

RESEARCH ARTICLE

Estimating the effects of smolt size and migration timing on salmon marine survival using a multivariate mixed-effect model

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Handling Editor: Paulo S. Pompeu**Abstract**

1. When the conditions encountered by a migratory species are highly variable, the timing of migration and migrant condition are critical to survival. Spring/summer-run Chinook salmon in the Snake River of the Northwestern United States are listed as threatened under the US Endangered Species Act because of decades of poor adult returns; juvenile smolt-to-adult survival is often 0.5% or less. Juveniles pass through eight dams en route to the ocean, and despite changes to the hydropower system, there has been little recent improvement in survival. We analysed the effect of migration date, fish length and their interaction on the survival to adulthood of 409,747 wild juvenile Chinook salmon as they migrated through a large, dynamic riverine ecosystem and through the ocean, measured over 20 years.
2. Parametric 2D smoothers are often used to quantify unexplained heterogeneity across space; however, these same statistical models can be applied to 2D datasets to uncover patterns of covariance of two biological processes important to management actions. We employ Gaussian Markov random fields (GMRF) and a 2D smoother to estimates of fish survival to identify the nature of variation in survival with respect to length and date.
3. We found significant effects of fish length, migration date and the date-by-length interaction on resulting riverine and marine survival. Unlike the gradual shifts in survival in relation to length and timing that marginal estimates demonstrate, we show that within year, changes in survival with length and timing are often more abrupt than previously thought.
4. *Synthesis and applications:* Inter-annually, we identified distinct combinations of fish length and migration timing leading to elevated smolt-to-adult survival. Often these 'hotspots' are compressed into fish sizes greater than 100mm and passage timings of only a week or two, demonstrating that even modest shifts in body size and migration timing can have a significant effect on survival. Further research can concentrate on these distinct annual periods to identify sources of mortality that have previously been elusive.

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KEYWORDS

carryover effects, Gaussian Markov random fields, migration timing, Pacific salmon, phenology, size dependent survival, survival

1 | INTRODUCTION

Despite the energetic costs of moving (Dodson, 1997), migration has selective advantages across taxa (Dingle, 2014) by reducing competition, avoiding predators and disease (Altizer et al., 2011), and exploiting seasonally and spatially variable growth opportunities (Newton, 2006). Ultimately, migration is thought to arise from a trade-off in survival and growth opportunities between alternate habitats (Gross et al., 1988). For individuals, migration is regulated by a combination of environmental cues and internal mechanisms (Fudickar et al., 2021), and our ability to model these effects is critical to understanding their ecology, which can lead to more effective management.

Pacific salmon (*Oncorhynchus* spp.) are semelparous (only reproduce once) fishes, whose anadromy leads to long migrations between their natal freshwater systems and marine systems where the majority of their growth occurs (Quinn, 2018). The cultural and economic value of these species often collides with the stresses from hydropower operations (Williams et al., 2005), climate change (Crozier et al., 2021) and predation (Hostetter et al., 2023) associated with the freshwater environments they rear and migrate through. Some populations of salmon may initiate their migration from rearing streams thousand or more kilometres from the marine environment. In preparation for migration they undergo smolting, a series of energetically expensive physiological changes (e.g. coloration, seawater tolerance and body shape) requiring weeks or months of development prior to and during the migration. Therefore, the body condition needed to smolt at the appropriate time is determined by conditions experienced throughout freshwater rearing (Metcalf & Thorpe, 1992), with the initiation of downstream movement related to seasonal cues (i.e. photoperiod and temperature) that will allow fish to arrive at sea when conditions are optimal for growth and survival (Ibbotson et al., 2006). Because marine survival is typically low (e.g. <1%–5%), strong evolutionary pressure exists to migrate at an optimal size and timing such that the timing of smolts entering the ocean may determine the success or failure of a cohort (Beamish & Mahnken, 2001; Satterthwaite et al., 2014). Despite these pressures, considerable variation exists within populations in the timing and body size at migration (Scheuerell et al., 2009), possibly due to the interannual variation in conditions experienced during the freshwater incubation and rearing period.

In the interior Columbia River basin in the Pacific Northwest of the United States, the majority of Snake River spring/summer-run Chinook salmon (*O. tshawytscha*) leave tributary rearing habitats in spring, entering mainstem rivers to migrate to sea for 1–4 years. Juveniles emigrating from the Snake River, the largest tributary of the Columbia River, traverse eight mainstem dams to reach marine waters (Figure 1). Following its listing as a threatened species under the federal Endangered Species Act in 1992, agencies began costly

restoration and mitigation efforts to improve tributary spawning and rearing habitats as well as survival through the hydropower system. In addition, researchers began tagging juveniles with passive integrated transponder (PIT) tags at traps and dams. These uniquely identified tags are permanently implanted into a fish's peritoneal cavity, and individual movements are recorded when fish pass near monitoring transceivers primarily located in dams (Axel et al., 2005). Previous work demonstrated an increase in juvenile-to-adult survival with increasing juvenile size in Snake River spring–summer Chinook (Gosselin et al., 2018; Zabel & Williams, 2002). However, few studies have been able to adequately disentangle the effects of downstream migration timing and smolt size on survival to the adult life stage at the fine timescales that are meaningful for managers and further research. While it is common to include more than one covariate (e.g. timing of migration, body size and physical environment) as a predictor for survival; to our knowledge, previous studies of salmon survival have not considered how the covariance between variables may affect survival.

To understand how survival is affected by behaviours like migration, we typically contend with a mismatch between the scale at which processes occur and our ability to sample them. For example, we may observe individuals at specific points in space and time, but from a conservation perspective, we need to make inferences about population survival over a geographic range where data may be sparse. Mixed-effects models offer a generalized framework for modelling these unobservable/latent processes that may bias our estimates of derived variables that are important to managers (Kéry & Schaub, 2011; Thorson & Minto, 2015). Additionally, mixed-effects models examine the correlation between latent processes (e.g. temporal, spatial or both) that, if ignored, violate the assumptions related to statistical independence of the model's residuals (Hui et al., 2015). Computational advances in optimizing the parameters in the joint likelihood for mixed-effect models (Kristensen et al., 2016; Lindgren & Rue, 2015) have led to improvements in unbiased estimates of abundance (Thorson et al., 2015), growth (Webber & Thorson, 2016) and survival (Stock et al., 2021). When modelling survival as a function of migration, mixed-effects models have been used to quantify effects such as phenology, morphology, location and environmental conditions across a broad range of taxa (Balbontín et al., 2009; Knight et al., 2019; Melnychuk & Welch, 2018). However, while most of the studies we reviewed may include one or more latent processes for migration in their survival analysis, none of them included estimates of the covariance between latent processes.

The use of stochastic partial differential equations (SPDEs) as approximations to Gaussian Markov random fields (GMRF) has emerged as an efficient methodology for examining the correlation between continuous latent variables associated with ecological processes (Rue & Held, 2005). A common application has been

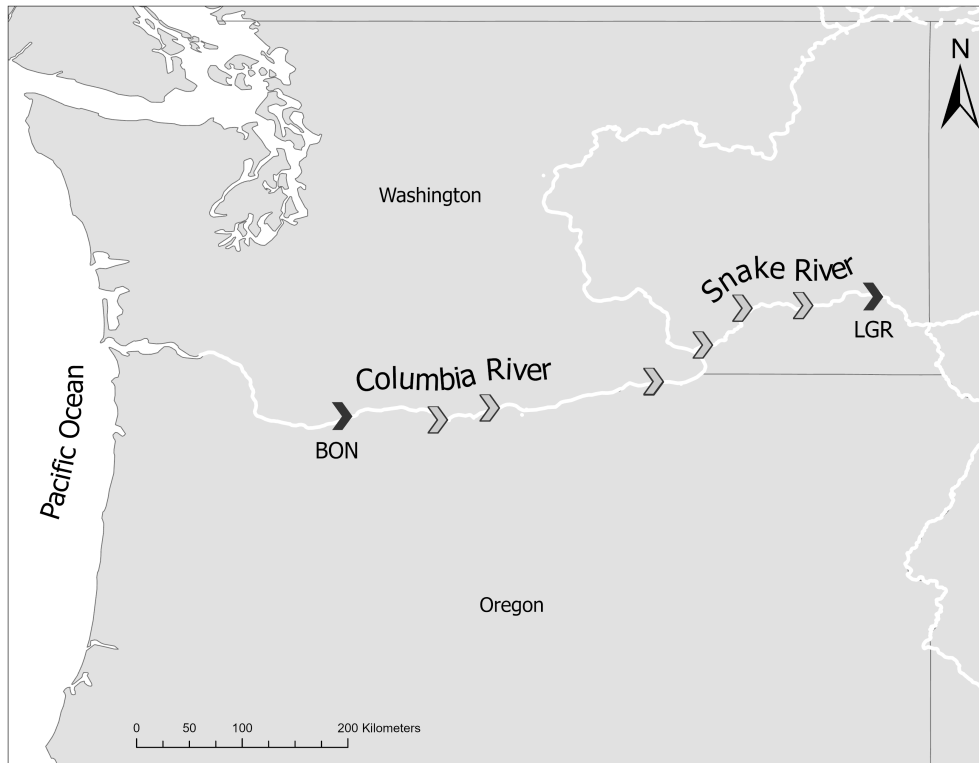


FIGURE 1 Map of the Pacific Northwest study region. Chevrons indicate mainstem dams where monitoring of passive integrated transponder tags occurs for adults moving through fish ladders. The primary study dams Lower Granite Dam (LGR) and Bonneville (BON) are shown in black. A small number of fish were not detected as adults at Bonneville dam, but were detected as adults at other mainstem dams (grey) and were included as having survived to Bonneville.

the description of the stochastic variation in species distributions across space (i.e. 2D spatial models; Lindgren & Rue, 2015), or space and time (i.e. 3D spatiotemporal models; Cressie & Wikle, 2011). Within the fisheries research community, the SPDE approximation of GMRF is most commonly used to examine the spatiotemporal distribution of species in response to changing habitat (Ward, Jannot, et al., 2015). However, a recent application of 2D spatial smoothers and GMRF models has been to the interaction between temporal latent processes associated with survival (e.g. age and year effects on yellow flounder mortality; Stock et al., 2021, or month and year effects on Chinook salmon mortality; Chasco et al., 2021). In these applications, estimated survival was less biased compared with models that treated the covariates as independent latent processes. Our objective for this paper was to extend GMRF models of mortality to include length and arrival timing as correlated latent processes that may affect annual marine survival of Chinook salmon.

2 | MATERIALS AND METHODS

2.1 | Fish data

Estimating the effect of length and timing on smolt-to-adult survival of wild spring/summer-run Snake River Chinook salmon necessitated evaluating fish measured and PIT tagged at or near

Lower Granite Dam (LGR, Figure 1) in the Snake River. Tagged fish were monitored for survival after migrating through the remaining 460 km of freshwater habitats, 234 km of estuary and 2–4 years of marine migration before returning to the Columbia River as mature adults. We included fish PIT-tagged during migration Years 1998 to 2019, which included 3215 surviving adults from 409,747 tagged out-migrating smolts. Later in each migration season, in an effort to increase downstream survival, some fish observed at LGR are placed into barges for transportation through the remaining seven downstream dams and released in the estuary. Scheduled barging of fish is episodic and governed by a very different process than the natural migration of fish passing LGR. Therefore, we chose to exclude these fish by screening our dataset with PitPro software (Westhagen & Skalski, 2009) that uses combinations PIT-tag antennas at dams to determine which fish were placed on barges. The final data included (i) detection date at Lower Granite as juveniles, (ii) fish fork length in mm (hereafter referred to as length) at tagging and (iii) detection in any one of the eight dams in the Columbia River or Snake River, which we determined as the criteria for fish to have survived the marine stage. The PIT-tag detection probability for adults at mainstem dams ranges between 0.989 and 0.998 (Crozier et al., 2016); therefore, we assume all returning adults are detected. Our model estimates random processes for the day, length and year effects, and initial analyses demonstrated improved model performance and estimation speed

if we excluded the extremes of migration timing where data are particularly sparse. We excluded fish tagged prior to March 25 and after June 8 (4.2% of the total observations). Although our study focused on naturally produced Snake River spring–summer Chinook, fall-run Chinook, which emigrate at a smaller body size, unmarked hatchery fish also migrate through LGR concurrently. To minimize inclusion of those fish, we excluded all fish less than 80 mm length (to eliminate fall-run Chinook) and greater than 125 mm length (likely hatchery-reared fish misidentified as wild fish [T. Marsh, NWFSC, personal communication]), resulting in the elimination of 1.9% of the total observations. Although our sample includes over 400,000 individuals, juvenile-to-adult survival is so low that the number of surviving adults from any year, length and day combination is small. Therefore, to further increase our sample size, we included some fish (13.1% of juveniles) that were PIT-tagged at traps in the Snake River upstream of LGR and detected, but not measured, at LGR. To ensure that their length measured at the trap was representative of length at arrival at LGR, we only included fish tagged within 21 days prior to detection at LGR, and applied a growth rate of $2 \text{ mm} \cdot \text{week}^{-1}$ (N. Beer, personal communication). Fish at all sites were tagged by the National Marine Fisheries Service and Idaho Department of Fish and Game under their own permitting and animal care authorization, and data were accessed via the PIT Tag Information System (PTAGIS, www.ptagis.org) repository. All final data and code used in these analyses are available in a permanent repository (Chasco et al., 2024).

2.2 | Statistical model

We describe the smolt-to-adult-return (SAR) for i th individual as a linear model

$$p_i = f^{-1}(\mathbf{X}_i \boldsymbol{\beta} + \omega_{b(i),l(i)} + v_{b(i),j(i)} + \zeta_{b(i),y(i)} + \lambda_{b(i),s(i)} + \epsilon_{y(i),b(i),s(i)}) \quad (1)$$

where $b(i)$ indicates whether a fish was tagged above or at LGR, $l(i)$ is the length, $j(i)$ is the migration day passing LGR, $y(i)$ is the migration year, and $s(i)$ is the 'location' for a particular length/day combination. The design matrix \mathbf{X}_i includes mean survival and a binary indication of tagging location (LGR or above LGR), and $\boldsymbol{\beta}$ is a vector of coefficients. The random effects include length ($\omega_{b(i),l(i)}$), day ($v_{b(i),j(i)}$), year ($\zeta_{b(i),y(i)}$), the 'equilibrium' interaction between length and day across all years ($\lambda_{b(i),s(i)}$), and the interaction between length and day for each year ($\epsilon_{b(i),y(i),s(i)}$) for the i th individual. A logit transformation f^{-1} ensures the expected survival (p_i) based on the linear model for the i th fish is between zero and one.

2.3 | Process models

For each random process, we investigated the independence and correlation between migration pathways using different statistical models. Using the length random effect ($\omega_{b(i)}$) for illustrative purposes, the

statistical models can be generalized to the migration day and year effects. Additionally, for clarity and compactness, we have removed the i from subscript indicating the i th fish. For models where tagging location is assumed to not affect survival, the univariate random process can be written as either a random walk ($\omega_{\cdot,j} \sim N(\omega_{\cdot,j-1}, \sigma_{\omega}^2)$, $\forall b$), AR1 ($\omega_{\cdot,j} \sim N(\phi_{\omega} \omega_{\cdot,j-1}, \sigma_{\omega}^2(1 - \phi_{\omega}^2))$, for $|\phi_{\omega}^2| < 1$ and $\forall b$) with correlation ϕ_{ω} and variance equal to $\sigma_{\omega}^2(1 - \phi_{\omega}^2)$, or i.i.d. with mean zero ($\omega_{\cdot,j} \sim N(0, \sigma_{\omega}^2)$, $\forall b$). Alternatively, including the effect of tagging location at or above LGR, the multivariate versions for the vectors of random effects are: random walk ($\boldsymbol{\omega}_i \sim \text{MVN}(\boldsymbol{\omega}_{i-1}, \boldsymbol{\Sigma}_{\omega}^2)$), AR1 ($\boldsymbol{\omega}_i \sim \text{MVN}(\phi_{\omega}^2 \boldsymbol{\omega}_{i-1}, \boldsymbol{\Sigma}_{\omega}^2(1 - \phi_{\omega}^2))$, for $|\phi_{\omega}^2| < 1$) or i.i.d. ($\boldsymbol{\omega}_i \sim \text{MVN}(\mathbf{0}, \boldsymbol{\Sigma}_{\omega}^2)$). Here, $\boldsymbol{\omega}_i$ is the vector of length two for the LGR PIT-tagged fish and the fish tagged above LGR, $\boldsymbol{\Sigma}_{\omega}^2$ is the covariance matrix with the variance parameter σ_{ω}^2 and a correlation between locations equal to ψ_{ω} . The between year correlation, ϕ_{ω}^2 , is the same as the univariate example. Statistically, the random effects for day ($v_{b,j}$) and year ($\zeta_{b,y}$) are the same as the aforementioned example, except with separate variance parameters for length (v) and year (ζ) random effects (σ_v^2 and σ_{ζ}^2 respectively), within tagging location correlation (ϕ_v and ϕ_{ζ}), and between tagging location correlation (ψ_v and ψ_{ζ}).

Previous applications of GMRF approximations using SPDE from the INLA R package (Rue et al., 2009) have addressed questions of spatial covariance between observations using the Matérn function with smoothness (ν) equal to one and parameters for range (κ) and anisotropy (h_1 and h_2), and scaled by an estimate of precision (τ) (Cressie & Wikle, 2011; Thorson et al., 2015). The variance estimate (σ) for the GMRF is a derived variable that is a function of the precision parameter τ and the range parameter κ , with $\sigma = \tau(2\kappa\sqrt{\pi})^{-1}$.

Here, we expand the use of the INLA package by applying the SPDE approximation of a GMRF to temporal deviates in a 2D field for length and migration day. We examined several models, starting with an equilibrium state for the interaction between length and day that is the same for each tagging location and year ($\lambda \sim \text{MVN}(\mathbf{0}, \tau_{\lambda} \mathbf{R}(\kappa, \mathbf{H}))$, $\forall b$), where $\mathbf{R}(\kappa, \mathbf{H})$ is the correlation matrix for the length/day GMRF field assuming a Matérn function for the decorrelation with parameters for range (κ), a linear transformation of the anisotropic differences between length and timing (Thorson et al., 2015), scaling parameter (τ_{λ}) and smoothness (ν) equal to one. Next, we treat the equilibrium deviates for each tagging location as separate but correlated processes ($\lambda \sim \text{MVN}(\mathbf{0}, \tau_{\lambda} \mathbf{R}(\kappa, \mathbf{H}) \otimes \mathbf{R}_{\lambda})$), where \mathbf{R}_{λ} is a 2×2 correlation matrix for the tagging locations with a correlation parameter ψ_{λ} , and $\mathbf{R}(\kappa, \mathbf{H}) \otimes \mathbf{R}_{\lambda}$ is the Kronecker product of the length/day matrix and the tagging location matrix. For temporal variation in the length/migration day deviates, we only considered the situations where the temporal deviates were i.i.d. with mean zero in the univariate case where the annual deviates were equal for the two tagging locations ($\epsilon_y \sim \text{MVN}(\mathbf{0}, \tau_{\epsilon} \mathbf{R}(\kappa, \mathbf{H}))$, $\forall b$), where τ_{ϵ} is a measure of precision, and the multivariate model for tagging location \mathbf{R}_{ϵ} is the correlation matrix with correlation between tagging location with correlation ψ_{ϵ} ($\epsilon_y \sim \text{MVN}(\mathbf{0}, \tau_{\epsilon} \mathbf{R}(\kappa, \mathbf{H}) \otimes \mathbf{R}_{\epsilon})$).

For the i th observation, we assumed that the likelihood of the estimated survival (p_i) given the total number of smolts (n_i) that

survived to be detected as adults 1 to 3 years later (k_i) was binomially distributed,

$$L(p_i | n_i, k_i) = \Pi_i \text{Binomial}(k_i; p_i, n_i) \quad (2)$$

2.4 | Model fitting

We used the non-linear optimization package TMB (Kristensen et al., 2016) built for R (R Core Development Team, 2015, version 3.6.0) to estimate the fixed and random effects of the model. The standard errors for the fixed effects are estimated directly from the inverse of the Hessian, while standard errors for random effects were estimated using the delta method while incorporating the variance of fixed effects (Kass & Steffey, 1989). Model convergence was determined by positive definite Hessian and a maximum gradient of 0.0001 for the fixed effects. We used the marginal Akaike's information criterion (AIC) for the fixed effects (Akaike, 1974) from the 'TMBhelper package' to compare models and select the most parsimonious fit to the data.

2.5 | Simulation testing

In addition to Kolmogorov–Smirnov tests (K–S test) for the residual normality and model classification tests based on the area under the receiver operator curve (AUC), we conducted a simulation experiment for the model with the lowest AIC. We simulated 50 datasets from the conditional likelihood. That is, the fixed and random effects were equal to their maximum likelihood estimates (MLE),

and data were generated from the observation model (Equation 2). We then examined the parameter bias between the MLE parameters for the observed data and the range of MLE parameters for the simulated data.

Efforts aimed at advancing migration timing and increasing fish size are regarded as strategies to bolster juvenile-to-adult survival rates (Scheuerell et al., 2009; Zabel & Williams, 2002). To investigate the impact of parameters influencing variability in the length/day interaction for the GMRF, τ and κ , we simulated the 22-year time series of smolt survival data, repeated 50 times. This involved setting the year, length and day random effects to their MLE values for the model with the lowest AIC. Subsequently, we determined the average survival rates for observed samples when migration timing was shifted 7 days earlier and fish length increased by 4 mm (roughly equivalent to one standard deviation for each parameter).

3 | RESULTS

After a preliminary analysis exploring the estimability of the parameters and model convergence, we tested nine different models with different combinations of random effects and statistical descriptions of the variations for tagging locations that addressed both biological and management questions related to juvenile-to-adult survival for wild Snake River spring/summer Chinook salmon. Of the models we tested, Model 1 (Table 1) had the lowest AIC—with a single parameter for the mean survival, tagging location-specific multivariate random effects for migration day and random effects for the length/migration day interactions for each year that were

TABLE 1 Top five models with the lowest Akaike's information criterion (AIC) values of the 60 model combinations we tested by varying the random effects, whether random effects were univariate or multivariate (i.e. separate but correlated migration pathways), and the correlation between random deviates (i.e. random walk, AR1 or i.i.d.). (table_AIC_comp.r).

Model input	Process	Model				
		1	2	3	4	5
Random effects	Year	Included	Included	Included	Not included	Included
	Day	Included	Included	Included	Not included	Not included
	Length	Included	Included	Included	Not included	Not included
	Length/day	Not included	Not included	Not included	Not included	Included
	Length/day/year	Included	Included	Included	Included	Not included
Temporal correlation	Year	I.I.D.	I.I.D.	I.I.D.	NA	I.I.D.
	Day	AR1	AR1	AR1	NA	NA
	Length	AR1	AR1	AR1	NA	NA
Tagging location covariance	Year	Univariate	Multivariate	Univariate	NA	Univariate
	Day	Multivariate	Multivariate	Multivariate	NA	NA
	Length	Univariate	Univariate	Multivariate	NA	NA
	Length/day	NA	NA	NA	NA	Multivariate
	Length/day/year	Multivariate	Univariate	Multivariate	Multivariate	NA
AIC		14,800.9	14,801.6	14,802.2	14,853.1	14,888.0
Δ AIC		0.0	0.7	1.3	52.2	87.1

tagging location-specific. Models 2 and 3 had $\Delta AIC \leq 2$, implying plausible alternative modelling solutions, including the same random effects for year, length, migration day and length/day interactions, but differed in terms of which of the random processes had a multivariate effect for tagging location. Diagnostics for Model 1 using the Kolmogorov–Smirnov test for normality (K–S p -value=0.09; Figure S1) suggests the estimates are similar to observed data, and the AUC curve statistic (AUC=0.76; Figure S2) produces an acceptable level of model classification. Furthermore, the distribution of parameter estimates in the bias simulation test was similar to the MLEs and standard errors for the parameters from the estimation model using the observed data (Figure S3).

To describe the correlation between the migration pathways, our analysis identified that the model with the lowest AIC incorporated multivariate processes for the day effect ($\psi_v = 0.22$) and the day/length interaction for each year ($\psi_\varepsilon = 0.60$) (Table 2). Notably, a distinct lack of correlation between the day effect for the two pathways is evident from the divergence in the marginal survival estimates. Specifically, fish tagged at LGR exhibit continuously declining survival rates over the migration season, while those utilizing the by-pass pathway experience a survival peak around May 1 (see Figure 2).

Conversely, the random effects for length and year were assumed to be univariate for both pathways. High temporal correlation was estimated for length and day ($\phi_v = 0.99$ and $\phi_\omega = 0.99$, respectively), with the year effect treated as independent and identically distributed. Notably, the standard deviation of the year effect was largest ($\sigma_y = 0.85$), followed by the standard deviation of the length effect ($\sigma_\omega \sqrt{1 - \phi_\omega^2} = 0.08$), and finally, the day effect ($\sigma_v = 0.07$; Table 2).

While all year and migration pathways show variability in the survival across length/day domain (see Figures S4 and S5 for all years), 1998, 1999, 2018 and 2019 highlight notable differences

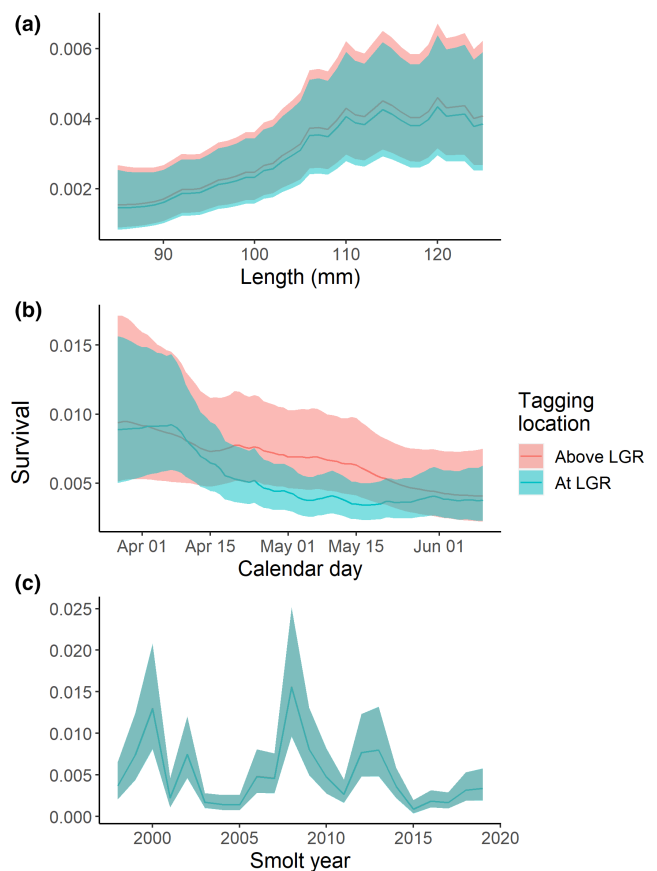


FIGURE 2 Marginal survival estimates (mean and 90% CI) for length (a), migration day (b) and year (c) for the two tagging locations. Because the random effects for length and migration day are AR1 processes with deviates not equal to zero for the means of the data, the marginal estimates are conditional on the average migration days of May 2 and May 4 for fish tagged at and above Lower Granite Dam (LGR), respectively, with an average length of 107 mm For all tagged fish.

Description	Process	Symbol	Model 1
Expected survival		μ	0.003 (0.002, 0.005)
Variance/precision	Length	σ_v^2	0.05 (0.07, 0.09)
	Day	σ_ω^2	0.11 (0.08, 0.15)
	Year	σ_ζ^2	0.07 (0.05, 0.09)
	Length/day	$\sigma_\lambda(\tau_\lambda, \kappa_\lambda)$	Not estimated
	Length/day/year	$\sigma_\varepsilon(\tau_\varepsilon, \kappa_\varepsilon)$	0.03 (0.02, 0.05)
Temporal correlation	Length	ϕ_v	Not estimated
	Day	ϕ_ω	Not estimated
	Year	ϕ_ζ	Not estimated
Multivariate correlation	Length	ψ_v	Not estimated
	Day	ψ_ω	0.22 (0.04, 0.62)
	Year	ψ_ζ	Not estimated
	Length/day	ψ_λ	Not estimated
	Length/day/year	ψ_ε	0.60 (0.10, 0.95)
Anisotropy vector		h_1	0.48 (0.20, 1.18)
		h_2	3.53 (0.62, 19.0)

TABLE 2 Maximum likelihood estimates and 95% confidence interval for Model 1 (Table 1).

in estimated survival patterns: from high, concentrated unimodal and bimodal patterns in 1998 and 1999, respectively, to lower and less concentrated survival in 2018 and 2019 (Figure 3). The standard deviation for the length/day interaction random effect (σ_ϵ) was 0.14 and the 'range' at which the decorrelation between the interaction effects decreases to 10% was ± 11.4 days along the migration day axis, and ± 229 mm along the length axis (Figure S6). Evidence of annual variability in survival across the length/day interaction can be summarized using a Moran I statistic—a measure of autocorrelation between adjacent estimates length/day combinations in the 2D field with values between -1 and 1 . We found the Moran I to be positive for all years, with the highest level of autocorrelation in 2007 and 2012, and the lowest level autocorrelation in Year 2004 and 2008 (Figure S7). All Moran I estimates were statistically significant ($p < 0.001$), indicating that the patterns were not the result of random chance. Visually, the random deviates in survival between years appear like shifting vertical bands of higher and lower random deviates highlighting more variability along the day than the length axis (Figures S8 and S9).

We examined the effect of management actions on survival through changes in the timing (± 7 days) and the size (± 4 mm) of

smolts arriving at LGR. Aggregating across all years, we found that both increasing length of the fish by 4 mm and moving the migration timing 7 days earlier would increase the survival by as much as 23% (Figure 4). Conversely, decreasing the size by 4 mm and moving the migration timing 7 days later would decrease survival by 19%. For the remaining management actions, the different combinations of length and timing resulted in changes in survival to a lesser degree. In most years, survival benefitted from moving the observed arrival distribution 7 days earlier and increasing the size by 4 mm (Figure 5), with the exception for fish tagged at LGR 1999 and 2010. In 1999 in particular, this is due to the higher than average survival between May 1 and May 15 (Figure 5), which also coincided with the peak of the smolt migration in that year.

With no alteration to the parameters τ and κ that influence the variability of the length/day interaction, 50 simulations of the 22-year time series were conducted to assess a specific management action. This action involved increasing the length by 4 mm and shifting the arrival timing 7 days earlier. The results indicated that approximately 10% of the simulations exhibited lower survival compared with scenarios without the management action, based on MLE parameter estimates (Figure 6).

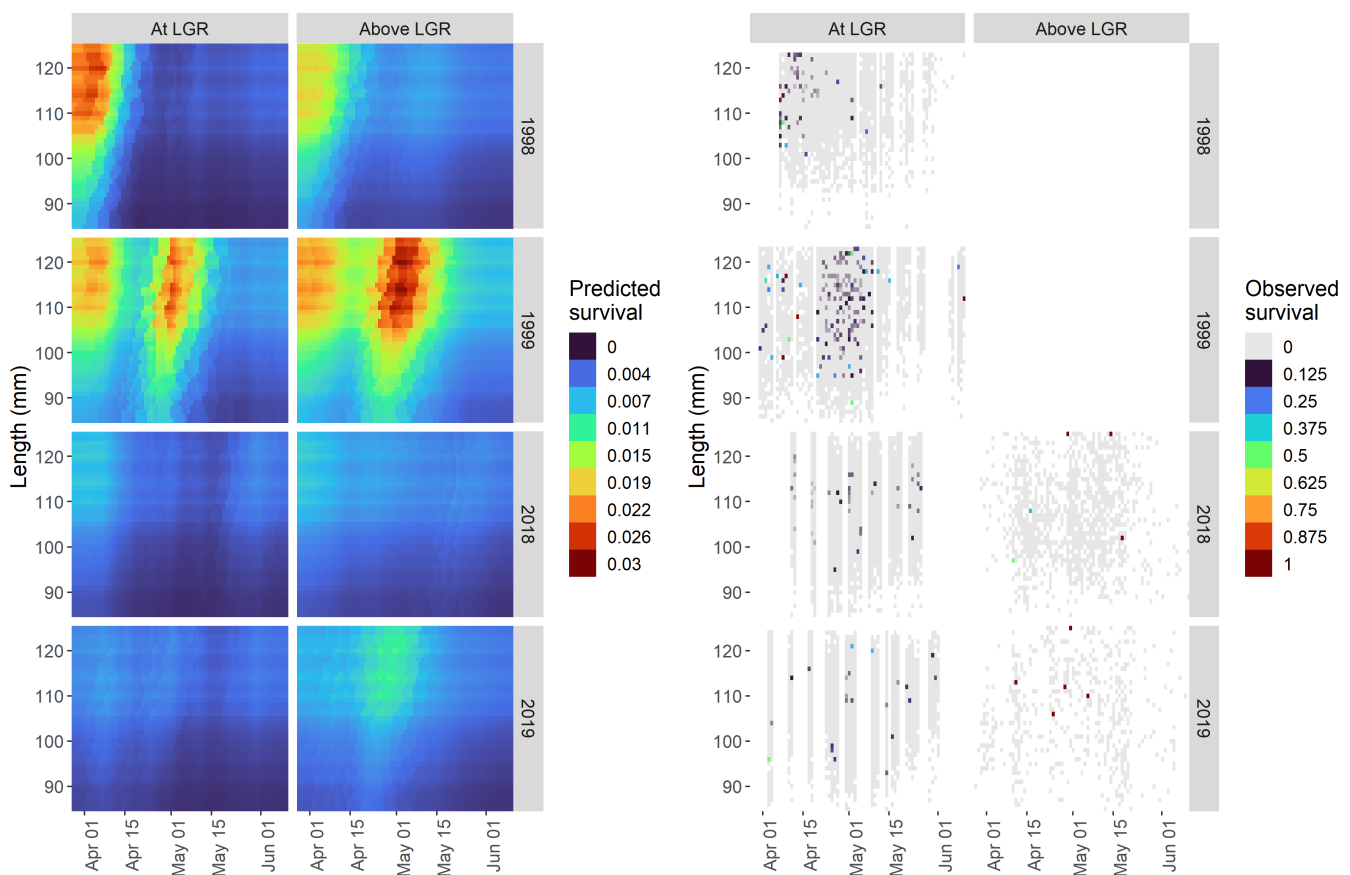


FIGURE 3 Predicted (panel a) and observed (panel b) survival of spring/summer Chinook salmon conditional on the length (y-axis) and migration date (x-axis) during smolt migration Years 1998, 1999, 2018 and 2019 for fish tagged at or above Lower Granite Dam (LGR). For panel (b), because of low sample size for individual length/day combinations, values greater 0.2 (0.19% of the total observations) were set to 0.2 to improve contrast in the colour scale, and grey space indicates length/day combinations with zero survival, and white areas represent no data observed.

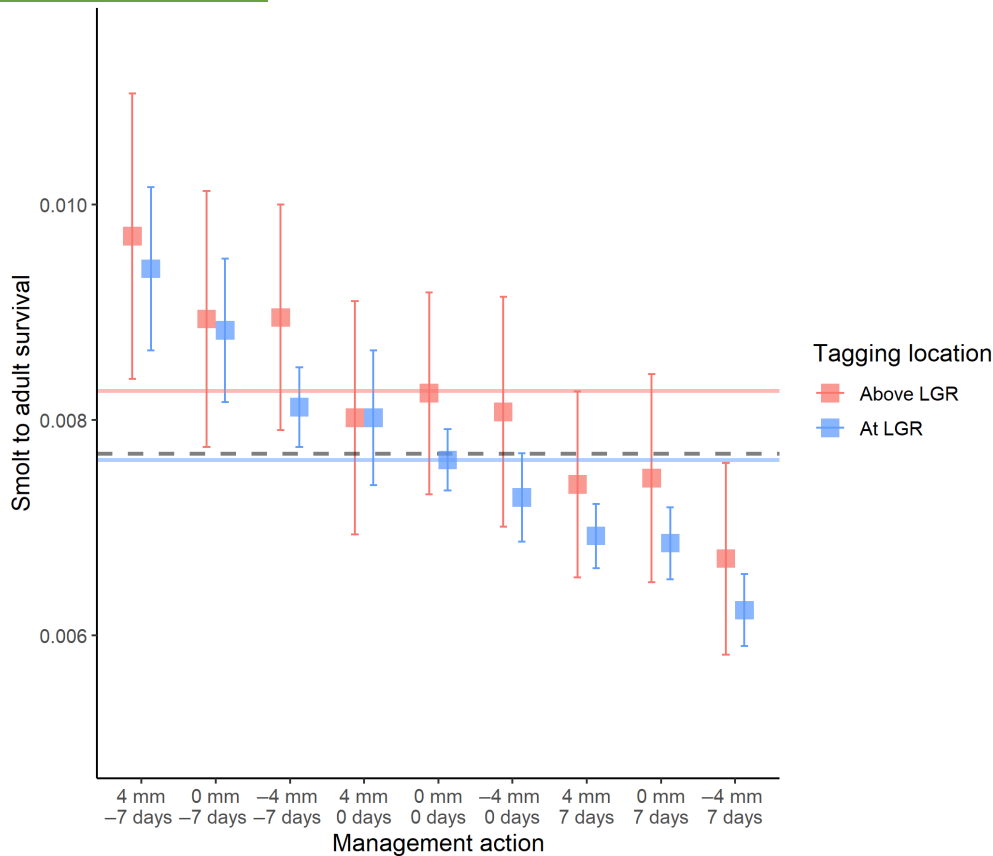


FIGURE 4 Predicted survival estimates (proportion of smolts surviving) as a function of different deviations in migration timing (+7 days later, 0 days difference and -7 days earlier) and migration size (-4 mm smaller, 0 size difference and +4 mm larger) aggregated by migration pathway and across all observations. Error bars represent the 90% confidence intervals in the estimates. Red and blue horizontal lines represent the observed aggregate survival by tagging location across all years, and the grey line represents the observed survival across all observations.

The standard deviation of the deviates for the length/day interactions is jointly controlled by τ and κ ($\sigma = (\tau 2\kappa \sqrt{\pi})^{-1}$). The range at which correlation between two locations in the 2D field decreases to 13% is determined by κ (range = $\sqrt{8}/\exp(\kappa)$). Holding the effects of range (κ) at their MLE value, we adjusted τ to increase the standard deviation of the 2D length/day interaction by 50% and 200%, and then fixed τ at its MLE value while adjusting κ to modify the range of the 2D interaction by 50% and 200%. Doubling the standard deviation or the range resulted in lower average survival rates for 23% and 29% of simulated years, respectively. Conversely, halving the standard deviation or the range only led to 0.2% and 1.4% of simulated years showing reduced survival rates, respectively (Figure 6).

4 | DISCUSSION

Our analysis uncovered complex dynamics in the relationship between survival from the juvenile to the adult stage and fish body size and migration timing. In particular, GMRF models found covariation in the length/timing 'field' that may result in biased survival estimates compared with models with independent processes for

length and time (Figure 5). Survival deviates are more sensitive to migration timing than to fish length as indicated by the vertical 'bands' in Figures S8 and S9, and the anisotropic estimates of decorrelation, a measure of the interaction effects of migration timing and size (Figure S6).

Another surprising result was that the seasonal relationship was quite variable from year to year. In some years, such as 1998 and 2014, the fish that arrived earlier experienced the highest marine survival. In other years, such as 2008 and 2011, late-arriving fish returned at higher rates. Although it was beyond the scope of this work, a fruitful question would be to ask whether any measurable factors, such as flow or water temperature, are useful in predicting this variation in the dominant seasonal pattern. Nonetheless, based on the marginal relationship (Figure 2), it appears that on average, early-arriving fish at LGR fare better than late-arriving ones.

The relationship between juvenile-to-adult survival and body size has been well established for Pacific salmonids (Ward et al., 1989; Zabel & Williams, 2002) and teleost fish in general (reviewed by Sogard, 1997). Scheuerell et al. (2009) demonstrated the benefit of arriving in the estuary earlier in the season for Snake River spring/summer Chinook and steelhead. The importance of

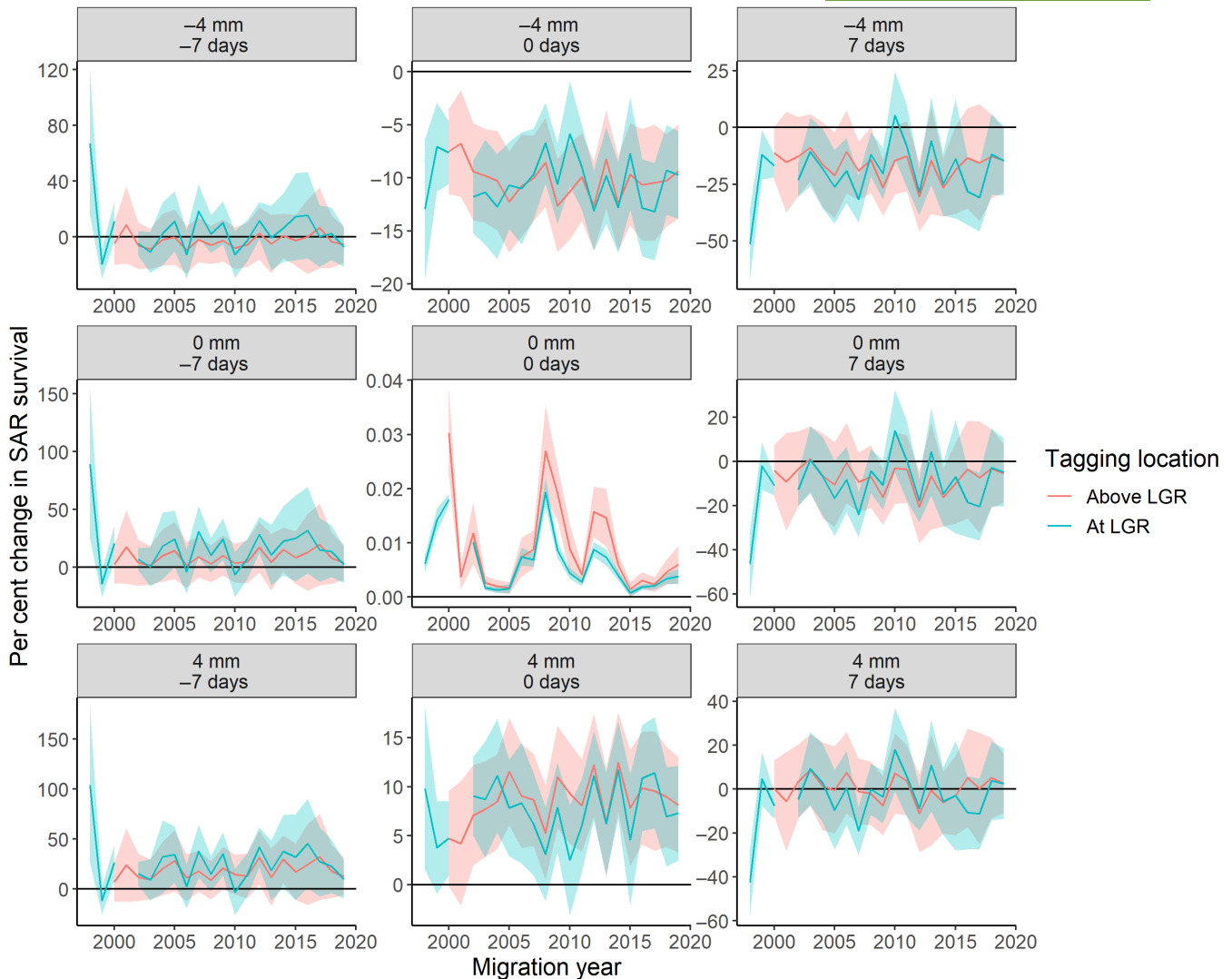


FIGURE 5 Per cent change in the annual survival for fish passive integrated transponder (PIT)-tagged at or above Lower Granite Dam (LGR) given changes in fish size (± 4 mm) and arrival timing (± 7 days) to LGR. The y-axes are different scales to highlight those years where the management action would lead to lower survival. The centre plot is the predicted smolt-to-adult-return (SAR) for fish tagged at and above LGR and meant to provide context for the relative changes in survival in the other panels.

arrival timing is consistent with the 'critical period' hypothesis formulated by Pearcy (1992), where conditions for survival are best during a time period that is conducive to fish growth and survival. Pearcy (1992) speculated that a substantial proportion of mortality occurs as salmonids enter the saltwater environment. We note that dams and reservoirs in the Snake and Columbia rivers have slowed ocean arrival timing by several weeks compared with a free-flowing river.

Because of the model's ability to 'borrow' information within and between years, we were able to make inferences about novel patterns in survival where the data were sparse and the sample sizes were low. For example, the number of juvenile Chinook salmon observed and surviving from the 2000 migration year was much higher than 2015, (Figure 2c), yet we could still detect sharp gradients in survival across the length/time domain for each year (Figure 2, column B). While size and migration timing are two

aspects of salmon that managers are most likely to be able to affect, simply mitigating for larger fish and later migrating fish carries risks of lower survival in some years (Figure 5). Rather, our research supports future studies looking to account for the heteroscedastic variation in length/day effects. Previous studies have shown that the volatility of habitat characteristics such as flow or temperature within a year are likely to explain annual differences in survival (Ward, Anderson, et al., 2015), possibly leading to the distinct intra-annual periods of low and high survival that we found in our analysis. However, the combination of physical drivers and predator phenology has been shown to spatiotemporally compress the overlap of predators and juvenile Chinook salmon and leads to shifts in survival through direct and apparent competition (Wells et al., 2017). In the Columbia River estuary, large sources of mortality on juvenile spring/summer Chinook salmon from predators such as marine mammals (Nelson et al., 2019), birds (Collis

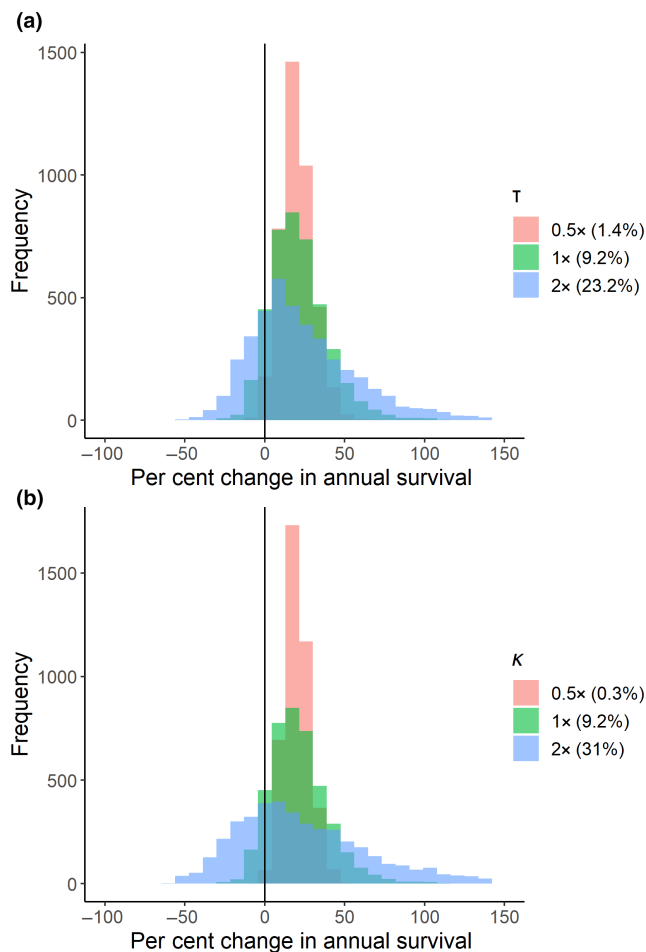


FIGURE 6 Frequency distributions of the estimated annual change in survival based on 50 simulated outcomes of a management strategy where the observed smolts migrate 7 days earlier and are four millimetres larger and given that the range ($\sqrt{8}/\exp(\kappa)$; panel a) or the variance ($(1/\tau)^2$; panel b) for the length/day interaction are: Reduced by half (0.5 \times), fixed to the maximum likelihood estimates (MLE) (1 \times), or doubled (2 \times). Values in parentheses reflect the percentage of simulated years where the management scenario results in lower survival.

et al., 2002; Roby et al., 2003) and piscivorous fishes (Emmett & Sampson, 2007) are well documented. If the survival gradients for size and timing are being driven by predation, our analysis provides a guide for examining predator phenology during certain periods as well as sources of apparent competition when predators may switch from prey sources such as American shad (*Alosa sapidissima*) to Chinook salmon (Rub et al., 2019).

The data available for this study necessitated the analysis of the combined survival of juveniles through the mainstem Snake and Columbia Rivers, the Columbia River estuary, and the 2–4 years of ocean migration prior to adult re-entry to the Columbia River. Unsurprisingly, the vast majority of the mortality among these phases is incurred in the 2–4 years individuals spend in the marine environment before returning to freshwater (Chasco et al., 2021).

A recent analysis demonstrated that survival during the ocean life stage (Crozier et al., 2021), which is contained in the survival we measured here, was by far the most influential life stage in terms of shaping population dynamics under climate change. Given that there are few actions we can take in the marine life stage, we focused on ‘carry over’ effects—that is improvements made in one life stage that can have positive effects in a later life stage.

4.1 | Management implications

Although the migration speed of naturally produced Chinook does typically increase throughout the season (Zabel et al., 1998), hydro-power operations in the Snake and Columbia Rivers have slowed the migration overall, likely delaying their ocean arrival compared with a historical free-flowing river state. Juvenile salmon are developmentally and physiologically constrained in their ability to shift to earlier migration timing, which squeezes fish between the pressure to grow large enough to migrate, and to migrate early enough to take advantage of favourable marine conditions. One potential mitigation action currently being tested is the use of increased dam spillway flow, which encourages fish to migrate through spillway routes rather than the powerhouse, likely decreasing direct mortality. The additional benefit of increased spill, however, may be a more rapid transit through the river and earlier arrival in marine habitats, potentially leading to an increase in survival.

Zabel and Achord (2004) previously demonstrated a consistent negative relationship within populations of Snake River spring/summer Chinook salmon between juvenile fish length in tributary streams and arrival date at LGR the following spring. Coupled with our analysis, increased early life growth may result in earlier migration and higher marine survival in many years. There are several management and restoration tools available to increase growth rates of juveniles in freshwater. Artificial nutrient enhancement could increase growth rates of Snake River spring/summer Chinook salmon because they rear in relatively nutrient-poor, high elevation streams (Chittaro et al., 2014). Additionally, increasing seasonal access to off-channel habitats that often have favourable temperatures and primary productivity that may increase juvenile salmon growth rates. In-channel and off-channel habitats may both benefit from seasonally increased streamflow from water management programmes. If these restoration and management actions can produce better growing conditions and subsequently larger individuals in the tributary rearing stage, it would manifest in both larger body size and earlier arrival date at LGR the next year, benefitting survival in most years and moving wild spring/summer Chinook salmon closer towards recovery goals.

AUTHOR CONTRIBUTIONS

Richard W. Zabel and Morgan H. Bond conceived and designed the research. Brandon Chasco and Morgan H. Bond conducted the analyses. All authors wrote and revised the manuscript. All authors approve of the manuscript to be published.

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CONFLICT OF INTEREST STATEMENT

All authors are employees of the United States Federal government and declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

DATA AVAILABILITY STATEMENT

All PIT-tag files and R code are available in a Zenodo Repository: <https://doi.org/10.5281/zenodo.12738322> (Chasco et al., 2024).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Distributions for the parameter estimates for the simulated data from the operating model (box and whisker plots where whiskers represented the 90% quantiles) and the maximum likelihood estimates and 90% C.I. for the parameters (red dots and lines) for Model 1 (Table 1).

Figure S2. Area under the curve plot (AUC=0.7556) for the receiver operator curve (ROC).

Figure S3. QQplot showing little deviation from the expected distribution for the simulated SAR values for the model with the lowest AIC value.

Figure S4. Estimated survival for spring/summer Chinook salmon tagged at Lower Granite Dam as smolts between 1998 and 2019 using the model with the lowest AIC value in Table 1.

Figure S5. Estimated survival for spring/summer Chinook salmon tagged above Lower Granite Dam (LGR) and detected at LGR within two weeks of tagging for smolt migration years 1998 to 2019 using the model with the lowest AIC value in Table 1.

Figure S6. Estimated anisotropy in the length/day domain as represented by the 10% decorrelation along length and day axes.

Figure S7. Moran statistic values for the spatial autocorrelation in fish length and migration date deviates (see Figure S8 for the 2d fields for each year) for fish tagged at LGR.

Figure S8. Estimated length/day deviates for spring/summer Chinook salmon tagged at Lower Granite Dam as smolts between 1998 and 2019 using the model with the lowest AIC value in Table 1.

Figure S9. Estimated length/day deviates for spring/summer Chinook salmon tagged above Lower Granite Dam as smolts between 1998 and 2019 using the model with the lowest AIC value in Table 1.

Table S1. Annual sample sizes for the number of smolts tagged at and above Lower Granite Dam, and the number of adults that survived and return two to three years later.

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