Integrated Population Models with application to Skagit River Chinook Recovery Evaluation

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Abstract

To understand fish and wildlife population dynamics we must determine which internal and external factors most influence demographic rates, and therefore drive changes in populations. Integrated population models (IPMs) incorporate multiple data types throughout animals’ life cycles, and incorporate separate process variability and sampling uncertainty, allowing for increased accuracy of parameter estimates. The goal of this project was to develop, apply, and evaluate a Bayesian state-space life cycle IPM for Skagit River Chinook Salmon \( (Oncorhynchus tshawytscha) \) to enable inference about population dynamics from multiple sources of life stage specific data including age composition, smolt abundance, escapement, and harvest. We used non-least squares models to test effects of density dependence on freshwater and marine productivity and determined that freshwater productivity was best described by a non-density dependent function, while marine productivity was best described by a Ricker model. To determine the ability of the IPM to detect influences of environmental covariates on productivity, we compiled data on temperature, river flow, weather, and ocean condition indices. We developed a state-space life cycle IPM that incorporated freshwater and marine life stages with environmental covariates, and included functions for random process and observation error. We evaluated if our model successfully described and linked freshwater and marine life stages of Chinook Salmon using model convergence and fit metrics, comparison to parallel non-least squares model results, and examined the ability of the model to correctly identify parameters from simulated datasets. We found that the IPM successfully converged, fit the data well, and appeared to estimate similar covariate coefficients and non-density dependent productivity to single-stage NLS models. However, productivity and density dependence for simulated datasets were poorly predicted, indicating poor parameter identifiability. Future work on this model will involve improving parameter identifiability, further exploring the effects of covariates on life cycle stages, and adding additional data.
Introduction

The conservation and management of fish and wildlife is increasingly focused on population dynamics, which include changes in abundance over time and the demographic causes of those changes (Lindén and Knappe 2009). Changes in population size over time are the direct result of demographic processes (i.e., births and deaths), which are described by demographic rates (i.e., survival and productivity) (Cappuccino and Price 1995). To understand fish and wildlife population dynamics, we must determine which internal and external factors most influence demographic rates, and therefore drive changes in population abundance (Lindén and Knappe 2009; Lebreton and Gimenez 2013). Demographic rates, and the factors that influence them, likely change throughout an animal’s life, and therefore it is beneficial for management of populations to understand which life stages may be influenced by internal and external factors (Cappuccino and Price 1995). This understanding likely requires several disparate data sources such as change in population abundance, survival and fecundity rates at specific stages, or individual growth (Maunder and Deriso 2011; Polansky et al. 2019).

Integrated population models (IPMs) are a relatively new tool used by researchers that can connect two or more different data types describing population dynamics through a link function (Abadi et al. 2010; Buhle et al. 2018). These models incorporate multiple data types throughout animals’ life cycles, and incorporate separate process variability and sampling uncertainty, allowing for increased accuracy of parameter estimates (Maunder and Deriso 2011; Schaub and Abadi 2011). Integrated population models can be particularly useful for species with complex life cycle dynamics, such as Pacific Salmon (*Oncorhynchus* spp.), which have multiple life history types that encompass both freshwater and marine environments (Cunningham et al. 2018; Quinn 2018; Friedman et al. 2019).

In the Puget Sound, Chinook Salmon (*Oncorhynchus tshawytscha*) were listed as Threatened under the Endangered Species Act in 1999 (National Oceanic and Atmospheric Administration 2005). However, maintaining and recovering natural populations of Puget Sound Chinook Salmon is becoming more challenging due to contemporary threats of habitat loss due to human land use practices and climate change, requiring improved tools to evaluate populations (Beechie et al. 2006). Though studies have sought to evaluate drivers of population dynamics at individual life stages separately (Zimmerman et al. 2015; Greene et al. 2016; Ruff et al. 2017), or as a single stage encompassing the entire Chinook Salmon life cycle (Jorgensen et al. 2021), to date, there has been no concerted effort to integrate all existing disparate life-stage specific abundance data for Skagit River Chinook Salmon into a single framework.

The goal of this project was to develop, apply, and evaluate a Bayesian state-space life cycle IPM for Skagit River Chinook Salmon to provide an update of population dynamics from a series of sequential observations (time series) with error in measurements (Figure 1). This model may be applied in the future to evaluate recovery actions. Multiple sources of life stage specific data including age composition, smolt abundance, escapement, and harvest for Skagit River Chinook Salmon were integrated into this model to quantify the ability of a life-cycle IPM to identify drivers of Salmon populations. Here, we outline the current state of the IMP, our evaluation of the model following steps outlined in a Quality Assurance Project Plan (Lemoine et al. 2020) and highlight next steps in IMP development. Any results presented in this document
should only be used for model assessment and are not an evaluation of Skagit Chinook Salmon population dynamics nor the factors influencing those populations dynamics.

Figure 1. Conceptual diagram for multi-stage state-space integrated population model for Chinook Salmon.

Methods

Study Area

The Skagit River watershed is the largest river system in Puget Sound and includes 3,100 mi$^2$ of watershed area and 126 mi$^2$ of freshwater tidal delta and estuary (Figure 2). Hydroelectric projects occur on the upper-Skagit River near Newhalem, WA and on the Baker River near Concrete, WA. Most of the Skagit River watershed is forested with the lower watershed dominated by agriculture and urban development. The estuarine ecosystem of the Skagit River consists of delta and the nearshore and pelagic areas of the Whidbey basin. Vegetation within the delta comprises river riparian communities to open flat salt marsh communities.

Six populations of Chinook Salmon are currently delineated in the Skagit Basin exhibiting run timings of spring, summer and fall (Ruckelshaus et al. 2006). Skagit Chinook Salmon are part of
the Puget Sound Evolutionary Significant Unit (ESU) that was listed as threatened under the Endangered Species Act in 1999. In 2007, a recovery plan for Puget Sound Chinook Salmon and Skagit specific Chinook Recovery was adopted (Shared Strategy for Puget Sound 2007).

![The Skagit River Watershed](image)

Figure 2. Skagit river watershed within Washington State.

**Data sources**

Time series count data was collected during 1994–2016 and included estimates of outmigration abundance, adult returns, age structure, and harvest data. Annual estimates of outmigrating fry and parr (“smolts”) collected from the mainstem Skagit River rotary screw trap operated by Washington Department of Fish and Wildlife (WDFW). Adult escapement estimates and age structure data were derived from Skagit River system regional comanagers’ redd counts. Harvest data were comanager-agreed to estimates of harvest from the Fisheries Regulation Assessment Model (FRAM) from commercial and sport fisheries sampling (Pacific Fishery Management Council et al. 2022). We also estimated recruitment for each brood year using an age-structured population reconstruction (Fleischman et al. 2013).
To determine the ability of the IPM to predict productivity responses to environmental covariates, we compiled a suite of environmental covariates that have been found to predict productivity for freshwater and marine life stages including temperature, flow, weather, and ocean productivity (Table 1).

For the freshwater life stage, we used air temperatures from Sedro Woolley, WA from the Western Regional Climate Center (Western Regional Climate Center 2023) to calculate average annual and January–April air temperature. Water temperature data for the Skagit River were unavailable over the time period of our data, and air temperature correlates with, and can act as a proxy for, water temperature (Morrill et al. 2005). We calculated average flows in the Skagit River from the Mount Vernon USGS station (#12200500) during February–June (U.S. Geological Survey 2023) to test if higher flows during freshwater rearing decreased freshwater productivity.

Large flow events may move substantial amounts of substrate and therefore influence egg and embryo survival (Montgomery et al. 1996). Flows that maximize sediment movement (i.e. flooding events) are difficult to directly estimate, therefore we calculated proportion of maximum daily flows during August—February that were above the 1-year recurrence interval (RI) flows and calculated RIs of peak flows during each year (Soar and Thorne 2011) by applying Weibull’s formula (Natural Resource Conservation Service 2007) to yearly peak flows during 1941–2021. We used hourly data on flows to calculate proportion of days where the maximum flow exceeded the 1-year RI (U.S. Geological Survey 2023). Flow for a recurrence interval of 1 year was 835 m$^3$ per second. We also determined the maximum annual August—February flow. We advanced flow and temperature metrics by one year to account for time lag between incubation and smolt outmigration.

For the marine life stage, we used a variety of temperature and ocean productivity metrics. Delta water temperatures representing thermal rearing conditions for Chinook Salmon fry within the Skagit River Delta were calculated from spot measures taken during fish surveys as average temperatures during February–August surveys (Greene et al. 2016). Ocean condition indices included localized metrics, such as the Cumulative Upwelling Transport Index (CUTI), the Biologically Effective Upwelling Transport Index (BEUTI) (Jacox et al. 2018), Pacific and Washington Coast sea surface temperatures averaged annually across the region (Clayson et al. 2016; Huang et al. 2017); and basin-scale metrics, such as the North Pacific Gyre Oscillation (NPGO)(Di Lorenzo et al. 2008), Oceanic El Niño Index (ONI)(National Oceanic and Atmospheric Administration and National Weather Service 2023), Pacific Decadal Oscillation Index (PDO)(Mantua and Hare 2002; National Oceanic and Atmospheric Administration 2023a), and Multivariate El Niño/Southern Oscillation Index (MEI)(Zhang et al. 2019; National Oceanic and Atmospheric Administration 2023b). Data were compiled from (Satterthwaite et al. 2020), which followed (Johnstone and Mantua 2014).
Table 1. Candidate set of environmental covariates with source of data, model life stage transition (T; freshwater [f] or marine [m]), Salmon life cycle life stage, and reference for data source for the Chinook Salmon multi-stage life cycle IPM, Skagit River system, Washington, USA, 1993–2016.

<table>
<thead>
<tr>
<th>Data</th>
<th>Covariate</th>
<th>T</th>
<th>Life stage</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Air temperature (°C) in Sedro Woolley</td>
<td>Annual mean temperature</td>
<td>f</td>
<td>Freshwater rearing</td>
<td>(Western Regional Climate Center 2023)</td>
</tr>
<tr>
<td></td>
<td>Jan–Apr mean temperature</td>
<td>f</td>
<td>Freshwater rearing</td>
<td></td>
</tr>
<tr>
<td>Skagit River discharge (m³/s) at Mount Vernon USGS station</td>
<td>Proportion of days above 1-year recurrence interval Aug–Feb</td>
<td>f</td>
<td>Redd</td>
<td>(U.S. Geological Survey 2023)</td>
</tr>
<tr>
<td></td>
<td>Recurrence interval for maximum annual stream flow</td>
<td>f</td>
<td>Redd</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Maximum flow Feb–Jun</td>
<td>f</td>
<td>Redd</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Annual mean flow Feb–Jun</td>
<td>f</td>
<td>Freshwater rearing</td>
<td></td>
</tr>
<tr>
<td>Delta temperature (°C)</td>
<td>Mean Skagit River Delta temp. Feb–Aug</td>
<td>m</td>
<td>Estuary rearing</td>
<td>(Greene et al. 2016)</td>
</tr>
<tr>
<td>Ocean temperature (°C)</td>
<td>Annual mean coastal Washington sea surface temperature</td>
<td>m</td>
<td>Estuary rearing/ Marine</td>
<td>(Johnstone and Mantua 2014; Clayson et al. 2016; Satterthwaite et al. 2020)</td>
</tr>
<tr>
<td></td>
<td>Annual mean northeast Pacific sea surface temperature</td>
<td>m</td>
<td>Marine</td>
<td></td>
</tr>
<tr>
<td>Pacific Decadal Oscillation Index (PDO)</td>
<td>Annual mean</td>
<td>m</td>
<td>Marine</td>
<td>(Mantua and Hare 2002; Huang et al. 2017; National Oceanic and Atmospheric Administration 2023a)</td>
</tr>
<tr>
<td>North Pacific Gyre Oscillation (NPGO)</td>
<td>Annual mean</td>
<td>m</td>
<td>Marine</td>
<td>(Di Lorenzo et al. 2008)</td>
</tr>
<tr>
<td>Biologically Effective Upwelling Transport Index (BEUTI)</td>
<td>Annual mean</td>
<td>m</td>
<td>Marine</td>
<td>(Jacox et al. 2018)</td>
</tr>
<tr>
<td>Coastal Upwelling Transport Index (CUTI)</td>
<td>Annual mean</td>
<td>m</td>
<td>Marine</td>
<td>(Jacox et al. 2018)</td>
</tr>
<tr>
<td>Oceanic El Niño Index (ONI)</td>
<td>Annual mean</td>
<td>m</td>
<td>Marine</td>
<td>(Huang et al. 2017; National Oceanic and Atmospheric Administration 2023a)</td>
</tr>
<tr>
<td>Multivariate El Niño/Southern Oscillation Index (MEI)</td>
<td>Annual mean</td>
<td>$m$</td>
<td>Marine</td>
<td></td>
</tr>
<tr>
<td>------------------------------------------------------</td>
<td>-------------</td>
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<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

(Zhang et al. 2019; National Oceanic and Atmospheric Administration 2023b)
**Integrated Population Model Specification**

Before fitting the IPM, we conducted model selection to determine which form of density dependence, if any, best fit the data for freshwater productivity (spawners to smolts) and estuarine/marine productivity (smolts to adults) by fitting non-least squares (NLS) models to two life stages separately. We tested linear (non-density dependent; Equation 1a), Beverton-Holt density dependent (Beverton and Holt 1993; Equation 1b), and Ricker density dependent (Ricker 1954; Equation 1c) models.

\[ N_{a+1,t} = \alpha N_{a,t} \]  
\[ N_{a+1,t} = \frac{aS_t}{1 + \beta S_t} \]  
\[ N_{a+1,t} = \frac{aS_t}{e^{\beta S_t}} \]

Where \( N_{a,t} \) describes number of individuals in the first life stage in time \( t \) (number of smolts for freshwater productivity model, number of adult recruits for a given brood year for the marine productivity model), \( N_{a+1,t} \) describes number of individuals in the first life stage (number of spawners for freshwater productivity model, number of smolts for marine productivity model), \( \alpha \) is a density-independent estimate of productivity from one life stage to the next, and \( \beta \) is the density dependence parameter. In the Ricker model, carrying capacity is estimated by the inverse of \( \beta \), and maximum productivity in the second life stage is estimated by \( \frac{\alpha}{\beta} \) (Quinn and Deriso 1999). In the Beverton-Holt model, maximum productivity is estimated as \( \frac{\alpha}{\beta} \), with no estimate of carrying capacity (Quinn and Deriso 1999).

For ease of computation and interpretation we fit natural-log transformations of the aforementioned models (Equations 2a–c).

\[ \ln(N_{a+1,t}) = \ln(\alpha) + \ln(N_{a,t}) \]  
\[ \ln(N_{a+1,t}) = \ln(\alpha) + \ln(N_{a,t}) - \ln(1 + \beta N_{a,t}) \]  
\[ \ln(N_{a+1,t}) = \ln(\alpha) + \ln(N_{a,t}) - \beta N_{a,t} \]

We determined initial values for NLS models using the FSA package implemented in program R (R Core Team 2022; Ogle, Derek H. et al. 2023). We examined fit of NLS models using R packages nlstools and FSAmisc (Baty et al. 2015; Ogle, Derek H. et al. 2023).

We originally considered a wide range of variables (Table 1). However, some variables were correlated (Supplementary Tables 1–2). We therefore used model selection on an a priori candidate model set fit using NLS methods to determine which combination of non-correlated variables (Pearson’s product-moment correlation coefficient < 0.7) may best predict freshwater and marine productivity (Tables 2–3), maximizing number of variables included to create a global uncorrelated model to capture all potential influences on productivity. We scaled all covariates around the mean. We selected the model with the lowest Akaike’s Information Criterion adjusted for small sample size (AICc) to include in the multi-stage model.
Table 2. Candidate model set for freshwater Chinook Salmon productivity, including predictors for flood recurrence interval (flood RI), proportion of days with maximum flows above a 1-year recurrence interval (prop. 1-year RI), mean spring flow, mean spring air temperature, mean annual air temperature, watershed landslide volume (landslide), 20-year lagged landslide volume (lagged landslide), and freshwater habitat index (freshwater habitat), with degrees of freedom (DF) and Akaike’s information criterion for small sample size (AICc) for each model, Skagit River system, Washington, USA, 1993–2016.

<table>
<thead>
<tr>
<th>Parameters</th>
<th>DF</th>
<th>AICc</th>
</tr>
</thead>
<tbody>
<tr>
<td>Flood RI, prop. 1-year RI, mean spring flow, mean spring air temp.</td>
<td>8</td>
<td>40.1</td>
</tr>
<tr>
<td>Peak winter flow, prop. 1-year RI, mean spring flow, mean spring air temp.</td>
<td>8</td>
<td>41.5</td>
</tr>
<tr>
<td>Peak winter flow, prop. 1-year RI, mean spring flow, mean spring air temp.</td>
<td>8</td>
<td>41.7</td>
</tr>
<tr>
<td>Flood RI, prop. 1-year RI, mean spring flow, mean annual air temp.</td>
<td>8</td>
<td>42.5</td>
</tr>
</tbody>
</table>

Table 3. Candidate model set for marine Chinook Salmon productivity, including predictors for the North Pacific Gyre Oscillation (NPGO), Coastal Upwelling Transport Index (CUTI), Biologically Effective Upwelling Transport Index (BEUTI), Multivariate El Niño/Southern Oscillation index (MEI), Oceanic Niño Index (ONI), mean annual sea surface temperature for coastal Washington (Washington sea surface temp.), mean annual sea surface temperature for the Northeast Pacific (sea surface temp.), and mean water temperature in the Skagit River delta during February–August (delta temp.) with degrees of freedom (DF) and Akaike’s Information Criterion for small sample size (AICc) for each model, Skagit River system, Washington, USA, 1993–2016.

<table>
<thead>
<tr>
<th>Parameters</th>
<th>DF</th>
<th>AICc</th>
</tr>
</thead>
<tbody>
<tr>
<td>NPGO, CUTI, MEI, sea surface temp.</td>
<td>8</td>
<td>7.0</td>
</tr>
<tr>
<td>NPGO, CUTI, MEI, Washington sea surface temp., delta temp.</td>
<td>9</td>
<td>7.7</td>
</tr>
<tr>
<td>NPGO, PDO, CUTI, MEI, delta temp.</td>
<td>9</td>
<td>8.0</td>
</tr>
<tr>
<td>NPGO, CUTI, ONI</td>
<td>7</td>
<td>9.3</td>
</tr>
<tr>
<td>NPGO, BEUTI, ONI</td>
<td>7</td>
<td>13.8</td>
</tr>
</tbody>
</table>

Following model selection, we applied a multi-stage state-space model (Rivot et al. 2004), with a process model to describe transitions of spawners to smolts and smolt to brood-year recruitment with a hidden transition between brood-year recruitment to returning spawners, and observation models to account for errors in estimates of smolt production, spawning escapement, and age composition.

We modeled the freshwater life stage transition \( (w) \) such that within brood year \( t \) the true number of smolts \( (N_{sm}) \) equals the product of a linear density independent function of the true number of spawners \( (N_{sp}) \) and covariates for the freshwater life stage \( C_{w,t} \):

\[
N_{sm,t} = \alpha N_{sp,t} e^{C_{w,t}}
\]

Where \( \alpha \) represents freshwater productivity, and the influence of covariates (Table 2–3) is applied as
\[ C_{a,t} = \sum_{l=1}^{K} \gamma_{a,l} X_{a,l,t} \]  

(4b)

where \( K \) refers to the number of covariates evaluated, and covariate effects for the given life stage \( (C_{a,t}, \text{where } a \text{ is either freshwater } [w] \text{ or marine } [m]) \) vary according to \( \gamma_{a,i} \), which is the effect of life stage specific covariate \( X_{a,i} \) measured at time \( t \).

For the estimate of freshwater productivity, we assumed independent process error draws around a log-normal distribution with an unknown variance such that

\[ \ln(\alpha_w) \sim \text{Normal}(\ln(\mu_{\alpha_w}), \sigma_w) \]  

(4a)

Where \( \mu \) is the estimated mean of freshwater productivity \( (\alpha_w) \), with variance \( \sigma \).

We modeled the marine life stage transition \( (m) \) such that within brood year \( t \) abundance of adult recruits \( (N_R) \) equals the product of a Ricker density dependent function of the number of smolts \( (N_{sm}) \) and time-varying stochastic error where \( \alpha \) describes density-independent productivity (slope) and \( \beta \) describes density dependence.

\[ N_{R,t} = \alpha N_{sm,t} e^{\epsilon_{m,t} - \beta N_{sm,t}} \]  

(5)

Process error was assumed to be non-zero and autocorrelated according to autocorrelation coefficient \( (\phi) \) and variance \( (\sigma_m) \), and was modeled as a function of the covariate structure shown in (2b), \( C_{m,t} \).

\[ \epsilon_{m,t} \sim \text{Normal}(C_{m,t} + \phi \epsilon_{m,t-1}, \sigma_{\epsilon_m}) \]  

(6a)

\[ \epsilon_{m,0} \sim \text{Normal}(0, \frac{\sigma_{\epsilon_m}}{1-\phi^2}) \]  

(6b)

To link estimated brood-year recruitment to annual escapement, we first established that estimated numbers of fish of ocean age \( A \) returning in year \( t \) \( (U_{A,t}) \) is a product of the total number of outmigration-year recruits \( (N_R) \) in year \( t - A \) from Equation (5) and the proportion of mature fish from that outmigration year that returned to spawn at ocean age \( A \) \( (\pi_{A,t-A}) \), such that

\[ U_{A,t} = N_{R,t-A} \pi_{A,t-A} \]  

(7)

Thus, in a table of true numbers-at-age by calendar year, \( \pi_A \) apportions total recruits \( (N_{R,t-A}) \) into appropriate age classes of future returns. Adult Chinook from the Skagit spend between 1 to 5 years maturing in the ocean prior to returning to the terminal river as adults, and therefore the vector of all age-specific return rates for outmigration year \( t \) is \( \pi_t = [\pi_1, \pi_2, \pi_3, \pi_4, \pi_5] \), which we will model as a hierarchical random effect whereby \( \pi_t \sim \text{Dirichlet}(\eta_t) \). The mean vector \( \eta \) is also distributed as a Dirichlet and is affected by the precision parameter \( \tau \); large values of \( \eta \) result in the \( \pi_t \) very close to \( \eta \) and small values of \( \tau \) lead to much more diffuse \( \pi_t \).

We obtained counts of fish in each age class \( A \) in year \( t \) \( (O_{A,t}) \) from scale analysis of 179–2910 harvested adult Chinook per year. These data were assumed to arise from a multinomial process with order \( Y_t \) and proportion vector \( d_A \), where
\( O_t \sim \text{Multinomial}(Y_t, d_t). \) (8)

The order of the multinomial is the sum of observed counts of aged fish across all ages returning in year \( t \):

\[ Y_t = \sum_{A=1}^{5} O_{A,t} \] (9)

The proportion vector \( d_t \) for the multinomial is based on the age-specific, model-derived estimates of adult returns in each age class in year \( t \) (run size; \( U_{A,t} \)) such that

\[ d_{A,t} = \frac{U_{A,t}}{\sum_{A=1}^{5} U_{A,t}}. \] (10)

The estimated true number of spawners for each year (escapement, \( N_{sp,t} \)) is calculated using estimated total run size (\( U_t \)) and annual harvest rate (\( r_{h,t} \)), where annual harvest rate is estimated from annual observed harvest (\( y_{h,t} \)) and true unobservable harvest is \( N_{h,t} \).

\[ N_{sp,t} = U_t - N_{h,t} \] (11)

Where \( U_t \) describes the total run size and equals the sum of \( U_{a,t} \) from Equation (7) over all age classes. Harvest rate was estimated from annual observed harvest data (\( y_{h,t} \)) and included lognormal process error such that

\[ y_{h,t} \sim \text{Normal}(N_{h,t}, 20) \] (12)

Annual estimates of observed harvest, spawner abundance and smolt production likely contain some measurement errors due to poor visibility, non-exhaustive sampling, etc. Therefore, we will assume that observed estimates (\( y \)) in each life stage \( i \) in time \( t \) are log-normally distributed about the true abundance for each life stage (\( N \)) with a variance of \( \sigma_y \).

\[ \ln(y_{l,t}) \sim \text{Normal}(\ln(N_{l,t}), \sigma_{y,i}) \] (13)

We fit models using Gibbs sampling using JAGS through the JagsUI package in program R (Kellner 2021; Plummer 2022) to fit state-space models. We used minimally informative uniform bounded (for productivity and density dependence), uninformative normally distributed (for covariates), and uninformative uniform (for error) priors with four chains, a thin rate of 300, a burn-in of 50,000, and 300,000 iterations. We used initial values informed by the original NLS models, where \( \alpha_f = 250, \alpha_m = 0.01, \beta_m = 1.5E10^{-7} \).

**Model testing and validation**

We used a multi-step approach to evaluate if our model successfully described and linked freshwater and marine life stages of Chinook Salmon. We first used traceplots, density plots and the Brooks-Gelman-Rubin convergence diagnostic (\( \hat{\rho} \)) values to determine if sampled chains successfully converged on a solution (Gelman et al. 2004; Kéry 2010), and determined effective sample sizes and time-lagged autocorrelation functions of Markov chains to evaluate autocorrelation between parameters (Kéry 2010). We then evaluated posterior predictive checks.
(Bayesian p-values) to check model fit (Gelman et al. 1996). To validate our results, we compared posterior distributions generated from the IPM to bootstrapped results from identical NLS models fit separately to individual life stages to ensure that the IPM was producing similar estimates for productivity, density dependence, and covariate coefficients. Similarly, we compared predicted estimates of abundance smolts and recruits from the IPM and NLS models.

We additionally generated multiple simulated datasets using the model structure previously described excluding covariates, with known freshwater and marine productivity and density dependence. We then specified the IPM without covariates or autocorrelated error structure (Equations 2a and 2c for freshwater and marine productivity respectively, with normally distributed error as indicated by 4a) and fit the simplified model to simulated datasets, then compared model-estimated parameters and parameters used to generate the dataset (Table E). All simulations had fixed age proportions (proportions age 2 = 0.1, 3 = 0.3, 4 = 0.5, 5 = 0.1, standard error = 0.01) and an age sample proportion of 0.05.

Results

*Model selection*

For the estuarine-marine productivity negative likelihood model, the Ricker and Beverton-Holt density dependence models were similar (ΔAICc < 1; Table 4) and were better than the linear model (ΔAICc = 12.7). We used the Ricker model for all remaining calculations as it had less autocorrelation structure between bootstrapped α and β parameters (1000 iterations).

For freshwater productivity, all three models fit similarly (ΔAICc < 1; Table 4). As there was no evidence of density dependence, we used the linear model for freshwater productivity.

Table 4. Initial values, AICc values, parameter estimates, and parameter correlation for linear, Beverton-holt (B-H), and Ricker models fit to freshwater and marine life stages of Chinook salmon, Skagit River system, Washington, USA, 1993–2014.

<table>
<thead>
<tr>
<th>Life stage</th>
<th>Model</th>
<th>Initial values</th>
<th>AICc</th>
<th>Parameter Estimates</th>
<th>Corr.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Freshwater</td>
<td>Linear</td>
<td>α_f = 150</td>
<td>35.3</td>
<td>α_f = 275.8</td>
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</tr>
<tr>
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<td>36.0</td>
<td>α_f = 378, β_f = 3.09E-5</td>
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</tr>
<tr>
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<td>Ricker</td>
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<td>36.0</td>
<td>α_f = 360, β_f = 2.15E-5</td>
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<td>B-H</td>
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<td>Ricker</td>
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<td>α_m = 0.016, β_m = 1.53E-7</td>
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</table>

For marine productivity, the best covariate model included NPGO, CUTI, MEI, and sea surface temperature. For freshwater productivity, the best covariate model included RI, proportion of days with a maximum flow above a 1-year RI, mean spring flow, and mean spring air temperature.

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1 We tested Ricker, Beverton-Holt, and linear models including covariates with similar results (AICc linear = 36.36, Beverton-Holt = 38.07, Ricker = 38.19).
Model fitting and validation

Inspection of traceplots and density plots revealed that the IPM successfully converged (all $\hat{r} < 1.01$) and Bayesian p-values indicated good model fit ($\text{smolt} = 0.51$, $\text{recruit} = 0.49$). Though time-lagged autocorrelation for all parameter estimates were low ($< 0.06$), the effective sample size for $\beta_m$ was estimated at 1, indicating low parameter identifiability (Kéry 2010). The IPM and NLS models converged on similar results, with all Bayesian credible intervals overlapping mean estimates from single-state NLS models (Figures 3–5). Both models appeared to appropriately estimate smolt and recruit abundances (Figure 6).

Analysis of simulated datasets revealed that while the IPM was able to identify freshwater productivity ($\alpha_f$) accurately, estimates of marine productivity ($\alpha_m$) and marine density dependence ($\beta_m$) had low identifiability, as the majority of 95% credible intervals of the posteriors from the IPM did not overlap the values used to generate the data (Table 5). Neither reducing variability in generated data nor increasing years of data improved parameter identifiability. Large changes in parameters for simulated data did alter model estimates accordingly, though estimates approached, but did not reach, true values.

![Figure 3. Posterior density distributions for freshwater productivity ($\alpha_f$), marine productivity ($\alpha_m$), and density dependence ($\beta_m$) from the Bayesian multistage integrated population model (IPM) and single stage non-least squares model (NLS; 1000 bootstrapped samples) with medians (lines) and 95% credible intervals (blue shading), Skagit River system, Washington, USA, 1993–2014.](image-url)
Figure 4. Posterior density distributions for covariate coefficients predicting freshwater productivity including flood recurrence interval (flood RI), proportion of days with flows above a 1-year recurrence interval (prop. above 1-yr RI), mean flow during February–June (mean spring flow) and mean air temperature during January–April (mean spring air temp.) from the Bayesian multistage integrated population model (IPM) and single stage non-least squares models (NLS; 1000 bootstrapped samples) with medians (lines) and 95% credible intervals (blue shading), Skagit River system, Washington, USA, 1993–2014.
Figure 5. Posterior density distributions for covariate coefficients predicting marine productivity including North Pacific Gyre Oscillation (NPGO), Coastal Upwelling Transport Index (CUTI), Multivariate El Niño/Southern Oscillation index (MEI), mean annual sea surface temperature for the Northeast Pacific (sea surface temp.) from the Bayesian multistage integrated population model (IPM) and single stage non-least squares models (NLS; 1000 bootstrapped samples) with medians (lines) and 95% credible intervals (blue shading), Skagit River system, Washington, USA, 1993–2014.
Figure 6. Model-estimated abundance of recruitment and smolts from the Bayesian multistage integrated population model (IPM) and single stage non-least squares models (NLS; 1000 bootstrapped samples) with medians (lines), 95% credible intervals (blue shading), and observed data, Skagit River system, Washington, USA, 1993–2014.
Table 5. Parameters used to generate simulated datasets to test state-space model performance for freshwater (f) and marine (m) life stage transitions including number of years, life stage productivity (α), density dependence (β), and harvest rate (r_h). All simulations had an initial spawner abundance of 15,000±1,000 and were generated with normally distributed random error around the mean. All simulations had fixed age proportions (proportions age 2 = 0.1, 3 = 0.3, 4 = 0.5, 5 = 0.1, standard error = 0.01) and an age sample proportion of 0.05.

<table>
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<th>n</th>
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<th>α_m</th>
<th>β_m</th>
<th>r_h</th>
<th>α_f</th>
<th>α_m</th>
<th>β_m</th>
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</table>

^ Model 18 failed to converge (f > 1.1) under 1 million iterations
Discussion

Though the IPM appeared to estimate similar covariate coefficients and non-density dependent productivity to single-stage NLS models, the low effective sample size for marine density dependence poor predictability of parameters for simulated datasets revealed that the IPM had difficulty differentiating effects of productivity and density dependence (Kéry 2010; Morita et al. 2012), which is commonly referred to as parameter identifiability or redundancy (Chis et al. 2011).

Parameter identifiability describes the ability of the mathematical model to estimate parameter(s) with sufficient accuracy and precision given finite and noisy data, which is commonly overlooked in ecology (Chis et al. 2011). Lack of parameter identifiability for productivity and density dependence is common for many models of density-dependent populations (Quinn and Deriso 1999; Delean et al. 2013; Thorson et al. 2014). Though observation and process error are accounted for separately in IPMs, when observation error is unknown, models can give biased, imprecise, and ecologically unrealistic parameter estimates (Knape 2008; Hosack et al. 2012; Delean et al. 2013). Additionally, in cases where a population is kept at or below carrying capacity by harvest, extent of density dependence and therefore carrying capacity is difficult to identify due to lack of data at high densities (Delean et al. 2013; Thorson et al. 2014).

There are multiple potential solutions that may improve parameter identifiability in models. As parameter estimates for productivity and density dependence may be largely dependent on prior information, when priors are correctly implemented, parameter identifiability, and therefore precision and accuracy, can be improved (Delean et al. 2013). Previous knowledge on marine productivity and carrying capacity for the Skagit River System could be used to apply informative priors for those parameters, therefore potentially improving parameter identification (Delean et al. 2013; Lebreton and Gimenez 2013). However, if priors are incorrectly specified, the model may produce biased estimates with high certainty, leading to erroneous conclusions (Rivot et al. 2004; Delean et al. 2013).

Parameter estimates may improve if observation error and its variance are estimated correctly. Observation error may be estimated within or outside the model using additional data types (Knape 2008), or alternatively, described by a model that more accurately describes the error structure (e.g. through use of a normal inverse Gaussian distribution; Hosack et al. 2012). Our model parameterization for marine productivity included time-varying productivity by incorporating autoregressive process error (Fleischman et al. 2013; Scheuerell et al. 2021). Other approaches, such as incorporating a Gaussian process to approximate the population growth function, may better incorporate process error, leading to more accurate and precise estimates (Thorson et al. 2014).

Our work acts as an initial foray into state-space integrated population modeling in a life-cycle framework for Skagit River Chinook Salmon, and conclusions about population dynamics or their drivers must not be drawn from our results. Planned future development on this model includes incorporating the auto-correlated error structure to freshwater productivity estimates (Fleischman et al. 2013) and prior sensitivity analysis using simulated and collected data to determine the impact that prior selection has on parameter estimation and identifiability (Delean et al. 2013; Lebreton and Gimenez 2013; Thorson et al. 2014).
Further directions for this model may include incorporating multiple data types, such as direct spawn-ground surveys or capture-mark-recapture smolt data, which may increase parameter identifiability (Macedo et al. 2022), or adding estuary fry density as a third life stage in the model between smolt and adult recruitment (Maunder and Deriso 2011). We may also examine impacts of predictors on abundance rather than productivity (Hamilton and Murphy 2018) and consider including habitat covariates to determine impacts of restoration on specific life stages. We may also attempt to divide fry and parr migrant life stages within the model, as parr and fry migrants may exhibit different degrees of density dependence (Zimmerman et al. 2015).

The IPM estimates productivity directly from count data from multiple life stages in a single model, and therefore acts as a retrospective analysis tool. The IPM is similar to other models that incorporate multiple life stages (i.e. Zabel et al. 2006; Crozier et al. 2008), but those models did not incorporate separate measures of process and observation error, which may lead to less accurate parameter estimates (Dennis et al. 2006; Lindén and Knappe 2009). Other life cycle models such as the Habitat Assessment and Restoration Planning (HARP) model require inputs of survival, productivity, and fish densities from previous research and expert opinion (Beechie et al. 2021). These models are especially effective to compare impacts of future and past scenarios, such as changes in river temperature due to climate change or habitat gains through restoration actions (Jorgensen et al. 2021; Beechie et al. 2023). However, they are unable to directly estimate productivity and true population numbers from available data (Jorgensen et al. 2021). The combination of IMP and HARP approaches could aid in evaluating risks to populations and their demographic responses to natural and anthropogenic changes (Benton and Grant 1999; Gerber et al. 2003).

Through ongoing collaboration and development, we can strengthen modeling frameworks to obtain more precise estimates of population parameters and more accurately determine external drivers of populations. Integrated population models that apply a state-space approach across multiple life stages of a species’ have wide-ranging applications to help determine what abiotic and biotic factors most influence demographic processes, and therefore population dynamics.
Works Cited


Supplementary Table 1. Table of Pearson product-moment correlation coefficients for predictors in the marine life stage model including mean annual indices for the North Pacific Gyre Oscillation (NPGO), Pacific Decadal Oscillation (PDO), Biologically Effective and Coastal Upwelling Transport Indices (BEUTI and CUTI respectively), Multivariate El Niño and Southern Oscillation Index (MEI), Oceanic Niño Index (ONI), mean Skagit delta temperature during February‒August (Delta T), and mean annual Washington state (WASST) and coastal Pacific coast sea surface temperatures (SST). Color scale denotates low correlation (green) to high correlation (red). Covariates correlated > 0.7 were not used in the same model.

<table>
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<th>BEUTI</th>
<th>CUTI</th>
<th>MEI</th>
<th>ONI</th>
<th>Delta T</th>
<th>WASST</th>
<th>SST</th>
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Supplementary Table B. Table of Pearson product-moment correlation coefficients for predictors in the freshwater life stage model including annual peak discharge during August‒February (PeakFlow), proportion of days with maximum flow above a 1-year recurrence interval (propRI1), estimated recurrence interval for annual peak flow (floodRI), mean flow during February‒June, and mean air temperatures during January‒April (airTJanApr) and annually (airTann). Color scale denotates low correlation (green) to high correlation (red). Covariates correlated > 0.7 were not used in the same model.

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