

MATHEMATICAL DESCRIPTION

STATE-SPACE LIFE CYCLE MODEL FOR GRANDE RONDE SPRING CHINOOK SALMON

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1 MODEL OVERVIEW

The purpose of the state-space life cycle model for Grande Ronde spring Chinook salmon is to synthesize the abundant and diverse biological data sets that have been collected as part of routine monitoring programs into a self-contained and internally consistent population dynamics model. Such a synthesis can provide richer insights about unobserved quantities (e.g., total parr recruitment abundance) and the relationships between them than allowed by more piecemeal analyses. Further, because the model estimates expected values and the magnitude of inter-annual variability in a time series framework, the output will be useful for structuring simulation models of future population dynamics. These simulation exercises will ultimately allow decision-makers to posit plausible future states of nature (e.g., climate change) or management strategies (e.g., habitat restoration or harvest policies) and to receive a distribution of possible future outcomes weighted by their probability of occurrence as suggested by historical population dynamics. The outputs of those analyses will be useful in decision frameworks that seek to prioritize certain actions over others, while helping to set reasonable expectations for what might likely occur in the face of future challenges. Although this is the ultimate goal and purpose of developing the state-space life cycle model described herein, we do not discuss this concept further, as it is beyond the scope of the statistical population dynamics model, which is the topic of this document.

The state-space life cycle model tracks the fates of n_y cohorts of fish from egg to adulthood within a statistical population dynamics model. The model is fundamentally statistical because it receives input data in the form of empirical observations (or externally derived estimates informed by empirical observations, with uncertainty in the external estimation propagated to this model) and estimates unknown parameters that must be internally consistent with the data and one another. The model is considered “state-space” because it captures two discrete types of variability: (i) process noise, i.e., variability in the biological and environmental processes that give rise to latent (i.e., true but unobserved) population dynamics and outcomes and (ii) observation error, i.e., variability in the measurement processes that result in the observed data representing an imperfect (but generally unbiased) perception of the true states and transitions among them. As such, the model is inherently a time series model: spawners in one year produce eggs, which then become parr, then smolt, ocean juveniles, and ultimately spawners in future years – along this life cycle, it is the same pool of fish at one life stage that is decremented (via survival rate transition probabilities) to become a pool of fish at a later stage of the life cycle.

Furthermore, the model has several dimensions and the majority of processes are assumed to operate differently (i.e., have varying numerical values) along each dimension. One dimension is age structure: anadromous Chinook salmon in the Grande Ronde basin return predominately as age-3, age-4, or age-5 adults, these outcomes are mutually exclusive but can occur for any fish from a given cohort. This important feature of Chinook salmon life history means monitoring activities in one year of adult returns sample fish that are progeny from from 3 consecutive brood (i.e., i.e., spawning) years; due to the resulting time linkages in the data this creates, it is essential that our model account for it. Another dimension is origin structure: adults returning in any given year may be the result of either natural spawning/rearing in the wild or via captive spawning/rearing in a hatchery setting. Critical outputs of the model are productivity (i.e., fish produced per fish) and capacity (i.e., declining productivity with increasing density) which makes it crucial that we track the fates of naturally and hatchery produced fish separately. Among naturally produced juveniles, an additional dimension is migratory strategy structure: some individuals rear over their first winter as free-swimming juveniles in the headwaters near where they were spawned, while others migrate to areas lower in the basin to rear overwinter; regardless, all individuals migrate out to sea the following spring as age-2 smolt. This phenological life history complexity is important to capture because these two groups of fish are monitored separately and they may have different survival outcomes while inhabiting heterogeneous habitats. A final dimension is population structure: there are several tributaries within the Grande Ronde basin that support spawning Chinook salmon, and local environmental conditions and genetic adaptations may result in their population dynamics differing in terms of productivity, capacity, or overall life cycle fitness. Four tributaries, which we consider to be distinct spawning populations, have been monitored using largely consistent methods for nearly three decades; these include Catherine Creek, Lostine River, Minam River, and Upper Grande Ronde River. Although we model their population dynamics separately, it is also

reasonable to expect that these populations should show some level of synchronicity in the conditions they face and the resulting production and survival outcomes. Thus, wherever possible we attempt to capture the covariability among population-specific dynamics.

The model is framed in the Bayesian mode of inference, as it is intuitive for the necessary integration over the many layers of uncertainty (i.e., process vs. observational variability). Further, Bayesian inference provides an intuitive framework to constrain population dynamics parameters to take on only biologically plausible values through the use of prior information – we intentionally employ nearly exclusively uninformative prior information, but in several rare cases we were required to bring in auxiliary information in the form of reasonably strong priors (Table 3). A final benefit of using the Bayesian framework is the seamless propagation of uncertainty from directly estimated parameters to derived quantities (of which there are many) – all unknown quantities, either estimated parameters or deterministic functions of estimated parameters, receive a posterior distribution in the Bayesian framework. Due to the analytical intractability of the complexity of the model, we employ Markov Chain Monte Carlo methods (implemented via the JAGS probabilistic programming language) to sample from the joint posterior distribution of all unknown quantities in the model.

We begin our description of the mathematical structure of the life cycle model with an overview of several syntax and statistical conventions we employ. In our mathematical representation of quantities in the model, we have striven for consistency, but this has created somewhat non-intuitive conventions which require devoted explanation. All quantities are defined (i.e., symbology and the specific equations that use them) in Tables 1, 2, 3, and 4 for reference and a catalog of all equations is provided in Table 5.

We have described the life cycle model calculations as divided into three distinct life “phases” (Figure 1): freshwater juvenile, ocean juvenile, and freshwater adult. For each life phase, we describe the process model dynamics as a set of stochastic and deterministic processes followed by how they are informed by empirical data as part of the observation model. Although we present these phases and model components in discrete sections, note that they are all components of a single integrated population dynamics model that is statistical in the sense that unknown quantities are estimated with uncertainty from input data.

2 SYNTACTICAL AND STATISTICAL CONVENTIONS

- For simplicity, we use the term “adult” to refer to any mature individual returning to spawn – this includes age-3 fish which are generally referred to as “jacks”.
- Life stage-specific states are defined by capital letters, e.g., parr (P), smolt (M), or spawners (S)
- Parameters (e.g., survival terms, non-survival transition probabilities, coefficients in relationships, etc.) are denoted by Greek symbols, e.g., ϕ for survival rates or ψ for maturation rates.
- Subscripts denote the structure of a quantity, e.g., y denotes a specific year and j a specific population.
- We use the convention b to indicate “before event” and a to indicate “after event” for a quantity that occurs at the same life stage. E.g., M^b represents smolt abundance *before* out-of-basin migration and M^a represents smolt abundance *after* out-of-basin migration. As such, superscripts are most often used syntactically, not mathematically. E.g., M^b is not “ M raised to the power b ”; if we must raise the quantity M^b to the power c , it will be written $(M^b)^c$.
- Survival terms to transition from state A to state B in year y for population j are denoted by $\phi_{y,j}^{A \rightarrow B}$.
- Most terms vary annually to capture process noise in population dynamics. We denote the deterministic (i.e., expected) value in the absence of process noise with a dot, e.g., $\dot{\phi}_j^{A \rightarrow B}$. We use the term “deterministic” in the sense that it is the expected value for a stochastic (i.e., with process noise) quantity; the deterministic quantity still has a posterior probability density function.
- In some cases, we specify calculations performed on vectors rather than scalars (i.e., a scalar being a single element from a vector or higher-dimensional array). Vectors are denoted via boldface, and the dimension of the vector is denoted using $1:n$ syntax. E.g., $\boldsymbol{\phi}_{y,1:n_j}^{A \rightarrow B}$ represents a vector of survival terms from state A to state B in year y , where each element of the vector represents the value for a given population.

- Mathematical operations performed on two vectors \mathbf{C} and \mathbf{D} are performed in an element-wise fashion, and the resulting vector will have identical dimensions to both \mathbf{C} and \mathbf{D} .
- In some cases, a calculation is performed differently for a subset of the possible index values. For example, to denote that k should take on only the values of 1 and 3 (not 2), we would write, $k \in [1, 3]$.
- $\log(x)$ represents the natural logarithm of x (i.e., $\log_e(x)$) and it is implied that the constraint $x > 0$ is satisfied.
- $\text{logit}(p)$ represents the log odds of p (i.e., $\log[p/(1-p)]$) and it is implied that the constraint $0 < p < 1$ is satisfied.
- All quantities that have been empirically observed (or externally estimated from empirically observed data, and supplied to the model as “data”) and are used in a likelihood component are denoted by a “hat”, e.g., a survival term ($\hat{\phi}_{y,j}^{A \rightarrow B}$) and its logit-normal standard error ($\hat{\sigma}_{\phi_{y,j}^{A \rightarrow B}}$, which we use as a direct estimate of observation error variability).
- Stochastic processes are represented by $x_y \sim \mathcal{F}(\theta_1, \theta_2)$, where x_y is a random variable, \mathcal{F} is some probability density (or mass) function (\mathcal{N} is univariate normal, \mathcal{MVN} is multivariate normal, \mathcal{B} is binomial, and \mathcal{M} is multinomial), and θ_1 and θ_2 are parameters of the probability distribution; generally θ_1 is a location parameter specifying the expected value of x_y and θ_2 is a dispersion parameter specifying the variability of x_y around the expected value.

Process noise is introduced by assuming year-specific values are multivariate logit-normal random variables around the deterministic value. This is done to enable modeling covariability in process noise among populations (or origins, in the few cases where population structure is not modeled). The covariance matrix of these random variables are denoted by Σ , and have a common structure for all model components. Take the hypothetical survival term $\phi_{y,j}^{A \rightarrow B}$ as an example. We denote its random variability across years and populations as:

$$\text{logit}(\phi_{y,1:n_j}^{A \rightarrow B}) \sim \mathcal{MVN}[\text{logit}(\phi_{y,1:n_j}^{A \rightarrow B}), \Sigma_{\phi^{A \rightarrow B}}] \quad (1)$$

where $\Sigma_{\phi^{A \rightarrow B}}$ is an $n_j \times n_j$ matrix with the structure:

$$\begin{bmatrix} \left(\sigma_{\phi_{j=1}^{A \rightarrow B}}\right)^2 & \sigma_{\phi_{j=1}^{A \rightarrow B}} \cdot \sigma_{\phi_{j=2}^{A \rightarrow B}} \cdot \rho_{\phi^{A \rightarrow B}} & \dots & \sigma_{\phi_{j=1}^{A \rightarrow B}} \cdot \sigma_{\phi_{j=n_j}^{A \rightarrow B}} \cdot \rho_{\phi^{A \rightarrow B}} \\ \sigma_{\phi_{j=2}^{A \rightarrow B}} \cdot \sigma_{\phi_{j=1}^{A \rightarrow B}} \cdot \rho_{\phi^{A \rightarrow B}} & \left(\sigma_{\phi_{j=2}^{A \rightarrow B}}\right)^2 & \dots & \sigma_{\phi_{j=2}^{A \rightarrow B}} \cdot \sigma_{\phi_{j=n_j}^{A \rightarrow B}} \cdot \rho_{\phi^{A \rightarrow B}} \\ \vdots & \vdots & \ddots & \vdots \\ \sigma_{\phi_{j=n_j}^{A \rightarrow B}} \cdot \sigma_{\phi_{j=1}^{A \rightarrow B}} \cdot \rho_{\phi^{A \rightarrow B}} & \sigma_{\phi_{j=n_j}^{A \rightarrow B}} \cdot \sigma_{\phi_{j=2}^{A \rightarrow B}} \cdot \rho_{\phi^{A \rightarrow B}} & \dots & \left(\sigma_{\phi_{j=n_j}^{A \rightarrow B}}\right)^2 \end{bmatrix} \quad (2)$$

That is, all populations (j) have unique variance terms $(\sigma_{\phi_j^{A \rightarrow B}})^2$ but we assume the correlation component of the covariance calculation ($\rho_{\phi^{A \rightarrow B}}$) is identical for all population pairs. In cases where a quantity varies annually and is different by origin but not by population, Σ would have dimensions $n_o \times n_o$:

$$\begin{bmatrix} \left(\sigma_{\phi_{o=1}^{A \rightarrow B}}\right)^2 & \sigma_{\phi_{o=1}^{A \rightarrow B}} \cdot \sigma_{\phi_{o=2}^{A \rightarrow B}} \cdot \rho_{\phi^{A \rightarrow B}} \\ \sigma_{\phi_{o=2}^{A \rightarrow B}} \cdot \sigma_{\phi_{o=1}^{A \rightarrow B}} \cdot \rho_{\phi^{A \rightarrow B}} & \left(\sigma_{\phi_{o=2}^{A \rightarrow B}}\right)^2 \end{bmatrix} \quad (3)$$

Although the stochastic process requires the Σ term, it is the component σ_j (or σ_o) and ρ terms that were assigned priors ($\mathcal{U}(0, 5)$ and $\mathcal{U}(-1, 1)$, respectively, Table 3) and the Σ matrices were constructed using the structures defined in eqs. 2 and 3.

3 FRESHWATER JUVENILE PHASE

3.1 Process Model

3.1.1 Reproduction and Parr Recruitment

Total egg production is the sum product of age-specific spawner abundance (from eq. 35, below), proportion female, and fecundity:

$$E_{y,j} = \sum_o^{n_o} \sum_k^{n_k} S_{y,k,o,j}^a \cdot \Omega_{k,j} \cdot f_k \quad (4)$$

The proportion of spawners at age that are female ($\Omega_{k,j}$) was calculated from carcass survey data and averaged across years and fecundity (f_k) was calculated from samples taken from Grande Ronde-origin hatchery broodstock. Both quantities were supplied to the model assuming no error or inter-annual variability.

Deterministic egg-to-parr survival is density-dependent and follows a Beverton-Holt relationship with productivity parameter α_j and capacity parameter β_j :

$$\phi_{y,j}^{E \rightarrow P^b} = \frac{1}{\frac{1}{\alpha_j} + \frac{E_{y,j}}{\beta_j}} \quad (5)$$

To facilitate later analyses (not documented here) investigating the effects of habitat restoration and climate change on population dynamics, we modeled parr capacity as a function of weighted usable habitat length (WUL_j). Derivation of WUL_j is too detailed to describe fully here, but briefly, the “value” of stream segments with different habitat characteristics were quantified by a complex generalized linear mixed model that treated detectability-adjusted snorkel counts as the response variable and habitat features (e.g., pool frequency, water temperature, large wood density, etc.) as predictor variables and weights were assigned to stream segments based on their relative value to the segment with the highest value; WUL_j was then the sum of segment-specific weight and length within the known spawning and rearing extent for each population. We modeled capacity (β_j) as a function of this WUL_j metric:

$$\log(\beta_j) \sim \mathcal{N} [\log(\lambda \cdot \text{WUL}_j), \sigma_\beta] \quad (6)$$

where λ is the expected change in parr capacity per 1 km change in weighted usable habitat length, and σ_β is the log-normal standard deviation of variability in this relationship not captured by WUL values.

Realized (i.e., with process noise) egg-to-parr survival was a multivariate logit-normal random variable around the deterministic value ($\phi_{y,j}^{E \rightarrow P^b}$) predicted by the Beverton-Holt function in eq. 5 with covariance matrix $\Sigma_{\phi^{E \rightarrow P^b}}$ (constructed of $\sigma_{\phi_j^{E \rightarrow P^b}}$ and $\rho_{\phi^{E \rightarrow P^b}}$ following eq. 2):

$$\text{logit}(\phi_{y,1:n_j}^{E \rightarrow P^b}) \sim \mathcal{MVN} \left[\text{logit}(\phi_{y,1:n_j}^{E \rightarrow P^b}), \Sigma_{\phi^{E \rightarrow P^b}} \right] \quad (7)$$

Parr recruitment ($P_{y,j}^b$) to the end of summer was then the product of total egg production and egg-to-parr survival:

$$P_{y,j}^b = \phi_{y,j}^{E \rightarrow P^b} \cdot E_{y,j} \quad (8)$$

3.1.2 Migratory Strategy Apportionment

Not all summer parr ($P_{y,j}^b$) stay in the headwaters to rear overwinter – some migrate out in the fall and rear farther downstream (termed “fall migrants” and indexed by $i = \text{fall}$) and others migrate out the following spring (termed “spring migrants” and indexed by $i = \text{spring}$). Due to this difference in migratory phenology, these two groups of fish are monitored separately. To enable building an observation model that could

accommodate this feature of the populations in our model, summer parr was apportioned to these two strategies:

$$P_{y,i,j}^a = P_{y,j}^b \cdot \pi_{y,i,j} \quad (9)$$

where $P_{y,i,j}^a$ is migratory strategy-specific parr abundance and $\pi_{y,i,j}$ is the proportion that take on each migratory strategy. For fall migrants, this proportion was a multivariate logit-normal random variable around a time-constant mean ($\dot{\pi}_{i=\text{fall},j}$) with covariance matrix $\Sigma_{\pi_{i=\text{fall}}}$ (constructed of $\sigma_{\pi_{i=\text{fall},j}}$ and $\rho_{\pi_{i=\text{fall}}}$ following eq. 2):

$$\text{logit}(\pi_{y,i=\text{fall},1:n_j}) \sim \mathcal{MVN} \left[\text{logit}(\dot{\pi}_{i=\text{fall},1:n_j}), \Sigma_{\pi_{i=\text{fall}}} \right] \quad (10)$$

and the proportion that are spring migrants was obtained as its complement ($\pi_{y,i=\text{spring},j} = 1 - \pi_{y,i=\text{fall},j}$).

3.1.3 Survival to Smolt Stage and Hatchery Inputs

Overwinter survival from the end of the parr year (i.e., age-1) to the start of the smolt year (i.e., age-2), denoted by $\phi_{y,i,j}^{P^a \rightarrow M^b}$, was modeled as a logit-linear function of parr density (scaled to the same metric of weighted usable habitat length [WUL_j] used in eq. 6). Deterministic overwinter survival was:

$$\text{logit}(\phi_{y,i,j}^{P^a \rightarrow M^b}) = \gamma_{0,i,j} + \gamma_{1,j} \cdot \left(\frac{P_{y,i,j}^a}{\text{WUL}_j} \right) \quad (11)$$

Note the migratory strategy-specific intercept ($\gamma_{0,i,j}$) but common slope terms ($\gamma_{1,j}$). Then, for each migratory strategy separately, overwinter survival was a multivariate logit-normal random variable around the deterministic logistic model prediction with covariance matrix $\Sigma_{\phi_i^{P^a \rightarrow M^b}}$ (each matrix constructed of $\sigma_{\phi_i^{P^a \rightarrow M^b}}$ and $\rho_{\phi_i^{P^a \rightarrow M^b}}$ following eq. 2):

$$\text{logit}(\phi_{y,i,1:n_j}^{P^a \rightarrow M^b}) \sim \mathcal{MVN} \left[\text{logit}(\dot{\phi}_{y,i,1:n_j}^{P^a \rightarrow M^b}), \Sigma_{\phi_i^{P^a \rightarrow M^b}} \right] \quad (12)$$

Natural-origin (indexed by $o = \text{NOR}$) parr surviving to the beginning of the following year was then:

$$M_{y,i,o=\text{NOR},j}^b = P_{y,i,j}^a \cdot \phi_{y,i,j}^{P^a \rightarrow M^b} \quad (13)$$

For populations with hatchery supplementation, hatchery-origin smolt releases (assumed known without error) were introduced at this point as well and stored in the variable $M_{y,i=\text{spring},o=\text{HOR},j}^b$; we assumed no hatchery-origin parr were released the prior year, thus $M_{y,i=\text{fall},o=\text{HOR},j}^b = 0$.

3.1.4 Seaward Migration

In-basin smolt ($M_{y,i,o,j}^b$) migrate to the ocean in the spring of the year they become age-2. We divide mortality experienced during this migration into two stages: (i) from in-basin to Lower Granite Dam (LGR), the first in a series of eight dams encountered in the downstream migration, and (ii) from LGR to the ocean. For parameter identifiability in mortality stage (i), we were required to assume that survival from in-basin to LGR was identical between natural-origin fall and spring migrants (i.e., $\phi_{y,i=\text{fall},o=\text{NOR},j}^{M^b \rightarrow M^a} = \phi_{y,i=\text{spring},o=\text{NOR},j}^{M^b \rightarrow M^a}$), but we were able to model natural-origin survival separately from hatchery-origin. We assume that year-specific realized survival values were multivariate logit-normal random variables around a time-constant and density-independent deterministic value ($\dot{\phi}_{o,j}^{M^b \rightarrow M^a}$) with covariance matrix $\Sigma_{\phi_o^{M^b \rightarrow M^a}}$ (constructed of $\sigma_{\phi_o^{M^b \rightarrow M^a}}$ and $\rho_{\phi_o^{M^b \rightarrow M^a}}$ following eq. 2):

$$\text{logit}(\phi_{y,o,1:n_j}^{M^b \rightarrow M^a}) \sim \mathcal{MVN} \left[\text{logit}(\dot{\phi}_{o,1:n_j}^{M^b \rightarrow M^a}), \Sigma_{\phi_o^{M^b \rightarrow M^a}} \right] \quad (14)$$

Thus, the abundance of smolt reaching LGR was:

$$M_{y,i,o,j}^a = M_{y,i,o,j}^b \cdot \phi_{y,o,j}^{M^b \rightarrow M^a} \quad (15)$$

After reaching LGR, we modeled survival during the downstream migration through the hydrosystem on the Snake and Columbia rivers as a single survival rate, specific to each year and origin but shared among populations ($\phi_{y,o}^{M^a \rightarrow O^0}$). We assumed these survival rates were multivariate logit-normal random variables around a time-constant and density-independent deterministic value ($\phi_o^{M^a \rightarrow O^0}$) with covariance matrix $\Sigma_{\phi^{M^a \rightarrow O^0}}$ (constructed of $\sigma_{\phi_o^{M^a \rightarrow O^0}}$ and $\rho_{\phi^{M^a \rightarrow O^0}}$ following eq. 3):

$$\text{logit} \left(\phi_{y,1:n_o}^{M^a \rightarrow O^0} \right) \sim \mathcal{MVN} \left[\text{logit} \left(\phi_{1:n_o}^{M^a \rightarrow O^0} \right), \Sigma_{\phi^{M^a \rightarrow O^0}} \right] \quad (16)$$

Thus, the abundance of fish reaching the ocean by origin was:

$$O_{y,o,j}^0 = \phi_{y,o}^{M^a \rightarrow O^0} \sum_i^{n_i} M_{y,i,o,j}^a \quad (17)$$

Note the summation across migratory strategies (i) in eq. 17, which indicates that the fates of fish with these different strategies were assumed to be the result of identical processes following arrival to LGR.

3.2 Observation Model

The observation model components for the freshwater juvenile life stage were fitted to two primary data types: (i) abundance of juveniles passing rotary smolt traps (located in each tributary) in either the fall or spring and (ii) survival of juveniles from several PIT tagging events to LGR. For both types, the information supplied to the model were externally compiled estimates (e.g., survival from Cormack-Jolly-Seber models) and the estimated standard error was supplied to the model as a measure of observation error variability.

3.2.1 Abundance Data Sources

Fish with the fall migratory strategy pass the screw trap in the fall and fish with the spring migratory strategy pass the screw trap the following spring. The estimated passage during these time periods were used in log-normal likelihoods by assuming:

$$\log \left(\hat{p}_{y,i=\text{fall},j}^a \right) \sim \mathcal{N} \left[\log \left(p_{y,i=\text{fall},j}^a \right), \hat{\sigma}_{p_{y,i=\text{fall},j}^a} \right] \quad (18)$$

for the fall screw trap estimate and

$$\log \left(\hat{M}_{y,i=\text{spring},o=\text{NOR},j}^b \right) \sim \mathcal{N} \left[\log \left(M_{y,i=\text{spring},o=\text{NOR},j}^b \right), \hat{\sigma}_{M_{y,i=\text{spring},o=\text{NOR},j}^b} \right] \quad (19)$$

for the spring screw trap estimate.

3.2.2 Survival Data Sources

Natural-origin juveniles have been PIT-tagged during four separate events in most years and populations: (i) at the end of summer prior to migratory strategy apportionment, (ii) as fall migrant parr pass the screw trap in the fall, (iii) at the start of winter in the headwaters (after fall migrants leave, so applies only to spring migrants; also not available for Minam River), and (iv) as spring migrant smolt pass the screw trap. Hatchery-origin smolt released in the spring have also been PIT-tagged. All five of these tag groups have their survival estimated from the time of tagging to their arrival at LGR. These estimates (and their associated standard errors) were used in logit-normal likelihoods by assuming:

$$\text{logit} \left(\hat{\phi}_{y,j}^{P^b \rightarrow M^a} \right) \sim \mathcal{N} \left[\text{logit} \left(\frac{\sum_i^{n_i} M_{y,i,o=\text{NOR},j}^a}{P_{y,j}^b} \right), \hat{\sigma}_{\phi_{y,j}^{P^b \rightarrow M^a}} \right] \quad (20)$$

for the summer tagging group,

$$\text{logit} \left(\hat{\phi}_{y,i=\text{fall},j}^{P^a \rightarrow M^a} \right) \sim \mathcal{N} \left[\text{logit} \left(\frac{M_{y,i=\text{fall},o=\text{NOR},j}^a}{P_{y,i=\text{fall},j}^a} \right), \hat{\sigma}_{\phi_{y,i=\text{fall},j}^{P^a \rightarrow M^a}} \right] \quad (21)$$

for the fall tagging group,

$$\text{logit} \left(\hat{\phi}_{y,i=\text{spring},j}^{P^a \rightarrow M^a} \right) \sim \mathcal{N} \left[\text{logit} \left(\frac{M_{y,i=\text{spring},o=\text{NOR},j}^a}{P_{y,i=\text{spring},j}^a \cdot \phi_j^{P^b \rightarrow P^a}} \right), \hat{\sigma}_{\phi_{y,i=\text{spring},j}^{P^a \rightarrow M^a}} \right] \quad (22)$$

for the winter tagging group (where $\phi_j^{P^b \rightarrow P^a}$ is a time-constant model-estimated survival from summer tagging to winter tagging for parr that ultimately become spring migrants and $j \in [\text{CAT}, \text{LOS}, \text{UGR}]$),

$$\text{logit} \left(\hat{\phi}_{y,i=\text{spring},o=\text{NOR},j}^{M^b \rightarrow M^a} \right) \sim \mathcal{N} \left[\text{logit} \left(\phi_{y,i=\text{spring},o=\text{NOR},j}^{M^b \rightarrow M^a} \right), \hat{\sigma}_{\phi_{y,i=\text{spring},o=\text{NOR},j}^{M^b \rightarrow M^a}} \right] \quad (23)$$

for the spring tagging group, and

$$\text{logit} \left(\hat{\phi}_{y,i=\text{spring},o=\text{HOR},j}^{M^b \rightarrow M^a} \right) \sim \mathcal{N} \left[\text{logit} \left(\phi_{y,i=\text{spring},o=\text{HOR},j}^{M^b \rightarrow M^a} \right), \hat{\sigma}_{\phi_{y,i=\text{spring},o=\text{HOR},j}^{M^b \rightarrow M^a}} \right] \quad (24)$$

for hatchery-origin smolt releases ($j \in [\text{CAT}, \text{LOS}, \text{UGR}]$).

Much quantitative research has been devoted to studying the survival of Chinook salmon smolts migrating through the hydrosystem located on the Snake and Columbia rivers. As a result, we thought it best to utilize the findings from some of this research as input data to our modeling effort rather than attempt to have our model freely estimate survival along this migration – doing so would give us the flexibility to more freely estimate quantities which have received less directed research, namely ocean survival. We used the output from the most recent Comparative Survival Study report (McCann et al., 2020, Table A.1 on page A-20 therein) to serve as empirical observations (with estimates of uncertainty) with which to inform this component of our model. Provided by McCann et al. (2020) are annual estimates of in-stream survival along the migration from LGR through Bonneville Dam (BON); separate time series are available for natural-origin (we used the “Aggregate Wild Chinook” estimates as none were available for Grande Ronde populations only, denoted $\hat{\phi}_{y,o=\text{NOR}}^{M^a \rightarrow O^0}$ here) and for hatchery-origin (we used the “Catherine Creek AP” estimates, denoted $\hat{\phi}_{y,o=\text{HOR}}^{M^a \rightarrow O^0}$ here). We treated these estimates as representative of the survival for each population, which implies an assumption that the different populations we model experience similar conditions during this migration and ignores any effect of barge-transporting fish. Similar to the other survival data sets, we assumed these estimates are made with logit-normal random error around the life cycle model estimate to build the likelihood:

$$\text{logit} \left(\hat{\phi}_{y,o}^{M^a \rightarrow O^0} \right) \sim \mathcal{N} \left[\text{logit} \left(\phi_{y,o}^{M^a \rightarrow O^0} \right), \hat{\sigma}_{\phi_{y,o}^{M^a \rightarrow O^0}} \right] \quad (25)$$

4 OCEAN JUVENILE PHASE

4.1 Process Model

Spring Chinook salmon in the Grande Ronde basin migrate to sea as age-2 smolts and can return as either age-3, age-4, or age-5 adults. That is, ocean juveniles spend between 1 and 3 winters at sea and some fraction will mature and make the return migration after each winter and before the following winter at sea (which we term the “maturation rate”). Thus, we divided ocean population dynamics into two types of demographic rates: survival and maturation rates. We treated survival in the first year with the most complexity and we vastly simplified survival in the second and third years for parameter identifiability purposes. Further, we wished to account for differences in ocean survival among natural- and hatchery-origin fish, but were

limited in the level of complexity that was estimable; thus we assumed natural- and hatchery-origin survival at sea was perfectly correlated over time, but shifted by a log-odds ratio.

First year natural-origin ocean survival was assumed to be a multivariate logit-normal random variable around a time-constant and density-independent deterministic value ($\phi_{o=\text{NOR},j}^{O^0 \rightarrow O^1}$) with covariance matrix $\Sigma_{\phi^{O^0 \rightarrow O^1}}$ (constructed of $\sigma_{\phi_j^{O^0 \rightarrow O^1}}$ and $\rho_{\phi^{O^0 \rightarrow O^1}}$ following eq. 2), but included a lag-1 autoregressive process as a means to account for ocean conditions that may affect survival in a temporally non-independent fashion (all $o = \text{NOR}$ in eq. 26, omitted for brevity):

$$\text{logit} \left(\phi_{y,o,1:n_j}^{O^0 \rightarrow O^1} \right) \sim \mathcal{MVN} \left\{ \text{logit} \left(\phi_{o,1:n_j}^{O^0 \rightarrow O^1} \right) + \kappa_{1:n_j}^{O^0 \rightarrow O^1} \cdot \left[\text{logit} \left(\phi_{y-1,o,1:n_j}^{O^0 \rightarrow O^1} \right) - \text{logit} \left(\phi_{o,1:n_j}^{O^0 \rightarrow O^1} \right) \right], \Sigma_{\phi^{O^0 \rightarrow O^1}} \right\} \quad (26)$$

We assumed process variation was negligible in the second and third year ocean survival terms, thus we forced the year-specific values of $\phi_{y,o=\text{NOR},j}^{O^1 \rightarrow O^2}$ and $\phi_{y,o=\text{NOR},j}^{O^2 \rightarrow O^3}$ to take on the same deterministic value each year (i.e., $\phi_{o=\text{NOR},j}^{O^1 \rightarrow O^2}$ and $\phi_{o=\text{NOR},j}^{O^2 \rightarrow O^3}$, respectively). We further discovered that not all maturity and ocean survival terms were uniquely identifiable based solely on adult return abundance and age composition – we thus relied on reasonably strong priors to inform $\phi_{o=\text{NOR},j}^{O^1 \rightarrow O^2}$ and $\phi_{o=\text{NOR},j}^{O^2 \rightarrow O^3}$ (Table 3). To obtain hatchery-origin ocean survival each year, we adjusted the natural-origin survival by a log-odds ratio (δ_j) that was common across all ocean years and brood years but varied by population:

$$\begin{aligned} \text{logit} \left(\phi_{y,o=\text{HOR},j}^{O^0 \rightarrow O^1} \right) &= \text{logit} \left(\phi_{y,o=\text{NOR},j}^{O^0 \rightarrow O^1} \right) + \delta_j \\ \text{logit} \left(\phi_{y,o=\text{HOR},j}^{O^1 \rightarrow O^2} \right) &= \text{logit} \left(\phi_{y,o=\text{NOR},j}^{O^1 \rightarrow O^2} \right) + \delta_j \\ \text{logit} \left(\phi_{y,o=\text{HOR},j}^{O^2 \rightarrow O^3} \right) &= \text{logit} \left(\phi_{y,o=\text{NOR},j}^{O^2 \rightarrow O^3} \right) + \delta_j \end{aligned} \quad (27)$$

Maturation rates (i.e., the proportion of fish from a given brood year alive and in the ocean at the beginning of a year that make the return migration that year) were assumed to vary by ocean age, origin, brood year, and population and were treated as multivariate logit-normal random variables around time-constant and density-independent deterministic values ($\psi_{o,j}^{O^w}$, w is the number of winters spent in the ocean) with covariance matrix $\Sigma_{\psi_o^{O^w}}$ (one matrix per origin, each constructed of $\sigma_{\psi_{o,j}^{O^w}}$ and $\rho_{\psi_o^{O^w}}$ following eq. 2):

$$\begin{aligned} \text{logit} \left(\psi_{y,o,1:n_j}^{O^1} \right) &\sim \mathcal{MVN} \left[\text{logit} \left(\psi_{o,1:n_j}^{O^1} \right), \Sigma_{\psi_o^{O^1}} \right] \\ \text{logit} \left(\psi_{y,o,1:n_j}^{O^2} \right) &\sim \mathcal{MVN} \left[\text{logit} \left(\psi_{o,1:n_j}^{O^2} \right), \Sigma_{\psi_o^{O^2}} \right] \end{aligned} \quad (28)$$

Since we assumed age-5 to be the last age of maturity, all fish alive and in the ocean after the third year at sea must mature and return that year (i.e., all $\psi_{y,o,j}^{O^3} = 1$).

Now that we have defined the sources of process noise in the ocean demographic rates, we can define the process equations that result in transitioning ocean juveniles through the various ocean ages. We modeled ocean population dynamics as a sequence of survival, maturation of surviving fish, and survival of non-maturing fish:

$$\begin{aligned} O_{y,o,j}^1 &= O_{y,o,j}^0 \cdot \phi_{y,o,j}^{O^0 \rightarrow O^1} \\ O_{y,o,j}^2 &= O_{y,o,j}^1 \cdot (1 - \psi_{y,o,j}^{O^1}) \cdot \phi_{y,o,j}^{O^1 \rightarrow O^2} \\ O_{y,o,j}^3 &= O_{y,o,j}^2 \cdot (1 - \psi_{y,o,j}^{O^2}) \cdot \phi_{y,o,j}^{O^2 \rightarrow O^3} \end{aligned} \quad (29)$$

That is, fish reaching the ocean as age-2 juveniles ($O_{y,o,j}^0$) must survive one winter to become age-3 ocean juveniles ($O_{y,o,j}^1$); if they do not mature at age-3 ($1 - \psi_{y,o,j}^{O^1}$), then they must survive another winter to become age-4 ocean juveniles ($O_{y,o,j}^2$), and if they do not mature at that point ($1 - \psi_{y,o,j}^{O^2}$), they must survive a third winter to become age-5 ocean juveniles ($O_{y,o,j}^3$).

Now, we must place the maturing portion of each of $O_{y,o,j}^1$, $O_{y,o,j}^2$, and $O_{y,o,j}^3$ into the correct year and age of return to the mouth of the Columbia River ($R_{y,k,o,j}^b$). Fish spawned in year y will return as the k^{th} possible age at maturity in year $y + k_{\min} + k - 1$ (age-3 is the first possible total age of maturity, thus $k_{\min} = 3$). As an example, fish spawned in brood year $y = 2000$ will return in 2003 as age-3 ($k = 1$), in 2004 as age-4 ($k = 2$), or in 2005 as age-5 ($k = 3$). Thus, the abundance of fish spawned in brood year y returning as age-3, age-4, and age-5, respectively, was:

$$\begin{aligned} R_{y+k_{\min}+1-1,1,o,j}^b &= O_{y,o,j}^1 \cdot \psi_{y,o,j}^{O^1} \\ R_{y+k_{\min}+2-1,2,o,j}^b &= O_{y,o,j}^2 \cdot \psi_{y,o,j}^{O^2} \\ R_{y+k_{\min}+3-1,3,o,j}^b &= O_{y,o,j}^3 \cdot \psi_{y,o,j}^{O^3} \end{aligned} \quad (30)$$

Note, however, that this leaves 12 age/year combinations per origin unpopulated (the first 3 missing years for age-3 returns, first 4 missing years for age-4 returns, and first 5 missing years for age-5 returns). This is because the life cycle dynamics must start somewhere, and no juvenile process model outcomes existed that would ultimately become these $R_{y,k,o,j}^b$ values in these early years. Thus, to initialize the adult returns for natural-origin fish (and as a result, the rest of the life cycle), we estimated these 12 year/age return abundances as free parameters with fairly restrictive priors (Table 3) with boundaries loosely informed by the ranges of adult returns at age observed in the early years of the data time series. Initial abundance of hatchery-origin returns was handled by the “straying model”, described below.

4.2 Observation Model

No data sources were used to inform ocean juvenile population dynamics – estimation of these quantities was enabled by (i) reasonably precise information about the abundance and composition of fish entering the ocean and returning to natal tributaries, (ii) the simplifying assumptions described above (i.e., time-constant second and third year ocean survival and perfectly correlated but offset origin-specific survival), and (iii) through the use of reasonably strong priors for second and third year ocean survival (Table 3).

5 FRESHWATER ADULT PHASE

5.1 Process Model

There are several sources of mortality that occur on the upstream migration between the mouth of the Columbia River and the natal tributaries in the Grande Ronde basin. Downstream of Bonneville Dam (BON, the first dam encountered in this upstream migration), returning adults are subject to predation mortality (survival denoted by $\phi_{y,j}^{SL}$) from sea lions and harvest mortality from fisheries (harvest rate after sea lion predation denoted by $U_{y,k,o}$). We compiled the best available estimates of these quantities, but did not fit to them explicitly as part of the observation model (as we do with many other data sources) – instead we passed them to the model as non-stochastic quantities that were assumed to be known without error. Once fish reach BON, however, their survival to LGR has been monitored (since 2000; $y = 10$) via PIT tags and so we did fit to those data and estimate the survival rate between BON and LGR as multivariate logit-normal random variables around deterministic values ($\phi_o^{R^b \rightarrow R^a}$) with covariance matrix $\Sigma_{\phi^{R^b \rightarrow R^a}}$ (constructed of $\sigma_{\phi_o^{R^b \rightarrow R^a}}$ and $\rho_{\phi^{R^b \rightarrow R^a}}$ following eq. 3). In years without these PIT tag counts, however, the survival from BON to LGR is confounded with ocean survival, and so we assumed BON to LGR survival was equal to the deterministic expectation in these years for parameter identifiability purposes:

$$\text{logit} \left(\phi_{y,1:n_o}^{R^b \rightarrow R^a} \right) \begin{cases} = \text{logit} \left(\phi_{1:n_o}^{R^b \rightarrow R^a} \right) & \text{if } y < 10 \\ \sim \mathcal{MVN} \left[\text{logit} \left(\phi_{1:n_o}^{R^b \rightarrow R^a} \right), \Sigma_{\phi^{R^b \rightarrow R^a}} \right] & \text{if } y \geq 10 \end{cases} \quad (31)$$

Examination of the adult data indicated that hatchery-origin adults returned to Grande Ronde populations in years that could not be attributed to hatchery-origin smolt releases to these populations. Further, the Minam River population (which has no hatchery supplementation program) has had hatchery adults return in many of the years with adult data. Since there were non-zero observations of hatchery-origin adults in cases without a process model component to produce them, we required a process model mechanism to populate non-zero expected values for the observation model to remain valid based on the available data. We term this part of the model the “straying model”, and apply it only in years/populations in which there is no other way to explain the presence of hatchery-origin adults. We denote the total number of strays that enter population j in year y as $T_{y,o,j}$; we forced all $T_{y,o=\text{NOR},j} = 0$ and forced all $T_{y,o=\text{HOR},j} = 0$ in years where hatchery-origin smolt releases to population j could have explained non-zero hatchery-origin adult returns in year y at age k . We denote the age composition of these strays by $p_{k,j}^T$ (where $\sum_k p_{k,j}^T = 1$) and apportioned $T_{y,o,j}$ to age-specific values by $T_{y,k,o,j} = T_{y,o,j} \cdot p_{k,j}^T$.

We can now define the abundance of adults arriving to their natal spawning tributaries by age and origin ($R_{y,k,o,j}^a$) as:

$$R_{y,k,o,j}^a = R_{y,k,o,j}^b \cdot \phi_{y,j}^{SL} \cdot (1 - U_{y,k,o}) \cdot \phi_{y,o}^{R^b \rightarrow R^a} + (T_{y,o,j} \cdot p_{k,j}^T) \quad (32)$$

Upon arrival in the tributary, populations with a weir and hatchery program (all populations except the Minam River, indexed by $j = \text{MIN}$) have some number of adults removed each year for broodstock and as a means to minimize natural spawning of hatchery-origin fish. These weir removals (denoted by $B_{y,k,o,j}$) were passed to the model as perfectly known values and $B_{y,k,o,j=\text{MIN}} = 0$. Thus, the abundance of fish passed upstream of the weir and that would have a chance to spawn each year was (the maximum constraint was used to ensure all $S_{y,k,o,j}^b > 0$):

$$S_{y,k,o,j}^b = \max(R_{y,k,o,j}^a - B_{y,k,o,j}, 1) \quad (33)$$

As a final step before spawning, these fish on the spawning grounds must survive the challenges of finding adequate spawning habitat and avoid succumbing to stress and mortality prior to spawning. We term this phenomenon “pre-spawn survival”, denoted by $\phi_{y,j}^{S^b \rightarrow S^a}$, which we assume are multivariate logit-normal random variables around a time-constant and density-independent deterministic value ($\phi_j^{S^b \rightarrow S^a}$) with covariance matrix $\Sigma_{\phi^{S^b \rightarrow S^a}}$ (constructed of $\sigma_{\phi_j^{S^b \rightarrow S^a}}$ and $\rho_{\phi^{S^b \rightarrow S^a}}$ following eq. 2):

$$\text{logit}(\phi_{y,1:n_j}^{S^b \rightarrow S^a}) \sim \mathcal{MVN} \left[\text{logit}(\phi_{1:n_j}^{S^b \rightarrow S^a}), \Sigma_{\phi^{S^b \rightarrow S^a}} \right] \quad (34)$$

Thus, the abundance of total successfully spawning individuals ($S_{y,k,o,j}^a$) was:

$$S_{y,k,o,j}^a = S_{y,k,o,j}^b \cdot \phi_{y,j}^{S^b \rightarrow S^a} \quad (35)$$

It is this $S_{y,k,o,j}^a$ value from which total egg production ($E_{y,j}$) is calculated in eq. 4 to complete the life cycle.

5.2 Observation Model

The adult observation model relies on three primary data types: (i) total abundance of adult returns to the natal tributaries, (ii) information about survival on the upstream migration between LGR and BON as well as on the spawning grounds, and (iii) composition data to inform the relative abundance of adults of different ages and origins.

5.2.1 Abundance Data Source

Total return abundance is estimated annually external to the model using a combination of weir counts, mark-recapture methods, and spawning ground surveys. For each population and year, these have been compiled into a point estimate ($\hat{R}_{y,j}^a$; note the lack of o or k indices – this indicates the estimate is aggregated across these

dimensions) and an estimate of observation uncertainty ($\hat{\sigma}_{R_{y,j}^a}$, expressed as a log-normal standard error). We assumed the point estimate is made with log-normal observation error around the model-predicted total returns to the tributary to build the likelihood for this component:

$$\log(\hat{R}_{y,j}^a) \sim \mathcal{N} \left[\log \left(\sum_o^{n_o} \sum_k^{n_k} R_{y,k,o,j}^a \right), \hat{\sigma}_{R_{y,j}^a} \right] \quad (36)$$

5.2.2 Survival Data Sources

For the observation model component informing migration survival upstream through the hydropower system, we relied on counts of PIT tag detections of known Grande Ronde-origin fish passing BON ($\hat{x}_{y,o}^{\text{BON}}$) and LGR ($\hat{x}_{y,o}^{\text{LGR}}$). We assumed the latter was a binomial random variable to build the likelihood component for this data set:

$$\hat{x}_{y,o}^{\text{LGR}} \sim \mathcal{B} \left(\phi_{y,o}^{R^b \rightarrow R^a}, \hat{x}_{y,o}^{\text{BON}} \right) \quad (37)$$

The other survival data set informing the freshwater adult observation model was for spawning success, i.e., pre-spawn survival. In annual spawning ground carcass surveys, surveyors record the counts of total females encountered ($\hat{x}_{y,j}^{\text{carcass,total}}$) and counts of those found to have successfully spawned ($\hat{x}_{y,j}^{\text{carcass,spawned}}$). Females are counted this way because it is too difficult to tell if a male has successfully spawned based on their gonads alone, thus we assumed that males and females experience the same pre-spawn survival. We assumed these counts were gathered using binomial sampling to build the likelihood:

$$\hat{x}_{y,j}^{\text{carcass,spawned}} \sim \mathcal{B} \left(\phi_{y,j}^{S^b \rightarrow S^a}, \hat{x}_{y,j}^{\text{carcass,total}} \right) \quad (38)$$

5.2.3 Composition Data Sources

Since the model is both age- and origin-structured, we required data to inform the relative abundance of adults returning according to these different classes. These took the form of two sources: (i) those collected at the weirs located within three of the four populations we model ($\hat{x}_{y,k,o,j}^{R^a}$) and (ii) those collected during carcass surveys ($\hat{x}_{y,k,o,j}^{S^a}$), given the Minam River population does not have a weir. We assumed the weir sampled fish representatively with respect to age and origin composition, however we discovered there was an age sampling bias for carcass surveys relative to the weir. We fitted to these data assuming multinomial sampling in which there were $n_{ko} = 6$ possible outcomes: $n_k = 3$ ages of return by $n_o = 2$ origins. Further, we chose to use the observed sample size ($\sum_{ko}^{n_{ko}} \hat{x}_{y,k,o,j}^{R^a}$) as the multinomial sample size rather than attempting to adjust it for non-independent sampling. The model-expected composition by age and origin ($p_{y,k,o,j}^{R^a}$) was calculated from the return abundance by age and origin, reorganized such that age and origin fell along the same array dimension ($R_{y,k,o,j}^a$) rather than along two dimensions as shown in the process model ($R_{y,k,o,j}^a$):

$$p_{y,k,o,j}^{R^a} = \frac{R_{y,k,o,j}^a}{\sum_{ko}^{n_{ko}} R_{y,k,o,j}^a} \quad (39)$$

which we used as the multinomial expected frequency to build the likelihood:

$$\hat{x}_{y,1:n_{ko},j}^{R^a} \sim \mathcal{M} \left(p_{y,1:n_{ko},j}^{R^a}, \sum_{ko}^{n_{ko}} \hat{x}_{y,k,o,j}^{R^a} \right) \quad (40)$$

Due to the age sampling bias of carcass surveys we discovered, we required a correction to ensure reliable fits to all data sets while still recovering unbiased true age composition data for the Minam River population, which had only carcass composition data (the other three populations had both weir and carcass composition data). For the three populations with paired composition data (i.e., $j \in [\text{CAT}, \text{LOS}, \text{UGR}]$), we estimated correction factors in a hierarchical fashion:

$$z_{k,j} \sim \mathcal{N}(\hat{z}_k, \sigma_{z_k}) \quad (41)$$

where $k = 1$ or $k = 3$ ($k = 2$ was treated as the baseline category), $z_{k,j}$ are age- and population-specific coefficients, \bar{z}_k are their expectations across populations, and σ_{z_k} are their standard deviations across populations. These coefficients were used in the following log-linear model to derive the correction factors ($\zeta_{k,j}$):

$$\log(\zeta_{k,j}) = z_{k=1,j} \cdot \text{age}3_k + z_{k=3,j} \cdot \text{age}5_k \quad (42)$$

where $k \in [1, 2, 3]$, $\text{age}3_{1:n_k} = [1 \ 0 \ 0]$ is a dummy variable indicating whether each value of k corresponds to age-3, and $\text{age}5_{1:n_k} = [0 \ 0 \ 1]$ is a dummy variable indicating whether each value of k corresponds to age-5. These correction factors were averaged across populations to obtain the correction factors for the Minam River population:

$$\zeta_{k,j=\text{MIN}} = \text{mean}(\zeta_{k,j \in [\text{CAT}, \text{LOS}, \text{UGR}]}) \quad (43)$$

We used these correction factors to calculate the expected proportions by age and origin for carcass surveys ($p_{y,ko,j}^{S^{a'}}$):

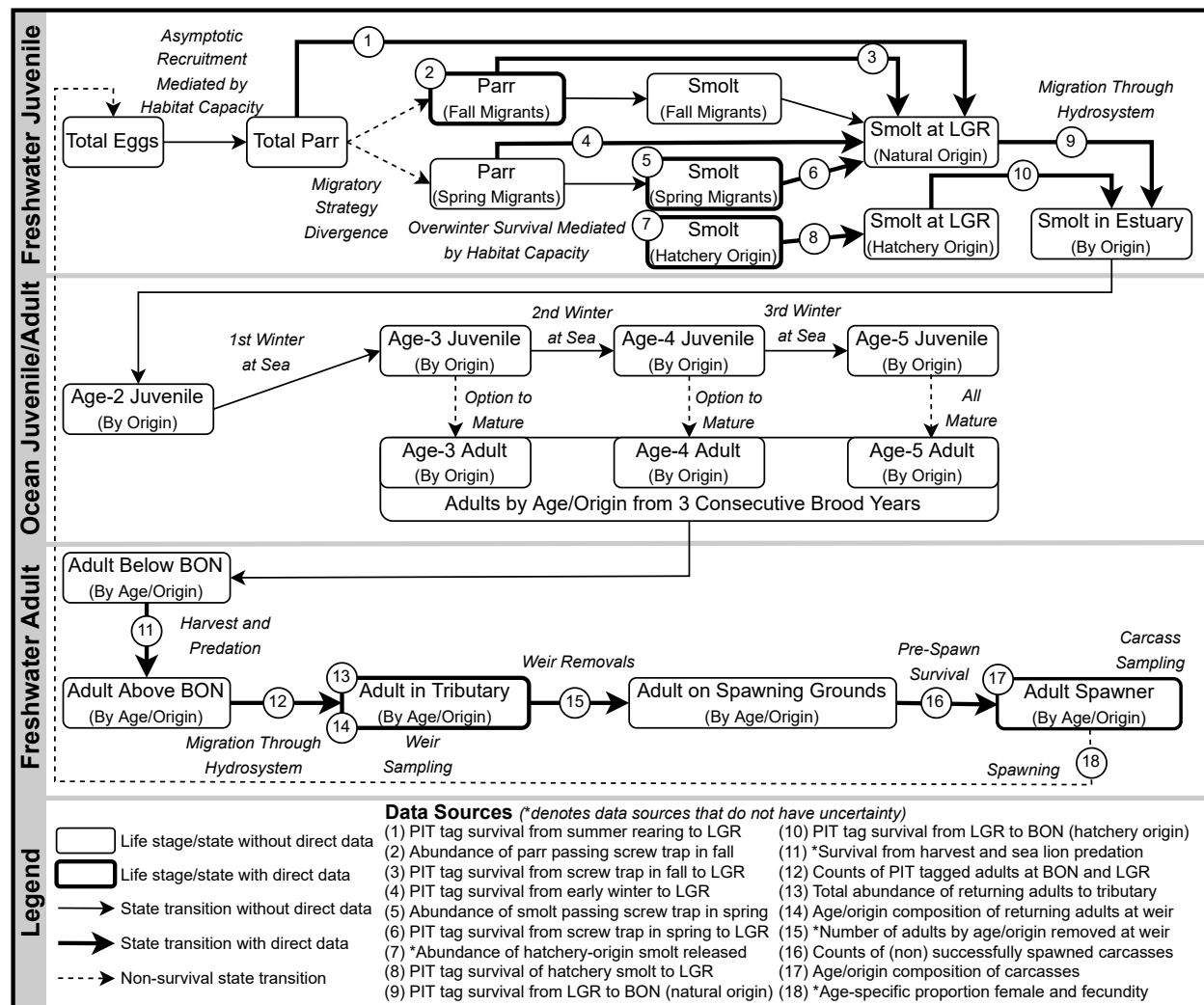
$$p_{y,ko,j}^{S^{a'}} = \frac{S_{y,ko,j}^a \cdot \zeta_{k,j}}{\sum_{ko}^{n_{ko}} S_{y,ko,j}^a \cdot \zeta_{k,j}} \quad (44)$$

which we used as the multinomial expected frequency to build the likelihood by assuming:

$$\hat{\mathbf{x}}_{y,1:n_{ko},j}^{S^{a'}} \sim \mathcal{M} \left(\mathbf{p}_{y,1:n_{ko},j}^{S^{a'}}, \sum_{ko}^{n_{ko}} \hat{\mathbf{x}}_{y,ko,j}^{S^{a'}} \right) \quad (45)$$

FIGURES

FIGURE 1. Schematic of the primary states and transitions among states that are captured in the state-space life cycle model for Grande Ronde spring Chinook salmon.



TABLES

TABLE 1. The various indices and dimensional constants used in defining the structure and scope for the state-space life cycle model for Grande Ronde spring Chinook salmon.

Type	Symbol	Description
Indices	j	¹ Population; $j \in [\text{CAT}, \text{LOS}, \text{MIN}, \text{UGR}]$
	y	² Year; $y \in [1, \dots, n_y]$
	k	³ Age of maturation; $k \in [1, \dots, n_k]$
	i	⁴ Juvenile migratory strategy; $i \in [\text{fall}, \text{spring}]$
	o	⁵ Origin type; either natural- or hatchery-origin; $o \in [\text{NOR}, \text{HOR}]$
	ko	⁶ Unique age/origin combinations; $ko \in [1, \dots, n_{ko}]$
Scoping Constants	w	Number of winters spent at sea prior to maturation; $w \in [1, 2, 3]$
	y_{\min}	² First year modeled; equal to 1991 here; first brood year with juvenile data
	y_{\max}	² Last year modeled; equal to 2019 here; last return year with adult data
	k_{\min}	³ Minimum total age of maturation; equal to 3 here
Dimensional Constants	k_{\max}	³ Maximum total age of maturation; equal to 5 here
	n_j	¹ Number of populations modeled; equal to 4 here
	n_y	² Number of years modeled; equal to 29 here
	n_k	³ Number of ages at maturation modeled; equal to 3 here
	n_i	⁴ Number of migratory strategies modeled; equal to 2 here
	n_o	⁵ Number of origins modeled; equal to 2 here
	n_{ko}	⁶ Number of unique age/origin combinations

¹ “Population” is used to distinguish among the tributaries within the Grande Ronde basin with sufficient data to model complete life cycle population dynamics. Abbreviations are as follows: Catherine Creek (CAT), Lostine River (LOS), Minam River (MIN), and Upper Grande Ronde River (UGR).

² “Year” refers to the year of spawning; for juvenile phases this is the year fish were spawned (i.e., brood year) and for adult phases this is the year of spawning (i.e., return or calendar year).

³ “Age” refers to the total age, i.e., the number of winters experienced post-spawning including the winter spent as an egg. For example, eggs fertilized in brood year 2000 are age-0 until they hatch in spring of 2001 (age-1), migrate to sea in spring/summer of 2002 (age-2), and return to spawn in one of 2003 (age-3), 2004 (age-4), or 2005 (age-5). $k = 1$ is the first age of maturation (age-3) and $k = 3$ is the last age of maturation (age-5).

⁴ “Migratory strategy” refers to the timing of migration from headwaters rearing areas – some fish (fall migrants) migrate out in the fall at age-1 and spend the winter downstream whereas others stay and migrate out at age-2 (spring migrants). Regardless of this migratory strategy, all fish make the seaward out-of-basin migration at age-2.

⁵ “Origin” refers to the type of spawning that produced the fish in question: natural-origin (NOR) are fish that were spawned in the wild and hatchery-origin (HOR) are fish that were spawned in a hatchery setting.

⁶ Most quantities treat age (k) and origin (o) as two separate dimensions of a larger array. However, for fitting to compositional data by age and origin, we collapse these two dimensions into one such that a single vector of proportions can represent the composition by age and origin. $k \in [1, 2, 3]$ represents age-3, age-4, and age-5 for natural-origin fish, respectively, and $k \in [4, 5, 6]$ represents these same ages for hatchery-origin fish, respectively.

TABLE 2. The symbology used to represent the key states (i.e., abundance at life stage/group) and rates (i.e., transition probabilities among states) in the presentation of the state-space life cycle model for Grande Ronde spring Chinook salmon. The majority of rates presented in this table are hierarchically structured/estimated, where the population- and/or origin-specific expected value and standard deviation are free parameters (or a function of free parameters) presented in Table 3. Equation numbers reference any equation that uses that quantity – these may include the equation where the quantity is first defined, where it is used in process model, or where it is used in the observation model.

Type	Symbol	Eqs.	Description
Freshwater Juvenile			
States	$E_{y,j}$	4, 5, 8	Total egg production
	$P_{y,j}^b$	8, 9, 20	Parr abundance at end of summer (<i>before</i> migratory strategy apportionment)
	$P_{y,i,j}^a$	9, 11, 13, 21, 22	Parr abundance <i>after</i> migratory strategy apportionment
	$M_{y,i,o,j}^b$	13, 15, 19	In-basin smolt abundance, immediately following over-winter mortality and <i>before</i> migration out of basin; hatchery-origin smolt releases introduced here
	$M_{y,i,o,j}^a$	15, 17, 20, 21, 22, 23, 24	Smolt abundance at Lower Granite Dam <i>after</i> migration out of basin
	$\phi_{y,j}^{E \rightarrow P^b}$	7, 8	Survival rate from egg to end of summer parr; density-dependent
	$\pi_{y,i,j}$	9, 10	Proportion of parr at end of summer that have migratory strategy i
	$\phi_{y,i,j}^{P^a \rightarrow M^b}$	12, 13	Overwinter survival from parr year to smolt year; i.e., to move from total age-1 to total age-2; density-dependent
	$\phi_{y,i,o,j}^{M^b \rightarrow M^a}$	14, 15, 23, 24	Migration survival from within basin to Lower Granite Dam
	$\phi_{y,o}^{M^a \rightarrow O^0}$	16, 17, 25	Migration survival downstream through hydrosystem to reach ocean
Ocean Juvenile			
States	$O_{y,o,j}^w$	17, 29, 30	Abundance of ocean juveniles after experiencing w winter(s) at sea, where $w \in [0, 1, 2, 3]$
Rates	$\phi_{y,o,j}^{O^w \rightarrow O^{w+1}}$	26, 27, 29	Survival of ocean juveniles from the end of winter w to the end of winter $w + 1$ at sea, where $w \in [0, 1, 2]$
	$\psi_{y,o,j}^{O^w}$	28, 29, 30	Proportion of ocean juveniles alive at the end of winter w at sea that make spawning migration before winter $w + 1$, where $w \in [1, 2, 3]$
Freshwater Adult			
	$R_{y,k,o,j}^b$	30, 32	Abundance of adults (i.e., mature) arriving at the estuary (<i>before</i> upstream main-stem migration)
	$R_{y,k,o,j}^a$	32, 33, 36, 39	Abundance of adults arriving at their natal tributary (<i>after</i> upstream main-stem migration)
	$T_{y,k,o,j}$	32	Abundance of adult strays
	$B_{y,k,o,j}$	33	Abundance of adults removed at weir, primarily for broodstock

(Continued on next page...)

TABLE 2. The symbology used to represent the key states (i.e., abundance at life stage/group) and rates (i.e., transition probabilities among states) in the presentation of the state-space life cycle model for Grande Ronde spring Chinook salmon. The majority of rates presented in this table are hierarchically structured/estimated, where the population- and/or origin-specific expected value and standard deviation are free parameters (or a function of free parameters) presented in Table 3. Equation numbers reference any equation that uses that quantity – these may include the equation where the quantity is first defined, where it is used in process model, or where it is used in the observation model. (*continued*)

Type	Symbol	Eqs.	Description
States	$S_{y,k,o,j}^b$	33, 35	Abundance of adults following weir removals (e.g., for hatchery broodstock but <i>before</i> pre-spawn mortality)
	$S_{y,k,o,j}^a$	4, 35, 44	Abundance of spawning adults <i>after</i> pre-spawn mortality
	$\phi_{y,j}^{SL}$	32	Survival past sea lion predation downstream of Bonneville Dam
	$U_{y,k,o}$	32	Fishery harvest rate downstream of Bonneville Dam
	$\phi_{y,o}^{R^b \rightarrow R^a}$	32, 37	Survival from all mortality sources during the migration between Bonneville Dam and arrival to natal tributaries
	$\phi_{y,j}^{S^b \rightarrow S^a}$	35, 38	Pre-spawn survival rate
Rates	$\Omega_{k,j}$	4	Proportion of spawners that are female
	f_k	4	Fecundity per female spawner

TABLE 3. All free parameters (i.e., that have a prior that is not function of other free parameters) estimated by the state-space life cycle model for Grande Ronde spring Chinook salmon.

Symbol	Prior ^{1,2,3,4,5}	Eqs.	Description
Freshwater Juvenile			
α_j	$b(1, 1)$	5	Maximum expected egg-to-parr survival rate; Beverton-Holt productivity
σ_β	$\mathcal{U}(0, 5)$	6	Among-population SD of parr capacity not explained by WUL_j
λ	$\mathcal{N}(0, 1 \times 10^{-8})$	6	Expected change in parr capacity per 1 km change in WUL_j ; prior bounded by $(0, \infty)$
$\sigma_{\phi_j^{E \rightarrow Pb}}$	$\mathcal{U}(0, 5)$	7	Among-year SD of egg-to-parr survival rate
$\rho_{\phi_j^{E \rightarrow Pb}}$	$\mathcal{U}(-1, 1)$	7	Among-population correlation of egg-to-parr survival rate
$\pi_{i=\text{fall},j}$	$b(1, 1)$	10	Expected proportion of summer parr that are fall migrants
$\sigma_{\pi_{i=\text{fall},j}}$	$\mathcal{U}(0, 5)$	10	Among-year SD of proportion of summer parr that are fall migrants
$\rho_{\pi_{i=\text{fall}}}$	$\mathcal{U}(-1, 1)$	10	Among-population correlation of proportion of summer parr that are fall migrants
$\phi_j^{Pb \rightarrow Pa}$	$b(1, 1)$	22	Survival from summer tagging to winter tagging for parr that become spring migrants
$\gamma_{0,i,j}$	$\mathcal{N}(0, 1 \times 10^{-3})$	11	Intercept of density-dependent overwinter survival relationship
$\gamma_{1,j}$	$\mathcal{N}(0, 1 \times 10^{-3})$	11	Slope of density-dependent overwinter survival relationship
$\sigma_{\phi_{ij}^{Pa \rightarrow Mb}}$	$\mathcal{U}(0, 5)$	12	Among-year SD of overwinter survival rate for migratory strategy i
$\rho_{\phi_i^{Pa \rightarrow Mb}}$	$\mathcal{U}(-1, 1)$	12	Among-population correlation of overwinter survival rate for migratory strategy i
$\phi_{o,j}^{Mb \rightarrow Ma}$	$b(1, 1)$	14	Expected migration survival from in-basin to LGR
$\sigma_{\phi_{o,j}^{Mb \rightarrow Ma}}$	$\mathcal{U}(0, 5)$	14	Among-year SD of migration survival from in-basin to LGR
$\rho_{\phi_o^{Mb \rightarrow Ma}}$	$\mathcal{U}(-1, 1)$	14	Among-population correlation of migration survival from in-basin to LGR
$\phi_o^{Ma \rightarrow O^0}$	$b(1, 1)$	16	Expected migration survival from LGR to ocean
$\sigma_{\phi_o^{Ma \rightarrow O^0}}$	$\mathcal{U}(0, 5)$	16	Among-year SD of migration survival from LGR to ocean
$\rho_{\phi^{Ma \rightarrow O^0}}$	$\mathcal{U}(-1, 1)$	16	Among-origin correlation of migration survival from LGR to ocean
Ocean Juvenile			
$\phi_{o=\text{NOR},j}^{O^0 \rightarrow O^1}$	$b(1, 1)$	26	Expected first year ocean survival for natural origin fish
$\sigma_{\phi_j^{O^0 \rightarrow O^1}}$	$\mathcal{U}(0, 5)$	26	Among-year SD of first year ocean survival
$\rho_{\phi^{O^0 \rightarrow O^1}}$	$\mathcal{U}(-1, 1)$	26	Among-population correlation in first year ocean survival
$\kappa_j^{O^0 \rightarrow O^1}$	$\mathcal{U}(-1, 1)$	26	Lag-1 autoregressive coefficient for first year ocean survival

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TABLE 3. All free parameters (i.e., that have a prior that is not function of other free parameters) estimated by the state-space life cycle model for Grande Ronde spring Chinook salmon. (*continued*)

Symbol	Prior ^{1,2,3,4,5}	Eqs.	Description
$\phi_{o=\text{NOR},j}^{O^1 \rightarrow O^2}$	$b(60, 15)$		Expected second year ocean survival for natural origin fish
$\phi_{o=\text{NOR},j}^{O^2 \rightarrow O^3}$	$b(60, 15)$		Expected third year ocean survival for natural origin fish
δ_j	$t(0, 1.57^{-2}, 7.76)$	27	Log-odds ratio to convert natural origin to hatchery origin ocean survival
$\psi_{o,j}^{O^w}$	$b(1, 1)$	28	Expected maturation rate after w winter(s) at sea ($w \in [1, 2]$)
$\sigma_{\psi_{o,j}^{O^w}}$	$\mathcal{U}(0, 5)$	28	Among-year SD of maturation rate after w winter(s) at sea ($w \in [1, 2]$)
$\rho_{\psi_o^{O^w}}$	$\mathcal{U}(-1, 1)$	28	Among-population correlation in maturation rate after w winter(s) at sea ($w \in [1, 2]$)
Freshwater Adult			
$R_{y,k=1,y,o,j}^b$	$\mathcal{U}(0, 50)$		Return abundance of natural-origin age-3 fish in years without process model link; only for $y \in [1, 2, 3]$ and $o = \text{NOR}$
$R_{y,k=2,y,o,j}^b$	$\mathcal{U}(0, 200)$		Return abundance of natural-origin age-4 fish in years without process model link; only for $y \in [1, 2, 3, 4]$ and $o = \text{NOR}$
$R_{y,k=3,y,o,j}^b$	$\mathcal{U}(0, 200)$		Return abundance of natural-origin age-5 fish in years without process model link; only for $y \in [1, 2, 3, 4, 5]$ and $o = \text{NOR}$
$\phi_o^{R^b \rightarrow R^a}$	$b(1, 1)$	31	Expected migration survival from BON to LGR
$\sigma_{\phi_o^{R^b \rightarrow R^a}}$	$\mathcal{U}(0, 5)$	31	Among-year SD of migration survival from BON to LGR
$\rho_{\phi^{R^b \rightarrow R^a}}$	$\mathcal{U}(-1, 1)$	31	Among-origin correlation of migration survival from BON to LGR
$T_{y,o,j}$	$\mathcal{U}(0, 500)$	32	Total hatchery-origin “strays”; only for $o = \text{HOR}$ and y where presence of HOR adults could not be explained by non-zero smolt releases
$p_{k,j}^T$	$\mathcal{D}(1, 1, 1)$	32	Age composition of hatchery-origin “strays”
$\phi_j^{S^b \rightarrow S^a}$	$b(1, 1)$	34	Expected pre-spawn survival
$\sigma_{\phi_j^{S^b \rightarrow S^a}}$	$\mathcal{U}(0, 5)$	34	Among-year SD of pre-spawn survival
$\rho_{\phi^{S^b \rightarrow S^a}}$	$\mathcal{U}(-1, 1)$	34	Among-population correlation of pre-spawn survival
\dot{z}_k	$\mathcal{U}(-10, 10)$	41	Across-population expected coefficient of log-linear carcass composition correction model; only for $k \in [1, 3]$
σ_{z_k}	$\mathcal{U}(0, 5)$	41	Across-population SD for coefficients of log-linear carcass composition correction model; only for $k \in [1, 3]$

Prior Distributions:

¹ Beta Distribution: $b(\text{shape}_1, \text{shape}_2)$

² Normal Distribution: $\mathcal{N}(\text{mean}, \text{precision})$

³ Uniform Distribution: $\mathcal{U}(\text{lower}, \text{upper})$

⁴ t -Distribution: $t(\text{mean}, \text{precision}, \text{degrees of freedom})$

⁵ Dirichlet Distribution: $\mathcal{D}(\text{shape}_1, \text{shape}_2, \text{shape}_3)$

TABLE 4. The symbology used to represent the data sources in the presentation of observation model components of the state-space life cycle model for Grande Ronde spring Chinook salmon. All data sources listed here have an explicit likelihood component and were thus assumed to be observed with error.

Type	Symbol	Eqs.	Description
Freshwater Juvenile			
Abundance	$\hat{P}_{y,i=\text{fall},j}^a$	18	Estimated smolt trap passage of parr in the fall
	$\hat{\sigma}_{P_{y,i=\text{fall},j}^a}$	18	Log-normal SE of estimated smolt trap passage of parr in the fall
	$\hat{M}_{y,i=\text{spring},o=\text{NOR},j}^b$	19	Estimated smolt trap passage of smolt in the spring
	$\hat{\sigma}_{M_{y,i=\text{spring},o=\text{NOR},j}^b}$	19	Log-normal SE of estimated smolt trap passage of smolt in the spring
	$\hat{\phi}_{y,j}^{P^b \rightarrow M^a}$	20	Estimated survival from summer tagging to LGR
	$\hat{\sigma}_{\phi_{y,j}^{P^b \rightarrow M^a}}$	20	Logit-normal SE of estimated survival from summer tagging to LGR
	$\hat{\phi}_{y,i=\text{fall},j}^{P^a \rightarrow M^a}$	21	Estimated survival from fall tagging to LGR
	$\hat{\sigma}_{\phi_{y,i=\text{fall},j}^{P^a \rightarrow M^a}}$	21	Logit-normal SE of estimated survival from fall tagging to LGR
	$\hat{\phi}_{y,i=\text{spring},j}^{P^a \rightarrow M^a}$	22	Estimated survival from winter tagging to LGR
	$\hat{\sigma}_{\phi_{y,i=\text{spring},j}^{P^a \rightarrow M^a}}$	22	Logit-normal SE of estimated survival from winter tagging to LGR
	$\hat{\phi}_{y,i=\text{spring},o=\text{NOR},j}^{M^b \rightarrow M^a}$	23	Estimated survival from spring tagging to LGR
	$\hat{\sigma}_{\phi_{y,i=\text{spring},o=\text{NOR},j}^{M^b \rightarrow M^a}}$	23	Logit-normal SE of estimated survival from spring tagging to LGR
	$\hat{\phi}_{y,i=\text{spring},o=\text{HOR},j}^{M^b \rightarrow M^a}$	24	Estimated survival of hatchery-origin smolt releases to LGR
	$\hat{\sigma}_{\phi_{y,i=\text{spring},o=\text{HOR},j}^{M^b \rightarrow M^a}}$	24	Logit-normal SE of estimated survival of hatchery-origin smolt releases to LGR
	$\hat{\phi}_{y,o}^{M^a \rightarrow O^0}$	25	Estimated aggregate survival of smolt through hydrosystem
Survival	$\hat{\sigma}_{\phi_{y,o}^{M^a \rightarrow O^0}}$	25	Logit-normal SE of estimated aggregate survival of smolt through hydrosystem
Freshwater Adult			
Abundance	$\hat{R}_{y,j}^a$	36	Estimated total adult return to tributary (all ages/origins)
	$\hat{\sigma}_{R_{y,j}^a}$	36	Log-normal SE of estimated total adult return to tributary
Survival	$\hat{x}_{y,o}^{\text{BON}}$	37	Count of Grande Ronde-origin PIT-tagged adults detected at BON
	$\hat{x}_{y,o}^{\text{LGR}}$	37	Count of Grande Ronde-origin PIT-tagged adults detected at LGR
	$\hat{x}_{y,j}^{\text{carcass,total}}$	38	Count of female carcasses examined for spawning success
	$\hat{x}_{y,j}^{\text{carcass,spawned}}$	38	Count of female carcasses found to have successfully spawned
	$\hat{x}_{y,ko,j}^a$	40	Count of sampled adults returning to tributary by age/origin; only for $j \in [\text{CAT}, \text{LOS}, \text{UGR}]$
Composition	$\hat{x}_{y,ko,j}^{S^a'}$	45	Count of sampled carcasses by age/origin

TABLE 5. Catalog of all equations presented, separated by life phase (freshwater juvenile, ocean juvenile, or freshwater adult) and model component (process model or observation model).

Model Component	Eq.	Description
Generic		
Syntax	1	Syntax for quantities assumed to follow a multivariate logit-normal distribution
	2	Covariance structure for quantities that vary across populations
	3	Covariance structure for quantities that vary across origins (but not populations)
Freshwater Juvenile		
Process	4	Obtain total egg production
	5	Obtain expected egg-to-parr survival; density-dependent via Beverton-Holt function
	6	Parr capacity as a stochastic function of weighted usable habitat length
	7	Add stochasticity to egg-to-parr survival
	8	Obtain total parr recruitment
	9	Obtain migratory strategy-specific parr abundance
	10	Add stochasticity to migratory strategy apportionment rates
	11	Obtain expected overwinter survival; density-dependent via logit-linear model
	12	Add stochasticity to overwinter survival
	13	Obtain natural-origin smolt abundance prior to out-of-basin migration
	14	Add stochasticity to migration survival from in-basin to LGR
	15	Obtain smolt abundance at LGR
	16	Add stochasticity to migration survival from LGR to ocean
	17	Obtain initial abundance of ocean juveniles
Observation	18	Assumption for fall screw trap count data likelihood
	19	Assumption for spring screw trap count data likelihood
	20	Assumption for summer tagging event survival data likelihood
	21	Assumption for fall tagging event survival data likelihood
	22	Assumption for winter tagging event survival data likelihood
	23	Assumption for spring tagging event survival data likelihood (NOR)
	24	Assumption for spring tagging event survival data likelihood (HOR)
	25	Assumption for migration through hydrosystem survival data likelihood
Ocean Juvenile		
	26	Add stochasticity to first year ocean survival
	27	Obtain HOR ocean survival
	28	Add stochasticity to maturation rates
	29	Obtain abundance of ocean juveniles by ocean age
	30	Obtain return abundance of adults by total age
Freshwater Adult		
Process	31	Add stochasticity to migration survival from BON to LGR
	32	Obtain return abundance to natal tributary
	33	Obtain abundance of potential spawners reaching spawning grounds
	34	Add stochasticity to pre-spawn survival
	35	Obtain abundance of successful spawners

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TABLE 5. Catalog of all equations presented, separated by life phase (freshwater juvenile, ocean juvenile, or freshwater adult) and model component (process model or observation model). (*continued*)

Model Component	Eq.	Description
	36	Assumption for natal tributary return abundance data likelihood
	37	Assumption for migration from BON to LGR survival data likelihood
	38	Assumption for pre-spawn survival data likelihood
	39	Obtain expected composition by age and origin of adults counted at weirs
	40	Assumption for age and origin composition at weir data likelihood
	41	Add stochasticity to carcass composition correction factor coefficients
	42	Obtain correction factors for populations with weir and carcass composition data
	43	Obtain correction factors for population with carcass composition data only
	44	Obtain expected composition by age and origin of carcasses
Observation	45	Assumption for age and origin carcass composition data likelihood

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