Cowley, 2022), could benefit from habitat management to provide clean gravels and encourage natural macrophyte assemblages throughout the juvenile growing period.

This study suggests that with sufficient data and understanding, we can disentangle and quantify the immediate and carry-over effects of habitat on populations of species with complex life histories (Norris and Taylor, 2006; Harrison et al., 2011). By quantifying the immediate habitat effects, we showed that sampling sites characterised by coarse substrate (gravel and cobbles) and, to a certain extent, faster water velocities, were positively associated with both greater YOY salmon abundance and mean length. Additionally, higher cover of the dominant macrophyte, *Ranunculus* spp., was linked to higher YOY salmon abundance. These findings confirmed our hypotheses of what constitutes good quality habitat in lowland rivers and are consistent with existing knowledge of juvenile salmon ecology, with macrophytes providing habitat complexity in the absence of large substrate in low-energy river systems (e.g. Heggenes et al., 1999; Beland et al., 2004; Riley et al., 2009; Marsh et al., 2021). Surprisingly, water depth was not retained as an influential variable describing YOY abundance, despite often being reported as an important habitat consideration for juvenile salmon (Armstrong et al., 2003). This could be an artifact of the data collection process, whereby electro-fishing surveys targeted YOY salmon in habitats with depths ranging from 11.4 to 71.2 cm (upper quartile = 45.6 cm), which was a limited range within the wider span of depths reportedly used by juvenile salmon (up to 100 cm; summarized in Armstrong et al., 2003).

Aside from immediate effects, we were also able to quantify carry-over effects of juvenile growing habitat. We have shown that the positive effects of habitat quality on mean YOY salmon length conveyed a positive influence on the probability to survive and subsequently be detected as a juvenile seaward migrant. This finding is consistent with

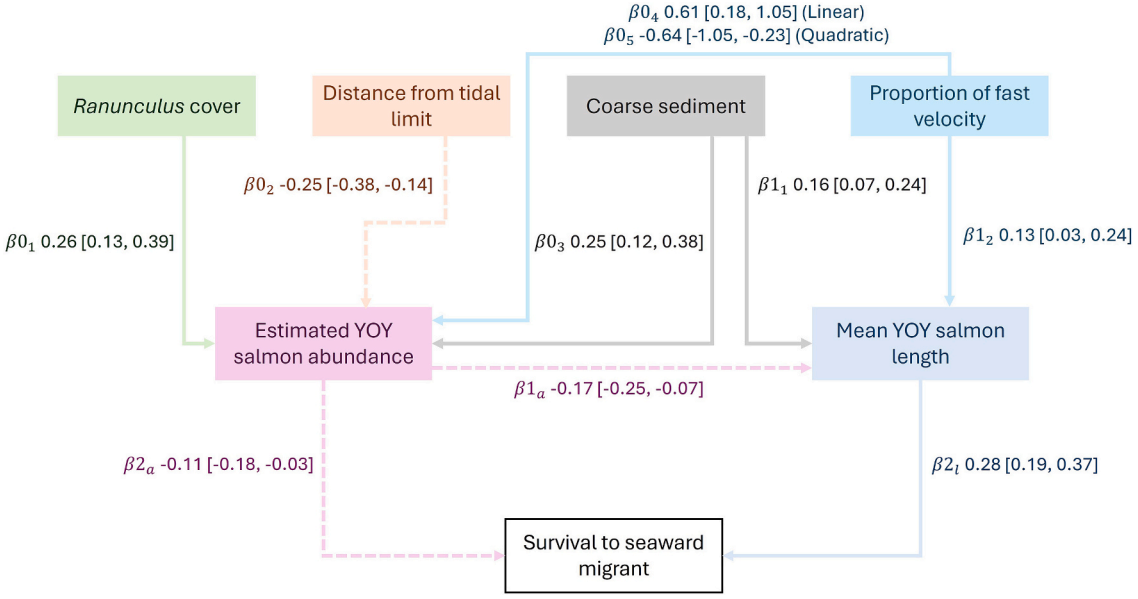


Fig. 4. Explanatory variables retained in each sub-model in the final integrated path analysis model describing young-of-year (YOY) salmon abundance, YOY mean salmon length, and the probability of YOY salmon surviving to be detected as a seaward migrant. Coefficient estimates (and 95% credible intervals) are shown for each pathway.

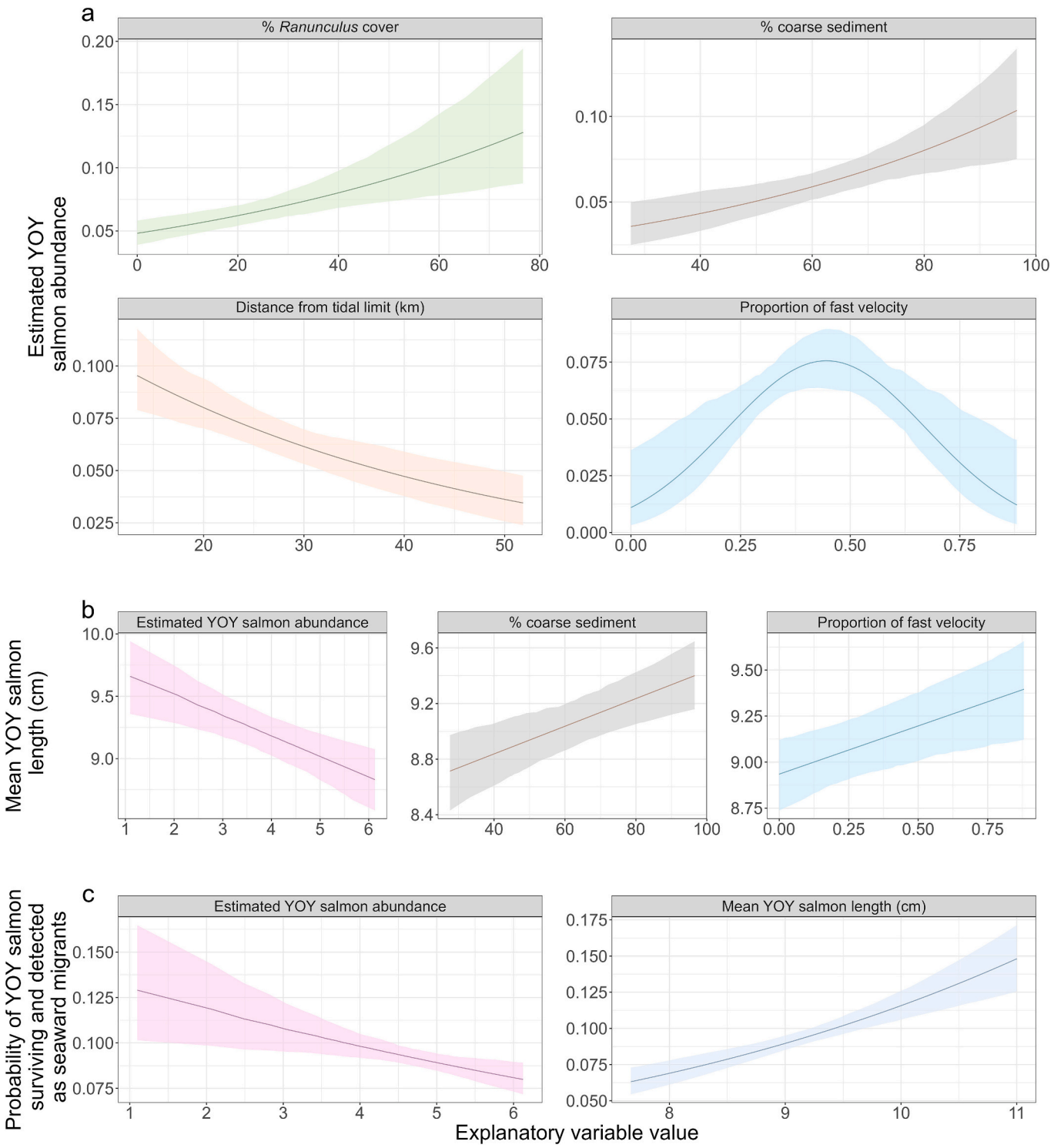


Fig. 5. Partial effects of the explanatory variables retained in the final integrated path analysis model for a) young-of-year (YOY) salmon abundance; b) mean YOY salmon length; and c) probability of YOY salmon surviving to be detected as a seaward migrant. Lines and shaded ribbons show the mean estimate and 95% credible intervals for continuous explanatory variables. The partial effects calculate the effect of a specific variable while holding all other explanatory variables constant at their mean effect size. In b) and c), the Estimated YOY salmon abundance explanatory variable is shown on the natural log scale.

studies on other salmonid species, which have reported size-dependent overwinter survival in juvenile coho salmon *Oncorhynchus kisutch* (Quinn and Pederson, 1996; Brakensiek and Hankin, 2007) and chinook salmon *O. tshawytscha* (Zabel and Achord, 2004). Interestingly, Zabel and Achord (2004) found no relationship between mean length and survival, but rather the relative size of an individual was related to their survival prospects, with smaller individuals at risk of greater overwinter mortality. Being a larger size might be advantageous if it reduces predation risk from gape-limited predators or provides physiological capabilities to more easily evade predation (Healey and Reinhardt, 1995). Furthermore, a larger body size might increase success in outcompeting smaller conspecifics for favourable territory (Blanchet et al., 2006), thereby resulting in less risk adverse foraging behaviour (Reinhardt and Healey, 1997). Consideration should also be given to size-dependent

Table 3
Indirect effects of habitat quality variables (R, Sd, D, F) and direct and indirect effects of estimated young-of-year (YOY) salmon abundance (A) on the probability of YOY salmon surviving and detected as seaward migrants (S), with mean YOY salmon length indicated as L. Indirect effects are the product of the partial path coefficients (shown above the arrow in each pathway) and the overall effects are the sum of all direct and indirect effects. Indirect and overall effects were calculated in the model estimation process.

Variable	Pathways	Direct/indirect effect	Overall effect
% *Ranunculus* cover (R)	$R \xrightarrow{0.26} A \xrightarrow{-0.11} S$	−0.03 [−0.06, −0.01]	−0.04 [−0.07, −0.01]
	$R \xrightarrow{0.26} A \xrightarrow{-0.17} L \xrightarrow{0.28} S$	−0.01 [−0.02, −0.00]	
% coarse sediment (Sd)	$Sd \xrightarrow{0.25} A \xrightarrow{-0.11} S$	−0.03 [−0.06, −0.01]	0.01 [−0.07, 0.05]
	$Sd \xrightarrow{0.25} A \xrightarrow{-0.17} L \xrightarrow{0.28} S$	−0.01 [−0.02, −0.00]	
	$Sd \xrightarrow{0.16} L \xrightarrow{0.28} S$	0.05 [0.02, 0.08]	
Distance from tidal limit (D)	$D \xrightarrow{-0.25} A \xrightarrow{-0.11} S$	0.03 [0.01, 0.05]	0.04 [0.01, 0.09]
	$D \xrightarrow{-0.25} A \xrightarrow{-0.17} L \xrightarrow{0.28} S$	0.01 [0.00, 0.02]	
Proportion of fast velocity (F)	$F \xrightarrow{-0.03} A \xrightarrow{-0.11} S$	0.00 [−0.01, 0.02]	0.04 [0.01, 0.08]
	$F \xrightarrow{-0.03} A \xrightarrow{-0.17} L \xrightarrow{0.28} S$	0.00 [−0.01, 0.01]	
	$F \xrightarrow{0.13} L \xrightarrow{0.28} S$	0.04 [0.01, 0.08]	
Estimated YOY salmon abundance (A)	$A \xrightarrow{-0.11} S$	−0.11 [−0.18, −0.03]	−0.15 [−0.23, −0.08]
	$A \xrightarrow{-0.17} L \xrightarrow{0.28} S$	−0.04 [−0.08, −0.02]	

tagging mortality, which Brakensiek and Hankin (2007) postulated could, in part, explain the lower apparent overwinter survival of juvenile coho salmon which were shorter at tagging.

To quantify immediate and carry-over effects, they must be disentangled from other population processes (Norris and Taylor, 2006). Density-dependence, usually negative and in the form of competition for limiting resources, is thought to be common in wild populations (Brook and Bradshaw, 2006), as in salmonids, particularly during their freshwater juvenile stages (Grossman and Simon, 2020). Here, we found higher YOY salmon abundance at the end of the growing period was associated with, on average, shorter YOY salmon and the reduced probability of YOY salmon surviving to be subsequently detected as a seaward migrant, suggesting density-dependent processes were evident throughout these juvenile life stages. Similar findings have been reported elsewhere. For example, a study on intraspecific competition found individual growth and food consumption rates were reduced with increasing density in Arctic charr *Salvelinus alpinus* (Amundsen et al., 2007), and a channel experiment has shown that juvenile Atlantic salmon are 27–33% larger in low relative to high density treatments (Puffer et al., 2015). Aside from negative density-dependence, we also hypothesised survival beyond the juvenile growing period to be positively related to conspecific abundance, i.e., positive density-dependence, as seaward migrating juveniles form shoals to reduce their predation risk during daylight hours (Riley et al., 2014). The effect of abundance, however, was estimated to be negative (albeit weak), which could suggest overwinter habitat limitation (Quinn and Pederson, 1996). In comparison with density-dependent growth, evidence for density-dependent mortality in salmonids has been less commonly reported in the literature (Grossman and Simon, 2020), potentially due to difficulties in detecting these effects (e.g. Teichert et al., 2013). The indirect effects of the habitat variables on the probability of YOY salmon to survive and subsequently be detected as seaward migrants were overall weak. This is likely because their effects are mediated by both positive and negative influences of salmon length and abundance, respectively, and changes in habitat during the intervening period (summer to spring), which was not considered here.

Overall, this study has shown that detailed population and habitat monitoring data can be used to disentangle and quantify immediate and carry-over effects from among myriad other regulatory processes in a case study species, the Atlantic salmon. We postulate that such findings could be useful in managing habitat in such a way as to maximise its beneficial (or minimise its detrimental) immediate effects, as well as carry-over effects, to different life stages of the target population. The approach presented here is applicable to other taxa, populations, and datasets. For example, path analysis of capture-mark-recapture data has been used to detect direct, indirect, and/or lagged effects of environmental conditions and individual traits on demographic rates in migratory marine seabirds (Gimenez et al., 2012; Layton-Matthews et al., 2024). When considering the widespread threats of climate change and pollution on the survival on adult great black-backed gulls (*Larus marinus*), Layton-Matthews et al. (2024) identified pollution as a key stressor which reduced survival rates both directly and indirectly via its negative influence on body mass. The ability to detect and account for possible effects of explanatory variables, even if we lack data to describe a covariate or if the mechanisms underpinning a relationship are unclear can help advance our understanding of population processes. This is particularly relevant for species that migrate or exhibit ontogenetic shifts in habitat use for which we have incomplete knowledge or scarce monitoring data. For example, Gimenez et al. (2012) tested for both an indirect lagged effect of sea surface temperature on the adult survival of Atlantic puffin (*Fratercula arctica*) mediated through changes in prey (herring *Clupea harengus*) availability, as well as a direct lagged effect of sea surface temperature on adult survival, although the mechanism that could drive this relationship was not specified. In the current investigation, we included data collected with imperfect sampling or missing important explanatory variables. To address the latter, we included year-within-site and site random effects to account for unmeasured (but potentially influential) variables when estimating YOY abundance and YOY capture probability, such as site-specific water temperature and electro-fishing operator, respectively. We recommend that similar detailed population and habitat datasets be (re)analysed to explore whether effects of habitat quality carry-over to subsequent life stages, thereby underscoring the importance of those habitats in population management.

For the River Frome salmon population, our finding that the increased quality of YOY growing habitat translates to higher probabilities of individuals becoming seaward migrants suggests that the restoration of YOY growing habitat would be a good candidate to improve juvenile salmon production and thereby the numbers of juveniles migrating that could return to this natal river to spawn. With a greater awareness of habitat effects that carry-over to subsequent life stages, it is hoped that we can get more “bang from our buck” when deciding how and where to restore habitats for population management, especially for migratory species with complex life histories of conservation concern, such as Atlantic salmon.

CRediT authorship contribution statement

Jessica E. Marsh: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Jonathan P. Gillson:** Writing – review & editing, Investigation. **William D. Riley:** Writing – review & editing, Investigation. **Sophie A.M. Elliott:** Writing – review & editing, Investigation. **Stephen D. Gregory:** Writing – review & editing, Methodology, Investigation, Data curation, Conceptualization.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2026.111822.

Data availability

Codes to simulate from and fit the models are available at https://github.com/CefasRepRes/marsh-salmon-habitat-carryovereffects. Data (Marsh et al., 2026) are available via the Zenodo repository https://doi.org/10.5281/zenodo.19205914.

References

Achord, S., Levin, P.S., Zabel, R.W., 2003. Density-dependent mortality in Pacific salmon: the ghost of impacts past? Ecol. Lett. 6, 335–342. https://doi.org/10.1046/j.1461-0248.2003.00438.x.

Amundsen, P.-A., Knudsen, R., Klemetsen, A., 2007. Intraspecific competition and density dependence of food consumption and growth in Arctic charr. J. Anim. Ecol. 76, 149–158. https://doi.org/10.1111/j.1365-2656.2006.01179.x.

Armstrong, J.D., Shackley, P.E., Gardiner, R., 1994. Redistribution of juvenile salmonid fishes after localised catastrophic depletion. J. Fish Biol. 45, 1027–1039. https://doi.org/10.1111/j.1095-8649.1994.tb01070.x.

Armstrong, J.D., Kemp, P.S., Kennedy, G.J.A., Ladle, M., Milner, N.J., 2003. Habitat requirements of Atlantic salmon and brown trout in rivers and streams. Fish. Res. 62, 143–170. https://doi.org/10.1016/S0165-7836(02)00160-1.

Arthington, A.H., Dulvy, N.K., Gladstone, W., Winfield, I.J., 2016. Fish conservation in freshwater and marine realms: status, threats and management. Aquat. Conserv. Mar. Freshwat. Ecosyst. 26, 838–857. https://doi.org/10.1002/aqc.2712.

Beall, E., Dumas, J., Claireaux, D., Barriere, L., Marty, C., 1994. Dispersal patterns and survival of Atlantic salmon (*Salmo salar* L.) juveniles in a nursery stream. ICES J. Mar. Sci. 51 (1), 1–9. https://doi.org/10.1006/jmsc.1994.1001.

Beland, K.F., Trial, J.G., Kocik, J.F., 2004. Use of riffle and run habitats with aquatic vegetation by juvenile Atlantic salmon. N. Am. J. Fish Manag. 24, 525–533. https://doi.org/10.1577/M02-196.1.

Belder, D.J., Pierson, J.C., Ikin, K., Lindenmayer, D.B., 2018. Beyond pattern to process: current themes and future directions for the conservation of woodland birds through restoration plantings. Wildl. Res. 45 (6), 473–489. https://doi.org/10.1071/WR17156.

Belder, D.J., Pierson, J.C., Rudder, A.C., Lindenmayer, D.B., 2021. Ongoing declines of woodland birds: are restoration plantings making a difference? Ecol. Appl. 31 (3). https://doi.org/10.1002/eap.2268.

Beltran, R.S., Kirkham, A.L., Breed, G.A., Testa, J.W., Burns, J.M., 2019. Reproductive success delays moult phenology in a polar mammal. Sci. Rep. 9, 5221. https://doi.org/10.1038/s41598-019-41635-x.

Blanchet, S., Dodson, J.J., Brosse, S., 2006. Influence of habitat structure and fish density on Atlantic salmon *Salmo salar* L. territorial behaviour. J. Fish Biol. 68, 951–957. https://doi.org/10.1111/j.0022-1112.2006.00970.x.

Bond, N.R., Lake, P.S., 2003. Local habitat restoration in streams: constraints on the effectiveness of restoration for stream biota. Ecol. Manag. Restor. 4, 193–198. https://doi.org/10.1046/j.1442-8903.2003.00156.x.

Brakensiek, K.E., Hankin, D.G., 2007. Estimating overwinter survival of juvenile coho salmon in a northern California stream: accounting for effects of passive integrated transponder tagging mortality and size-dependent survival. Trans. Am. Fish. Soc. 136, 1423–1437. https://doi.org/10.1577/T06-211.1.

Brook, B.W., Bradshaw, C.J.A., 2006. Strength of evidence for density dependence in abundance time series of 1198 species. Ecology 87, 1445–1451. https://doi.org/10.1890/0012-9658(2006)87[1445:SOEFDD]2.0.CO;2.

Bürkner, P., Gabry, J., Kay, M., Vehtari, A., 2023. Posterior: tools for working with posterior distributions. R package version 1.5.0. https://mc-stan.org/posterior/.

Burnett, N.J., Hinch, S.G., Bett, N.N., Braun, D.C., Casselman, M.T., Cooke, S.J., Gelchu, A., Lingard, S., Middleton, C.T., Minke-Martin, V., White, C.F.H., 2017. Reducing carryover effects on the migration and spawning success of sockeye salmon through a management experiment of dam flow. River Res. Appl. 33, 3–15. https://doi.org/10.1002/rra.3051.

Chelgren, N.D., Rosenberg, D.K., Heppell, S.S., Gitelman, A.I., 2006. Carryover aquatic effects on survival of metamorphic frogs during pond emigration. Ecol. Appl. 16, 250–261. https://doi.org/10.1890/04-0329.

Courchamp, F., Berec, L., Gascoigne, J., 2008. Allee Effects in Ecology and Conservation. Oxford University Press.

Cowley, P., 2022. River Frome SSSI Condition Assessment. Prepared by AECOM Limited for Natural England.

Crisp, D.T., 1995. Dispersal and growth rate of 0-group salmon (*Salmo salar* L.) from point-stocking together with some information from scatter stocking. Ecol. Freshw. Fish 3, 176–202. https://doi.org/10.1111/j.1600-0633.1995.tb00021.x.

Crozier, L.G., Siegel, J.E., 2023. A comprehensive review of the impacts of climate change on salmon: strengths and weaknesses of the literature by life stage. Fishes 8, 319. https://doi.org/10.3390/fishes8060319.

Darwall, W.R.T., 2023. *Salmo salar*. The IUCN Red List of Threatened Species 2023: e. T19855A67373433. https://doi.org/10.2305/IUCN.UK.2023-1.RLTS.T19855A67373433.en. Accessed on 17 August 2025.

Dingeldein, A.L., White, J.W., 2016. Larval traits carry over to affect post-settlement behaviour in a common coral reef fish. J. Anim. Ecol. 85, 903–914. https://doi.org/10.1111/1365-2656.12506.

Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J.R.G., Gruber, B., Lafourcade, B., Leitão, P.J., Münkemüller, T., McClean, C., Osborne, P.E., Reineking, B., Schröder, B., Skidmore, A.K., Zurell, D., Lautenbach, S., 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography 36, 27–46. https://doi.org/10.1111/j.1600-0587.2012.07348.x.

Dudgeon, D., Arthington, A.H., Gessner, M.O., Kawabata, Z.-I., Knowler, D.J., Lévêque, C., Naiman, R.J., Prieur-Richard, A.-H., Soto, D., Stiassny, M.L.J., Sullivan, C.A., 2006. Freshwater biodiversity: importance, threats, status and conservation challenges. Biol. Rev. 81, 163–182. https://doi.org/10.1017/S1464793105006950.

Gabry, J., Mahr, T., 2024. bayesplot: plotting for Bayesian models. R package version 1.11.1. https://mc-stan.org/bayesplot/.

Geist, J., Hawkins, S.J., 2016. Habitat recovery and restoration in aquatic ecosystems: current progress and future challenges. Aquat. Conserv. Mar. Freshw. Ecosyst. 26 (5), 942–962. https://doi.org/10.1002/aqc.2702.

Gillson, J.P., Basic, T., Davison, P.I., Riley, W.D., Talks, L., Walker, A.M., Russell, I.C., 2022. A review of marine stressors impacting Atlantic salmon *Salmo salar*, with an assessment of the major threats to English stocks. Rev. Fish Biol. Fish. 32, 879–919. https://doi.org/10.1007/s11160-022-09714-x.

Gimenez, O., Anker-Nilssen, T., Grosbois, V., 2012. Exploring causal pathways in demographic parameter variation: path analysis of mark-recapture data. Methods Ecol. Evol. 3, 427–432. https://doi.org/10.1111/j.2041-210X.2011.00150.x.

Glover, R.S., Fryer, R.J., Soulsby, C., Bacon, P.J., Malcolm, I.A., 2018. Incorporating estimates of capture probability and river network covariance in novel habitat – abundance models: Assessing the effects of conservation stocking on catchment-scale production of juvenile Atlantic salmon (*Salmo salar*) from a long-term electrofishing dataset. Ecol. Indic. 93, 302–315. https://doi.org/10.1016/j.ecolind.2018.05.013.

Gosselin, J.L., Buhle, E.R., van Holmes, C., Beer, W.N., Iltis, S., Anderson, J.J., 2021. Role of carryover effects in conservation of wild Pacific salmon migrating regulated rivers. Ecosphere 12, e03618. https://doi.org/10.1002/ecs2.3618.

Grabowski, R.C., Gurnell, A.M., 2016. Diagnosing problems of fine sediment delivery and transfer in a lowland catchment. Aquat. Sci. 78, 95–106. https://doi.org/10.1007/s00027-015-0426-3.

Gregory, S.D., Nevoux, M., Riley, W.D., Beaumont, W.R.C., Jeannot, N., Lauridsen, R.B., Marchand, F., Scott, L.J., Roussel, J.-M., 2017. Patterns on a parr: drivers of long-term salmon parr length in U.K. and French rivers depend on geographical scale. Freshw. Biol. 62, 1117–1129. https://doi.org/10.1111/fwb.12929.

Gregory, S.D., Ibbotson, A.T., Riley, W.D., Nevoux, M., Lauridsen, R.B., Russell, I.C., Britton, J.R., Gillingham, P.K., Simmons, O.M., Rivot, E., 2019. Atlantic salmon

return rate increases with smolt length. ICES J. Mar. Sci. 76, 1702–1712. https://doi.org/10.1093/icesjms/fsz066.
Grossman, G.D., Simon, T.N., 2020. Density-dependent effects on salmonid populations: a review. Ecol. Freshw. Fish 29, 400–418. https://doi.org/10.1111/eff.12523.
Hall, L.S., Krausman, P.R., Morrison, M.L., 1997. The habitat concept and a plea for standard terminology. Wildl. Soc. Bull. 25, 173–182.
Hansen, L.P., Quinn, T.P., 1998. The marine phase of the Atlantic salmon (*Salmo salar*) life cycle, with comparisons to Pacific salmon. Can. J. Fish. Aquat. Sci. 55, 104–118. https://doi.org/10.1139/d98-010.
Harrison, X.A., Blount, J.D., Ingre, R., Norris, D.R., Bearhop, S., 2011. Carry-over effects as drivers of fitness differences in animals. J. Anim. Ecol. 80, 4–18. https://doi.org/10.1111/j.1365-2656.2010.01740.x.
Healey, M.C., Reinhardt, U., 1995. Predator avoidance in naive and experienced juvenile chinook and coho salmon. Can. J. Fish. Aquat. Sci. 52, 614–622. https://doi.org/10.1139/f95-061.
Heggenes, J., Baglinière, J., Cunjak, R., 1999. Spatial niche variability for young Atlantic salmon (*Salmo salar*) and brown trout (*S. trutta*) in heterogeneous streams. Ecol. Freshw. Fish 8, 1–21. https://doi.org/10.1111/j.1600-0633.1999.tb00048.x.
Hogue, A.S., Breon, K., 2022. The greatest threats to species. Conserv. Sci. Pract. e12670. https://doi.org/10.1111/csp2.12670.
Ibbotson, A.T., Riley, W.D., Beaumont, W.R.C., Cook, A.C., Ives, M.J., Pinder, A.C., Scott, L.J., 2013. The source of autumn and spring downstream migrating juvenile Atlantic salmon in a small lowland river. Ecol. Freshw. Fish 22, 73–81. https://doi.org/10.1111/eff.12003.
ICES, 2024. Working group on North Atlantic Salmon (WGNAS). ICES Sci. Rep. 6 (36). https://doi.org/10.17895/ices.pub.25730247, 415 pp.
Klemetsen, A., Amundsen, P.-A., Dempson, J.B., Jonsson, B., Jonsson, N., O'Connell, M. F., Mortensen, E., 2003. Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L. and Arctic charr *Salvelinus alpinus* (L.): a review of aspects of their life histories. Ecol. Freshw. Fish 12, 1–59. https://doi.org/10.1034/j.1600-0633.2003.00010.x.
Layton-Matthews, K., Erikstad, K.E., Sandvik, H., Ballesteros, M., Hodges, K., Mesquita, M.D.S., Reiertsen, T.K., Yoccoz, N.G., Bustnes, J.O., 2024. Path analysis reveals combined winter climate and pollution effects on the survival of a marine top predator. J. Anim. Ecol. 93, 1351–1364. https://doi.org/10.1111/1365-2656.14159.
Lennox, R.J., Alexandre, C.M., Almeida, P.R., Bailey, K.M., Barlaup, B.T., Boe, K., Breukelaar, A., Erkinaro, J., Forseth, T., Gabrielsen, S.-E., Halfyard, E., Hanssen, E. M., Karlsson, S., Koch, S., Koed, A., Langaker, R.M., Lo, H., Lucas, M.C., Mahlum, S., Vollset, K.W., 2021. The quest for successful Atlantic salmon restoration: perspectives, priorities, and maxims. ICES J. Mar. Sci. 78 (10), 3479–3497. https://doi.org/10.1093/icesjms/fsab201.
Marsh, J.E., Lauridsen, R.B., Gregory, S.D., Beaumont, W.R.C., Scott, L.J., Kratina, P., Jones, J.I., 2020. Above parr: Lowland river habitat characteristics associated with higher juvenile Atlantic salmon (*Salmo salar*) and brown trout (*S. trutta*) densities. Ecol. Freshw. Fish 29, 542–556. https://doi.org/10.1111/eff.12529.
Marsh, J.E., Lauridsen, R.B., Gregory, S.D., Kratina, P., Scott, L.J., Cooling, D., Jones, J.I., 2021. High summer macrophyte cover increases abundance, growth and feeding of juvenile Atlantic salmon. Ecol. Appl. 32, e2492. https://doi.org/10.1002/eap.2492.
Marsh, J.E., Jones, J.I., Lauridsen, R.B., Grace, J.B., Kratina, P., 2022. Direct and indirect influences of macrophyte cover on abundance and growth of juvenile Atlantic salmon. Freshw. Biol. 67, 1861–1872. https://doi.org/10.1111/fwb.13979.
Marsh, J.E., Gillson, J.P., Riley, W.D., Elliott, S.A.M., Gregory, S.D., 2026. Data from: Understanding immediate and carry-over effects to prioritise habitat protection and restoration: a case study of threatened Atlantic salmon [Data set]. Biol. Conserv. https://doi.org/10.5281/zenodo.19205914. Zenodo.
Noe, E.E., Innes, J., Barnes, A.D., Joshi, C., Clarkson, B.D., 2022. Habitat provision is a major driver of native bird communities in restored urban forests. J. Anim. Ecol. 91 (7), 1444–1457. https://doi.org/10.1111/1365-2656.13700.
Norris, D.R., Taylor, C.M., 2006. Predicting the consequences of carry-over effects for migratory populations. Biol. Lett. 2, 138–151. https://doi.org/10.1098/rsbl.2005.0397.
Palmer, M.A., Bernhardt, E.S., Allan, J.D., Lake, P.S., Alexander, G., Brooks, S., Carr, J., Clayton, S., Dahm, C.N., Follstad Shah, J., Galat, D.L., Loss, S.G., Goodwin, P., Hart, D.D., Hassett, B., Jenkinson, R., Kondolf, G.M., Lave, R., Meyer, J.L., O'donnell, T.K., Pagano, L., Sudduth, E., 2005. Standards for ecologically successful river restoration. J. Appl. Ecol. 42, 208–217. https://doi.org/10.1111/j.1365-2664.2005.01004.x.
Parent, E., Rivot, E., 2013. Introduction to Hierarchical Bayesian Modeling for ecological data. CRC Press, Boca Raton.
Parry, E.S., Gregory, S.D., Lauridsen, R.B., Griffiths, S.W., 2018. The effects of flow on Atlantic salmon (*Salmo salar*) redd distribution in a UK chalk stream between 1980 and 2015. Ecol. Freshw. Fish 27, 128–137. https://doi.org/10.1111/eff.12330.
Pebesma, E., 2018. Simple features for R: standardized support for spatial vector data. R J. 10, 439–446. https://doi.org/10.32614/RJ-2018-009.
Plummer, M., 2003. JAGS: a program for analysis of Bayesian graphical models using Gibbs sampling. In: Proceedings of the 3rd International Workshop on Distributed Statistical Computing (DSC 2003), Vienna, 20–22 March 2003, pp. 1–10.
Plummer, M., 2023. rjags: Bayesian graphical models using MCMC. R package version 4-15. https://CRAN.R-project.org/package=rjags.
Powers, R.P., Jetz, W., 2019. Global habitat loss and extinction risk of terrestrial vertebrates under future land-use-change scenarios. Nat. Clim. Chang. 9, 323–329. https://doi.org/10.1038/s41558-019-0406-z.
Pretty, J.L., Harrison, S.S.C., Shepherd, D.J., Smith, C., Hildrew, A.G., Hey, R.D., 2003. River rehabilitation and fish populations: assessing the benefit of instream structures. J. Appl. Ecol. 40, 251–265. https://doi.org/10.1046/j.1365-2664.2003.00808.x.
Puffer, M., Berg, O.K., Huusko, A., Vehanen, T., Einum, S., 2015. Effects of intra- and interspecific competition and hydropeaking on growth of juvenile Atlantic salmon (*Salmo salar*). Ecol. Freshw. Fish 26, 99–107. https://doi.org/10.1111/eff.12258.
Quinn, T.P., Pederson, N.P., 1996. The influence of habitat complexity and fish size on over-winter survival and growth of individually marked juvenile coho salmon (*Oncorhynchus kisutch*) in Big Beef Creek, Washington. Can. J. Fish. Aquat. Sci. 53, 1555–1564. https://doi.org/10.1139/f96-09.
R Core Team, 2025. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.
Reinhardt, U.G., Healey, M.C., 1997. Size-dependent foraging behaviour and use of cover in juvenile coho salmon under predation risk. Can. J. Zool. 75, 1642–1651. https://doi.org/10.1139/z97-79.
Richard, A., O'Rourke, J., Caudron, A., Cattanéo, F., 2013. Effects of passive integrated transponder tagging methods on survival, tag retention and growth of age-0 brown trout. Fish. Res. 145 (37–42), 3. https://doi.org/10.1016/j.fishres.2013.03.001.
Riley, W.D., Pawson, P.G., Quayle, V., Ives, M.J., 2009. The effects of stream canopy management on macroinvertebrate communities and juvenile salmonid production in a chalk stream. Fish. Manag. Ecol. 16, 100–111. https://doi.org/10.1111/j.1365-2400.2008.00649.x.
Riley, W.D., Ibbotson, A.T., Maxwell, D.L., Davison, P.I., Beaumont, W.R.C., Ives, M.J., 2014. Development of schooling behaviour during the downstream migration of Atlantic salmon *Salmo salar* smolts in a chalk stream. J. Fish Biol. 85, 1042–1059. https://doi.org/10.1111/jfb.12457.
Riley, W.D., Ibbotson, A.T., Gregory, S.D., Russell, I.C., Lauridsen, R.B., Beaumont, W.R. C., Cook, A.C., Maxwell, D.L., 2018. Under what circumstances does the capture and tagging of wild Atlantic salmon *Salmo salar* smolts affect probability of return as adults? J. Fish Biol. 93, 477–489. https://doi.org/10.1111/jfb.13655.
Rogosch, J.S., Boehm, H.I.A., Tingley, R.W., Wright, K.D., Webb, E.B., Paukert, C.P., 2024. Evaluating effectiveness of restoration to address current stressors to riverine fish. Freshw. Biol. 69 (5), 607–622. https://doi.org/10.1111/fwb.14232.
Sayer, C., 2024. *Salmo salar* (Europe Assessment). The IUCN Red List of Threatened Species 2024: e.T19855A212864916. https://doi.org/10.2305/IUCN.UK.2024-2.RLTS.T19855A212864916.en. Accessed on 04 September 2025.
Suttle, K.B., Power, M.E., Levine, J.M., McNeely, C., 2004. How fine sediment in riverbeds impairs growth and survival of juvenile salmonids. Ecol. Appl. 14, 969–974. https://doi.org/10.1890/03-5190.
Teichert, M.A.K., Einum, S., Finstad, A.G., Ugedal, O., Forseth, T., 2013. Ontogenetic timing of density dependence: location-specific patterns reflect distribution of a limiting resource. Popul. Ecol. 55, 575–583. https://doi.org/10.1007/s10144-013-0387-0.
Thorstad, E.B., Bliss, D., Breau, C., Damon-Randall, K., Sundt-Hansen, L.E., Hatfield, E. M., Horsburgh, G., Hansen, H., Maoiléidigh, N.Ó., Sheehan, T., Sutton, S.G., 2021. Atlantic salmon in a rapidly changing environment—facing the challenges of reduced marine survival and climate change. Aquat. Conserv. Mar. Freshwat. Ecosyst. 31 (9), 2654–2665. https://doi.org/10.1002/aqc.3624.
Tyers, M., 2024. riverdist: river network distance computation and applications. R package version 0.16.3. https://CRAN.R-project.org/package=riverdist.
van Zyll de Jong, M., Cowx, I.G., 2016. Long-term response of salmonid populations to habitat restoration in a boreal forest stream. Ecol. Eng. 91, 148–157. https://doi.org/10.1016/j.ecoleng.2016.02.029.
Vehtari, A., Gelman, A., Simpson, D., Carpenter, B., Bürkner, P., 2021. Rank-normalization, folding, and localization: an improved Rhat for assessing convergence of MCMC (with discussion). Bayesian Anal. 16, 667–718. https://doi.org/10.1214/20-BA1221.
Vollset, K.W., Lennox, R.J., Thorstad, E.B., Auer, A., Bär, K., Larsen, M.H., Mahlum, S., Näslund, J., Stryhn, H., Dohoo, I., 2020. Systematic review and meta-analysis of PIT tagging effects on mortality and growth of juvenile salmonids. Rev. Fish Biol. Fish. 30, 553–568. https://doi.org/10.1007/s11160-020-09611-1.
Wentworth, C.K., 1922. A scale of grade and class terms for clastic sediments. J. Geol. 30, 337–424. https://doi.org/10.1086/622910.
Zabel, R.W., Achord, S., 2004. Relating size of juveniles to survival within and among populations of chinook salmon. Ecology 85, 795–806. https://doi.org/10.1890/02-0719.