
The Interplay between Climate Variability and Density Dependence in the Population Viability of Chinook Salmon

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Abstract: *The viability of populations is influenced by driving forces such as density dependence and climate variability, but most population viability analyses (PVAs) ignore these factors because of data limitations. Additionally, simplified PVAs produce limited measures of population viability such as annual population growth rate (λ) or extinction risk. Here we developed a “mechanistic” PVA of threatened Chinook salmon (*Oncorhynchus tshawytscha*) in which, based on 40 years of detailed data, we related freshwater recruitment of juveniles to density of spawners, and third-year survival in the ocean to monthly indices of broad-scale ocean and climate conditions. Including climate variability in the model produced important effects: estimated population viability was very sensitive to assumptions of future climate conditions and the autocorrelation contained in the climate signal increased mean population abundance while increasing probability of quasi extinction. Because of the presence of density dependence in the model, however, we could not distinguish among alternative climate scenarios through mean λ values, emphasizing the importance of considering multiple measures to elucidate population viability. Our sensitivity analyses demonstrated that the importance of particular parameters varied across models and depended on which viability measure was the response variable. The density-dependent parameter associated with freshwater recruitment was consistently the most important, regardless of viability measure, suggesting that increasing juvenile carrying capacity is important for recovery.*

Key Words: endangered species, *Oncorhynchus tshawytscha*, population viability analysis

La Interacción entre Variabilidad Climática y Denso Dependencia en la Viabilidad Poblacional de *Oncorhynchus tshawytscha*

Resumen: *La viabilidad de poblaciones esta influida por fuerzas conductoras como la denso dependencia y la variabilidad climática, pero la mayoría de los análisis de viabilidad poblacional (AVP) ignoran estos factores debido a limitaciones en la disponibilidad de datos. Adicionalmente, los AVP simplificados producen medidas limitadas de la viabilidad poblacional tales como la tasa anual de crecimiento poblacional (λ) o el riesgo de extinción. Aquí desarrollamos un AVP “mecanicista” de *Oncorhynchus tshawytscha* en el que, con base en datos detallados de 40 años, relacionamos el reclutamiento de juveniles en agua dulce con la densidad de reproductores, y la supervivencia en el océano al tercer año con índices mensuales de condiciones oceánicas y climáticas a amplia escala. La inclusión de la variabilidad climática en el modelo produjo efectos importantes: la viabilidad poblacional estimada fue muy sensible a las suposiciones de condiciones climáticas futuras y la autocorrelación contenida en la señal climática aumentó la abundancia poblacional promedio al mismo tiempo que incrementó la probabilidad de cuasi extinción. Sin embargo, debido a la presencia de denso densidad en el modelo no pudimos distinguir entre escenarios climáticos alternativos a través de los valores promedio de λ , lo que enfatiza la importancia de considerar medidas múltiples para dilucidar la viabilidad poblacional. Nuestros análisis de sensibilidad demostraron que la importancia de parámetros particulares varió en los modelos y dependió de la medida de viabilidad utilizada como variable de respuesta. El parámetro*

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de denso dependencia asociada con el reclutamiento en agua dulce consistentemente fue el más importante, independientemente de la medida de viabilidad, lo que sugiere que el incremento en la capacidad de carga de juveniles es importante para la recuperación.

Palabras Clave: análisis de viabilidad poblacional, especies en peligro, *Oncorhynchus tshawytscha*

Introduction

The viability of a population is governed by the interplay of driving forces, some intrinsic, such as density-dependent population regulation, and some extrinsic, such as environmental variability. Capturing these forces is essential for developing a “mechanistic” population viability analysis (PVA) model. Because populations and climate fluctuate, these forces are highly variable (Boyce 1992; Lande 2002), and because the forces typically apply to specific life stages (Stenseth et al. 2002), realistically modeling these important factors and their variability requires life-stage-specific data covering extended time periods (Beissinger & Westphal 1998; White et al. 2002). Most at-risk populations, however, are characterized by a paucity of data (Beissinger 2002; Morris et al. 2002), leading to a rarity of mechanistic PVA models (Ellner 2003). This is unfortunate because mechanistic PVAs offer several advantages over more simplified ones: they provide multiple viability measures in contrast to the limited outputs of deterministic demographic PVAs (Caswell 2001) or simple count-based PVAs (Dennis et al. 1991), and properly constructed and supported by strong data they produce more realistic representations of population dynamics and consequently more reliable viability measures (Coulson et al. 2001; Ellner 2003).

To demonstrate the advantages of mechanistic PVA models, we developed one for Snake River spring and summer Chinook salmon (*Oncorhynchus tshawytscha*), a federally listed evolutionarily significant unit (ESU) that has been monitored for more than 40 years. This migratory species spends significant portions of its life in both freshwater and saltwater habitats and thus is exposed to several distinct driving forces. We identified factors associated with life-stage-specific demographic rates that were important to the overall population dynamics and then incorporated them into a stochastic life-cycle model to conduct our PVA.

We identified the major freshwater driving force as density-dependent recruitment of juveniles during the spawning and rearing phase, a widespread phenomenon in stream-spawning salmonids. It is thought to occur through competition among females for spawning sites and after juveniles emerge from the spawning gravel (Milner et al. 2003). Therefore, we developed a nonlinear, density-dependent model relating the production of juveniles to the number of spawning adults.

We identified the major saltwater driving force as the relationship between survival during the first year in salt-

water and oceanic and climatic conditions. The population dynamics of a range of species, marine and terrestrial, are influenced by broad-scale climatic patterns such as the North Atlantic Oscillation (NAO) or the El Niño/Southern Oscillation (ENSO), which strongly influence temperature, precipitation, sea-level pressure, and major ocean currents (McGowan et al. 1998; Stenseth et al. 2002). There is a strong relationship between productivity of Pacific salmon and ocean and climate conditions of the northeastern Pacific (Beamish & Bouillon 1993; Mantua et al. 1997). The conditions appear to particularly affect survival during the critical first year at sea (Pearcy 1992). Previous modeling exercises recognized the estuary and ocean habitats as important, yet unexplained, sources of variation in survival of Snake River spring and summer Chinook salmon (Kareiva et al. 2000; Wilson 2003). Thus, we related early ocean survival to monthly indices of the Pacific Decadal Oscillation (PDO, Mantua et al. 1997), which has a 100-year historical record.

We believe that understanding the interplay between climate and density dependence is crucial for management of Snake River Chinook salmon, but previous PVAs of this economically and culturally important species (Kareiva et al. 2000; Ellner & Fieberg 2003; McClure et al. 2003; Wilson 2003) largely ignored these forces. Thus, we addressed the question, What do we gain by adding complexity to a PVA model? To answer this, we developed alternative models to examine the effects of assumptions of climate and density dependence on a suite of viability measures. Additionally, through a sensitivity analysis, we assessed the relative importance of each parameter to population viability. We present not only our modeling analyses and results but also a discussion of the usefulness of mechanistic PVAs for prioritizing management mitigation actions.

Life History of the Snake River Spring and Summer Chinook Salmon

The life history of a species forms the foundation of its life-cycle model, so we briefly present the life history of the Snake River spring-summer Chinook salmon, which has 31 defined extant populations (Interior Columbia Technical Recovery Team 2003). Its main life-history attributes are anadromy (juveniles migrate from freshwater to saltwater and adults return to freshwater) and semelparity. Adults return to spawning areas in Idaho and Oregon (Fig. 1) in the spring and summer (hence the designation) as 3- to 6-year-olds. Spawning occurs in the fall and fertilized

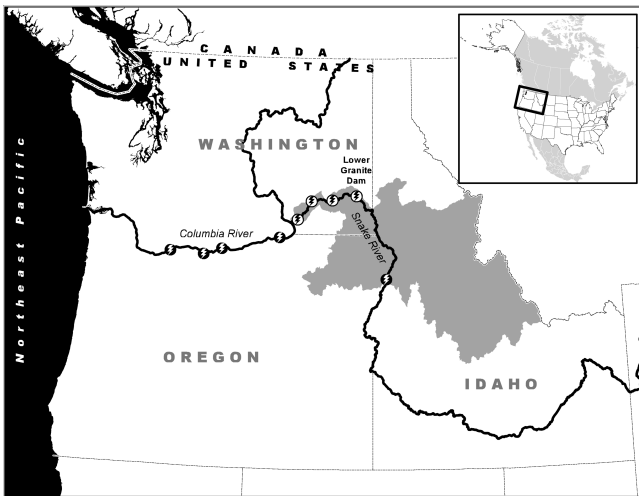


Figure 1. Northwestern United States highlighting the Snake River basin (shaded area) and hydroelectric dams (lightning bolt symbol) along the lower Snake and lower Columbia rivers.

eggs overwinter before fry emerge in early spring. During their second year smolts migrate as far as 1500 km to the Pacific Ocean, where the majority of growth occurs. This migratory life history has facilitated the collection of long-term data at several life-history stages because individuals are enumerated during the outmigration of juveniles and during the return migration of adults to freshwater.

This salmon ESU has experienced a long-term decline in abundance since at least the 1870s, with heavy fishing pressures apparently initiating the decline (Lichatowich 1999). Ongoing habitat alteration due to agriculture, grazing, mining, logging, and other human activities has reduced the quantity and quality of available freshwater habitat (National Research Council 1996). The mainstem Columbia and Snake rivers have been dramatically altered with the construction of hydroelectric dams (National Research Council 1996) that affect fish during both downstream and upstream migration. To mitigate for impacts of dams, a large proportion of juveniles are collected at the uppermost dam and transported in barges through the hydrosystem.

Methods

Estimating Counts of Adults and 2-Year-Olds (Smolts) at the Uppermost Dam

The primary data are estimates of wild smolt and adult abundances as they pass the uppermost dam on the Snake River. Estimates from 1964–1999 are from Petrosky et al. (2001), with recent estimates from Williams et al. (2005). Smolt counts are not available for 1985–1991, so we removed these years from the juvenile recruitment analysis.

The adult counts were divided into age classes (3-, 4-, and 5-year-olds, with the few 6-year-olds included with the 5-year-olds). Adult counts were adjusted yearly for harvest that occurred above the uppermost dam (obtained from Petrosky et al. 2001).

Estimating the Abundance of 1-Year-Olds

The period between adult entry to freshwater and smolt departure covers 2 years. Because the life-cycle model is based on yearly time steps, we partitioned the adult-to-smolt life stage into yearly increments. We partitioned the density dependence and stochasticity into the fertility term, which is the number of 1-year-olds (parr) produced per spawner. The remaining freshwater survival was assumed to be density independent and deterministic. This preserved the overall relationship (and associated variability) between smolts and spawners. Because we lacked reliable estimates of the number of parr, we used counts of smolts at the uppermost dam divided by mean parr-to-smolt survival (Levin et al. 2002) to estimate the number of parr.

Estimating Third-Year Survival

Estimates of third-year survival, $s_3(t)$, were based on smolt counts at year t and age-specific adult counts at years $t+1$, $t+2$, and $t+3$ at the uppermost dam. We note that $s_3(t) = n_3(t+1)/n_2(t)$, where $n_i(t)$ is the number of individuals of age i at time t . The $n_2(t)$ term is derived from the number of smolts as follows:

$$n_2(t) = s_d(t) \cdot \text{smolts}(t) \text{ and} \quad (1)$$

$$s_d(t) = p_T(t) \cdot s_T + (1 - p_T(t)) \cdot s_I(t), \quad (2)$$

where $s_d(t)$ is survival of downstream migrants through the hydrosystem, $p_T(t)$ is the portion of fish arriving at the uppermost dam that were transported (Marmorek et al. 1998; Williams et al. 2005), s_T is the survival of transported fish, and $s_I(t)$ is the survival of in-river migrants (based on Williams et al. 2001, 2005). Downstream survival estimates were lacking for 1981–1992, so we interpolated between the earlier period and the later period. The s_T parameter includes “delayed differential mortality” of transported fish (from Williams et al. 2005), accounting for the fact that transported fish return at lower rates than fish that migrated volitionally. Although this delayed mortality is most likely expressed during the early ocean life stage, we applied it to the downstream migration stage because it was more tractable and is mathematically equivalent. As mentioned above, smolt counts were lacking during 1985–1991. We estimated smolt abundances in these years based on the juvenile productivity relationship (described below) and the estimate of parr-to-smolt survival.

We back-calculated $n_3(t+1)$ from the number of adults returning as 3-year-olds in $t+1$ (designated $n_{A3}[t+1]$),

the number of 4-year-olds returning in $t + 2$ (designated $n_{A4}[t + 2]$), and the number of 5-year-olds returning in $t + 3$ (designated $n_{A5}[t + 3]$). These counts were then adjusted to account for mortality occurring during upstream migration (s_u , from Kareiva et al. [2000]), harvest rate in the river ($b_r[t]$) (from Petrosky et al. [2001] and Williams et al. [2005]), and ocean survival (s_o). In this manner, we estimated $n_3(t + 1)$ as

$$n_3(t + 1) = \frac{1}{s_u} \cdot \left[\frac{n_{A3}(t + 1)}{1 - b_r(t + 1)} + \frac{n_{A4}(t + 2)}{s_o \cdot [1 - b_r(t + 2)]} + \frac{n_{A5}(t + 3)}{s_o^2 \cdot [1 - b_r(t + 3)]} \right] \quad (3)$$

We assumed that $s_o = 0.8$ (Ricker 1976; Kareiva et al. 2000) and applied it according to the number of years spent in the ocean. This assumption may be unrealistic, but the overall smolt-to-adult survival rate is consistent with the data.

Density-Dependent Juvenile Recruitment

The juvenile recruitment phase is the rate of production of 1-year-olds from spawners (fertility). As mentioned above, adults return as 3-, 4-, and 5-year-olds. The model is not based explicitly on females because we did not have sex proportions of the adults, but we did not treat 3-year-olds as spawners because they were almost exclusively males that behave as “sneaker” spawners. Also, because older fish are more fecund, we converted adult counts to “effective” spawners at time t (spawners[t]) by multiplying the number of 5-year-old fish by 1.26 to account for their approximate 26% increase in fecundity compared with 4-year-olds (Kareiva et al. 2000).

We fitted several models of density-dependent recruitment to the spawner and juvenile recruit data: the Ricker (1954) model, the Beverton-Holt model (Beverton & Holt 1957), the hockey-stick and quadratic-hockey-stick models (Barrowman & Myers 2000), and a linear model (no density dependence). We removed one point from the analysis, corresponding to smolt migration in 1999, because it was a highly influential outlier. The Akaike Information Criterion (AIC) values for the alternative models were 431.2 (no density dependence), 416.0 (hockey stick), 418.0 (quadratic hockey stick), 406.0 (Ricker), and 402.4 (Beverton-Holt). Based on minimum AIC value, we chose the Beverton-Holt relationship to relate the number of 1-year-olds at time $t + 1$ ($n_1[t + 1]$) per spawner as a function of spawners:

$$\frac{n_1(t + 1)}{\text{spawners}(t)} = \frac{a}{1 + b \cdot \text{spawners}(t)}, \quad (4)$$

where the parameter a is juveniles per spawner at the origin, b is the density-dependent parameter, and a/b is the carrying capacity of the system. In analyses where we assumed no density dependence, we used a linear model, $n_1(t + 1)/\text{spawners}(t) = a$.

The goal of this analysis was to produce a submodel that we could then incorporate into a stochastic model. Thus, in addition to estimating the functional form of the model, we also modeled the error. We used transformations such that the resulting errors were independently and identically distributed as normal deviates. In the case of Eq. 4, the residuals were clearly not normally distributed and the variance decreased as effective spawners increased. The standard log-normal transformation did not rectify the problem, so we used a Box-Cox transformation (Box & Cox 1964; Seber & Wild 1989), which is equivalent to a weighted least-squares approach for nonlinear regressions. Based on a nonlinear regression with x the independent variable, y the dependent variable, f the nonlinear function, and θ the model parameters, the goal of this approach is to choose a parameter ϕ such that the residuals, ε_t , of the nonlinear regression equation,

$$y_t = f(x_t|\theta) + \varepsilon_t, \quad (5)$$

are distributed independently as $N(0, \sigma_1^2 \cdot f(x_t|\theta)^\phi)$. The model parameters and transformation parameter are estimated simultaneously (Seber & Wild 1989). Thus, in addition to estimating the Beverton-Holt parameters, we also estimated the parameters σ_1^2 and ϕ . We did not use the Box-Cox transformation in the linear, density-independent model.

Relationship between Third-Year Survival and Ocean Conditions

We related estuary and early ocean survival (third-year survival, $s_3[t]$) over the period 1966–2002 to monthly indices of the PDO (Mantua et al. 1997). This index measures broad-scale patterns of oceanic climate conditions. We used a logistic transformation of $s_3(t)$, which resulted in normally distributed residuals and ensured that the resulting (back-transformed) survival estimates were bounded on the range 0.0 to 1.0. Thus, our multiple regression between $s_3(t)$ and monthly PDO indices was

$$\ln \left[\frac{s_3(t)}{1 - s_3(t)} \right] = \beta_0 + \beta_{\text{APR}} \cdot \text{PDO}_{\text{APR}}(t) + \dots + \beta_{\text{MAR}} \cdot \text{PDO}_{\text{MAR}}(t + 1) + \varepsilon_t, \quad (6)$$

where t is the year of ocean entry, the β s are regression coefficients, $\text{PDO}_{\text{month}}(t)$ is the PDO index in the given month (e.g., April, APR) in year t , and ε_t is the error term distributed as $N(0, \sigma^2_3)$. In the full model, we included the 12 months of PDO values beginning with April, the month when fish first enter the estuary. Using multiple regression methods, we eliminated terms, one at a time, that were not significant ($\alpha = 0.05$). We always eliminated the term with the highest p value and then ran the regression again with the remaining terms until all terms in the regression model were significant. To apply these results predictively to the life-cycle model, we used the

monthly PDO indices for 1900–2002. We generated variability about the predicted survival based on Eq. 20.34 from Zar (1984), which is the standard error about predicted response values from a multiple regression that takes into account covariance among the independent variables. We also considered a case where $s_3(t)$ was variable across time but not related to the PDO. In this case, we used Eq. 6 with all the PDO terms removed.

Structure of the Stochastic Life-Cycle Model

The stochastic life-cycle model is expressed as

$$\mathbf{n}(t+1) = \mathbf{A}(t) \cdot \mathbf{n}(t), \quad (7)$$

where the vector $\mathbf{n}(t)$ represents the number of individuals at the end of time step t by age (referenced to date of fertilization), and $\mathbf{A}(t)$ is a five \times five population projection matrix (Caswell 2001) that varies at each time step. Based on the life history of Snake River spring and summer Chinook salmon, the matrix $\mathbf{A}(t)$ takes on the form

$$\mathbf{A}(t) = \begin{bmatrix} 0 & 0 & 0 & b_4 \cdot s_u \cdot F_4(t) & s_u \cdot F_5(t) \\ s_2 & 0 & 0 & 0 & 0 \\ 0 & s_3(t) & 0 & 0 & 0 \\ 0 & 0 & (1 - b_3) \cdot s_o & 0 & 0 \\ 0 & 0 & 0 & (1 - b_4) \cdot s_o & 0 \end{bmatrix}. \quad (8)$$

Each element of the matrix, a_{ij} , represents the transition of i -year-olds (columns) to j -year-olds (rows) during a yearly time step. In the simplest case this is just a survival rate, such as s_2 , which is survival of 1-year-old fish through to the second year. The s_o parameter is the ocean survival rate for 3-year-olds and 4-year-olds, and b_3 and b_4 are the propensity for adults to breed as 3- and 4-year-olds, respectively. Thus, for example, a proportion b_4 of the 4-year-olds spawn and then die, whereas $(1 - b_4)$ of the individuals remain in the ocean. The s_u parameter is the survival rate during upstream migration in the Columbia and Snake rivers. Elements that vary from year to year are designated as functions of t , such as $s_3(t)$, survival through the third year. The $F_4(t)$ and $F_5(t)$ terms are the fertilities of 4-year-olds and 5-year-olds, respectively. Fertility represents both fecundity and survival through the first year. The vital rates $s_3(t)$, $F_4(t)$, and $F_5(t)$ are submodels detailed above.

To complete the life-cycle model and apply it prospectively, we estimated several additional parameters that reflect current conditions (Table 1). For the survival of in-stream migrants (s_I) and transported fish (s_T), we used the mean of the past 5 years (obtained from Williams et al. 2005). We applied the proportion transported (p_T) used by Kareiva et al. (2000). We estimated mean propensity to breed by age based on an iterative approach similar to that presented in Eq. 3. Harvest in the river (H_r) was set to the mean of the last 5 years (Petrosky et al. 2001; Williams et al. 2005).

The stochasticity in the model is applied to specific life stages but is derived from variability in the adult-to-smolt (two-year-old) life stage and in the smolt-to-adult life stage. Because these life stages encompass the entire life cycle and because we made an effort to preserve the overall variability associated with these life stages, we believe the stochasticity in the model reflects the overall stochasticity of the population. Further, the survival rates in these two life stages were not significantly ($\alpha = 0.05$) correlated at any time lag, alleviating concerns that covariance between life stages could influence the overall variance in population abundance.

Population Viability Analysis

Once we estimated all the parameters for the stochastic life-cycle model, we simulated population trajectories. We began each simulation with 27,000 spawners, reflecting the most recently enumerated return year (2003). To populate the remaining age classes, we applied deterministic survival rates to the spawner numbers to back calculate abundances in the younger age classes, reflecting the long-term, stable age-class distribution. Each simulation began in 1900, the first year of available PDO data. Although we used historical climate data, we used current habitat conditions; thus, we considered our simulations as future population trajectories. We ran each simulation with $s_3(t)$, based on Eq. 6, for 103 yearly time steps to PDO year 2002, and parr-per-spawner numbers were obtained by applying the Beverton-Holt equation (Eq. 4) to the number of spawners.

Based on these 103-year population trajectories, we calculated four population performance measures. First, we recorded the mean number of spawners returning to Lower Granite Dam. Second, we calculated the first-order autocorrelation coefficient, ρ_1 (Chatfield 1989), from the adult recruits-per-spawner (R_t/S_t) time series. Adult recruits were defined as returning spawners from a given cohort (referenced to year of birth), and this provided a measure of lifetime survival by brood year. Third, we calculated a “running λ ” ($\lambda[t]$), which, for a given simulation year, was λ (mean annual population growth rate) calculated over the previous 20 years of the simulation:

$$\lambda(t) = \frac{1}{20} \sum_{i=t-19}^t \ln(\text{spawners}_t / \text{spawners}_{t-1}). \quad (9)$$

The initial $\lambda(t)$ began at year 20 of the simulation because we needed 20 previous years to calculate it. To assess population growth through the entire time period, we took the mean of $\lambda(t)$ across all time steps. Because the viability measures described above varied among simulations, we conducted 1000 simulations and took their means across simulations. The fourth population performance measure was the probability of falling below a threshold level of spawners, or probability of “quasi extinction.” We chose a threshold level of 3100, which is

Table 1. Model parameter values and their ranges for the stochastic life-cycle model of Chinook salmon.

Parameter	Value	Range	Description
Freshwater productivity			
<i>A</i>	887.6	693.4, 1081.8	Beverton-Holt parameters, fit to smolt and spawner data
<i>B</i>	4.62×10^{-5}	1.52×10^{-5} , 7.72×10^{-5}	
σ^2_1	2.07×10^{-2}	1.36×10^{-2} , 3.87×10^{-2}	density-independent parameters
ϕ	2.2		
<i>A</i>	485.7	396.1, 575.4	
σ^2_1	62,290	39,780, 111,300	
s_{p-s}	0.186	0.129, 0.208	
Downstream migration			
<i>s_I</i>	0.486	0.279, 0.578	downstream in-river survival (mean last 5 years) ^b
<i>s_T</i>	0.553	0.336, 0.683	survival of transported fish, included delayed effects ^b
<i>p_T</i>	0.729	0.704, 0.990	proportion of fish transported ^{b,c}
Estuary/early ocean			
β_0	-2.626	-2.794, -2.419	parameters used to derive third-year ocean survival from monthly PDO indices
β_{APR}	0.784	0.376, 1.190	variance associated with third-year survival no climate parameters
β_{MAY}	-1.773	-2.256, -1.904	
β_{JUN}	0.526	0.209, 0.825	
σ^2_3	0.257	0.173, 0.492	
β_0	-2.97	-3.267, -2.627	
σ^2_3	0.910	0.585, 1.534	
Ocean			
<i>s_o</i>	0.8	0.7, 0.9	ocean survival ^{c,d,e}
<i>b₃</i>	0.0345	0.0024, 0.087	propensity to breed as 3- and 4-year-olds, respectively; based on age composition data and ocean and upstream migration survival
<i>b₄</i>	0.4592	0.205, 0.842	
Adult migration			
<i>s_u</i>	0.794	0.78, 0.82	upstream migration survival ^{b,c}
<i>H_r</i>	0.07	0.03, 0.12	in-river harvest (mean last 5 years) ^{b,f}

^aLevin et al. (2002).

^bWilliams et al. (2005).

^cKareiva et al. (2000).

^dRicker (1976).

^ePacific Salmon Commission Joint Chinook Salmon Technical Committee (2002).

^fPetrosky et al. (2001).

100 spawners per population, well below the level considered detrimental for salmon populations (Wainwright & Waples 1998). We estimated this probability of quasi extinction by running 10,000 simulations and determining the proportion of simulations where the number of spawners fell below the threshold at some point during the 103-year period.

We also examined the effects of different climate and density-dependence assumptions. Because future climate conditions may not resemble those from the previous century ("historical" climate scenario), we created two alternative climate scenarios: a "bad" scenario in which future climate resembles the worst recently encountered period, 1977-1998, and a "recent" scenario in which future climate resembles the period 1964-2002, over which the smolt and adult data were collected. In both cases, we repeated the time series to generate 103 years of data, consistent with the above simulations. In addition, we ran

simulations in which we assumed no density-dependent effects, no climate effects, or neither.

Sensitivity Analysis

We conducted a sensitivity analysis to determine which model parameters, when varied, produced the greatest change in probability of quasi extinction or mean abundance. We modified the approach originally proposed by McCarthy et al. (1995), in which all parameters are varied randomly and simultaneously across specified ranges. The range of each parameter was based on its observed range, and typically greater ranges lead to greater sensitivity of the parameter. In each simulation every parameter is randomly sampled from a uniform distribution across its range. Following Cross and Beissinger (2001), for each set of randomly generated model parameters we ran the model 10 times. We generated 1000 such parameter sets

and in doing so created a data set with sample size of 10,000, in which the independent variables were the parameter values and the dependent variable was either mean population abundance or a binary variable indicating whether or not the population fell below the quasi extinction level.

For each response variable, we ran the analyses for the recent climate scenario, the density-independent model (with recent climate), and the no climate model. We then conducted regression analyses on these generated data sets (standard regression with normal error structure when the response variable was mean abundance and logistic regression when the response variable was quasi extinction), and the relative importance of each parameter was defined by its standardized regression coefficient (coefficient divided by its standard error, Cross & Beissinger 2001). The absolute value of the standardized regression coefficient determined the importance of the parameter and the sign determined the direction of the response in the response variable. Because standardized regression coefficients are not comparable across model constructs (Cross & Beissinger 2001), we further standardized them for ease of interpretation by dividing by the largest absolute value of all the standardized regression coefficients in each sensitivity analysis. Thus the most important parameter had an absolute value of 1.0, and all the rest were ≤ 1.0 .

We used several criteria to set the ranges of the parameters. For parameters that were estimated in the two submodels (a , b , σ_1 , β_0 , β_{APR} , β_{MAY} , β_{JUN} , σ_1), we set their ranges to the 95% CIs for the parameter estimates. Thus the range reflects the uncertainty in the parameter estimate. We varied only σ_1 of the Box-Cox transformation because this had the effect of linearly increasing variance in the density-dependent, fertility relationship. For all other parameters except s_o , we set the range based on the lowest and highest value of the parameter over the estimation time period. For s_o , we used the range of values adopted by the Pacific Salmon Commission Joint Chinook Salmon Technical Committee (2002) for age 3 and older Chinook salmon.

This type of sensitivity analysis is well suited for stochastic PVAs such as this one for several reasons (Cross & Beissinger 2001). First, because all parameters are varied simultaneously, important covariance relationships among parameters are maintained. Second, because parameters are varied across realistic ranges, the sensitivities represent realistic opportunities for viability improvements after mitigation actions (Reed et al. 2002). Finally, the approach easily accommodates nonlinear relationships such as those in density-dependent relationships (Cross & Beissinger 2001).

Results

We found strong evidence for density-dependent recruitment ($R^2 = 0.623$, Fig. 2; parameters listed in Table 1).

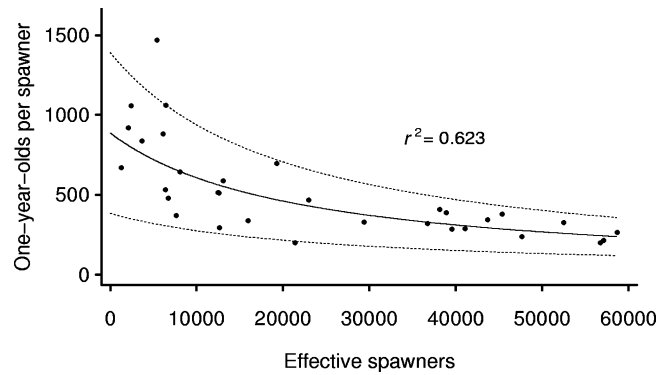


Figure 2. Relationship between 1-year-olds (juvenile recruits) per effective spawner (defined in text) versus effective spawners for Snake River spring and summer Chinook salmon. Solid line is the best-fit Beverton-Holt curve (see text).

Based on the Beverton-Holt model parameters, estimated carrying capacity for the entire ESU was approximately 19.2 million 1-year-olds (parr). The Box-Cox transformation resulted in homogeneous residuals (based on a lack of relationship between variance of residuals and spawners), normally distributed (based on visual inspection of the normal probability plot) and lacking any significant autocorrelation at any time lag. This transformation also decreased the AIC from 402.2 to 390.4. Residuals from the linear model exhibited serial correlation because of the positive-tending residuals associated with small numbers of spawners.

We also demonstrated a strong relationship between third-year survival and ocean conditions ($R^2 = 0.742$, Fig. 3a; coefficients listed in Table 1). Significant terms were related to April, May, and June, the first 3 months of salt-water residence. Although the time series of third-year survival exhibited significant autocorrelation ($p < 0.001$), the residuals did not ($p > 0.05$). Based on these results, we predicted third-year survival and 95% CIs over the period 1900–2002 (Fig. 3b).

Simulations

The simulated time series of spawners, recruits per spawner, and $\lambda(t)$ all varied considerably over time as demonstrated by the example simulation (Fig. 4). The relatively large values of recruits per spawner (Fig. 4b) occurred at combinations of low density and favorable ocean conditions. Although $\lambda(t)$ was quite variable, it generally hovered about the $\lambda(t) = 1.0$ line (Fig. 4c).

Climate conditions were clearly important, producing strong variability within the time series of abundance and strong effects when population performance measures were compared among scenarios (Fig. 5). For instance, mean population abundance was three times higher for the historical versus bad climate scenarios, and the probability of falling below the threshold of 3100 spawners increased from 0.309 to 0.880. The comparison between

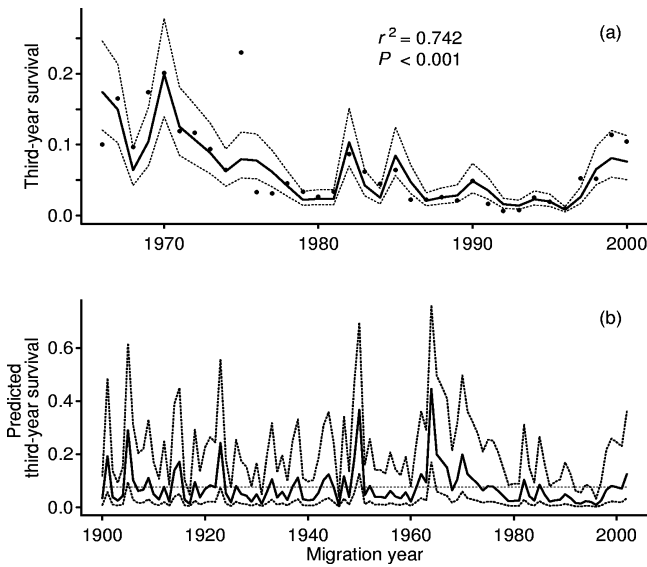


Figure 3. (a) Predicted (solid line) and observed (points) third-year survival, $s_3(t)$, for Snake River spring and summer Chinook salmon. Dashed line is 95% CI about the predicted relationship. (b) Modeled third-year survival based on the 103-year PDO record. Solid line is the deterministic estimate of third-year survival, and dashed lines are the 95% CI from which the modeled values were drawn.

the recent-climate scenario and the no-climate scenario based on the same time period demonstrated more important effects of including climate in the PVA. First, the variance associated with third-year survival (σ_3 , Table 1) was much larger under the no-climate scenario because all the variability attributed to climate in the climate-based model was subsumed in this variance term. Also, considerably more autocorrelation in recruits per spawner was associated with the recent-climate scenario compared with the no-climate scenario (Fig. 5). This autocorrelation led to a greater probability of experiencing several good years in a row and the associated exponential-like population growth. Consequently, the recent scenario had a greater mean abundance of spawners than the no-climate scenario (Fig. 5). The autocorrelation also led to a greater probability of experiencing several poor years in a row and a resulting increase in probability of quasi extinction (Fig. 5).

Density dependence was also clearly an important factor in determining population dynamics. When density dependence was removed, the model produced unrealistically high mean abundances (Fig. 5). Clearly, density dependence, as modeled, strongly regulated population abundance. When both density dependence and climate effects were removed, the model behaved like a random walk model and the autocorrelation in the recruits per spawner was close to 0.0.

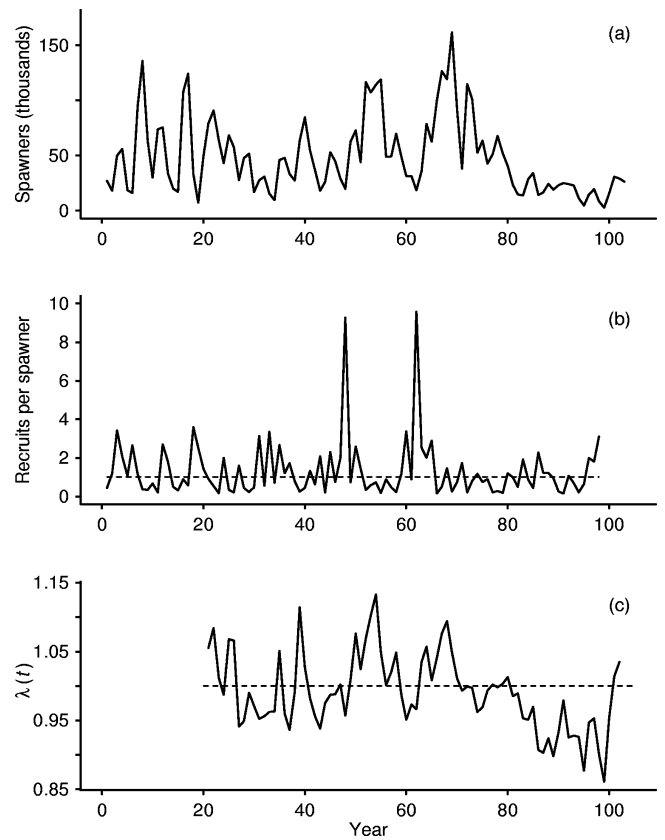


Figure 4. Examples of time-varying output of Chinook salmon from single simulations representing the "historical" scenario: (a) spawners by year, (b) adult recruits per spawner by year (dashed line is recruits per spawner = 1.0), and (c) running λ , $\lambda(t)$, by year (dashed line is $\lambda[t] = 1.0$).

Sensitivity Analyses

The sensitivity analyses demonstrated that the importance of some parameters varied considerably depending on the response variable (Table 2). The parameters associated with third-year survival under the full model exhibited this pattern. When the response variable was probability of extinction, the three parameters of the monthly PDO indices (β_{APR} , β_{MAY} , and β_{JUN}) were three of the four most important parameters. When the response variable was mean abundance, however, these parameters were among the least important.

The importance of some parameters varied substantially depending on the model (Table 2). The same third-year survival parameters mentioned above displayed this pattern when the response variable was probability of quasi extinction. Under the full model, the parameters were relatively important, but under the density-independent model, these parameters were far less important.

The parameters associated with freshwater productivity (a , b , and s_{p-s}) were always among the more important



Figure 5. Output from the stochastic life-cycle model of Chinook salmon based on various assumptions on the inclusion of density dependence (DD) and climate scenarios. The probability of quasi extinction is the probability of falling below 3100 spawners.

variables, but their relative importance did vary across response parameters and models (Table 2). The first-year, density-dependent parameter, *b*, was always among the top two most important parameters. The relative importance of this parameter when probability of extinction was the response variable suggests that increasing abundance during good periods can provide a buffer against extinction during poor periods. Under the full model, the first-year, density-independent parameter, *a*, was substantially less important, regardless of response variable.

The importance of the hydrosystem-related parameters varied across parameters (Table 2). Transportation survival, *p_T*, was always an important parameter, ranking among the top four most important parameter in all cases. The other parameters (*s_I*, *p_T*, and *s_U*) were generally unimportant. The in-river harvest parameter, *H_r*, was generally unimportant, reflecting the low levels of harvest of the past 5 years. If harvest were increased beyond this range, the importance of this parameter would surely increase.

Discussion

We demonstrated that when it is possible to relate variability in key demographic rates to important factors, intrinsic or extrinsic to a population, PVAs are more realistic and can provide a diverse assemblage of viability measures. Because each viability measure provides unique information, using a variety of measures provides a deeper understanding of population dynamics, which in turn will potentially allow for more efficient management of at-risk populations. We demonstrated the importance of considering several viability measures with our results for the four alternative climate scenarios. Across these scenarios, mean spawner abundances and quasi-extinction probabilities were highly variable, but in all four cases mean *λ* was close to 1.0. Although *λ* can provide important information over short time periods, such as whether a population is in imminent danger of extinction, it provides limited information on longer time scales, especially when density dependence is an important factor.

Table 2. Standardized coefficients from the sensitivity analysis of the stochastic population viability analysis for Chinook salmon.^a

Model parameter ^b	Quasi-extinction probability			Mean abundance		
	full model	no DD	no climate	full model	no DD	no climate
<i>a</i>	0.552	1.000	0.820	0.425	0.674	0.466
<i>b</i>	-0.791	NA ^b	-0.998	-1.000	NA ^b	-1.000
<i>σ</i> ₁	-0.045	-0.627	-0.006	0.022	-0.010	-0.026
<i>s_{p-s}</i>	0.613	0.776	0.863	0.497	0.937	0.534
<i>s_I</i>	0.132	0.214	0.192	0.135	0.102	0.111
<i>s_T</i>	0.734	0.987	0.988	0.623	1.000	0.662
<i>p_T</i>	0.113	-0.004	0.062	0.068	0.287	0.023
<i>β</i> ₀	0.487	0.593	1.000	0.315	0.175	0.608
<i>β</i> _{APR}	0.749	0.278	NA	0.056	0.365	NA
<i>β</i> _{MAY}	1.000	0.427	NA	-0.046	0.356	NA
<i>β</i> _{JUN}	0.604	0.153	NA	-0.038	-0.228	NA
<i>σ</i> ₃	-0.270	-0.002	-0.676	0.101	0.303	0.209
<i>s_o</i>	0.495	0.664	0.713	0.386	0.068	0.400
<i>b</i> ₃	-0.143	-0.174	-0.108	-0.135	0.189	-0.122
<i>b</i> ₄	-0.115	0.000	-0.031	0.099	0.480	0.048
<i>s_u</i>	0.131	0.093	0.098	0.049	0.199	0.047
<i>H_r</i>	-0.187	-0.108	-0.186	-0.092	-0.332	-0.128

^aAbbreviations: DD, density dependence; NA, not applicable.

^bValue and ranges in Table 1.

Our results support the premise that climate conditions can have extreme effects on the viability of natural populations. Results in the base-case scenarios (historical and recent climate conditions) were quite optimistic, but the results from the bad climate scenario provided a much more pessimistic outlook. Given the widely held prediction of continued global warming, the bad scenario, characterized by relatively warm ocean temperatures, might more realistically mimic future ocean conditions than the historical scenario (Meehl et al. 2001). Our results also emphasize that the impacts of climate go beyond just good or bad climate conditions. The autocorrelation associated with climate conditions leads to a greater tendency for populations to grow or decline exponentially, which clearly has important implications for population viability.

Our sensitivity analyses emphasized that the importance of particular vital rates may vary depending on which viability measure is the response variable. This distinction is important because the importance of viability measures will vary depending on population status. If a population is small and declining, mitigation efforts should focus on life stages deemed important for preventing abundances from falling below quasi-extinction thresholds. If a population is growing, priorities should shift toward promoting continued growth. Also, the life stages important to both preventing extinction and increasing overall abundance should receive the highest priority in recovery plans. In addition, the importance of some parameters varied across models, emphasizing that more complex models can provide additional information for setting priorities in conservation actions and highlighting the prevalence of model uncertainty in PVAs.

How can our results be used to help recover Snake River spring and summer Chinook salmon? Historical reductions in freshwater spawning and rearing habitat have contributed to the decline of Snake River spring and summer Chinook salmon (Ruckelshaus et al. 2002). Physical changes in habitat resulting from mining, forestry, grazing, and agricultural practices effectively reduced both the quantity and quality of spawning habitat (National Research Council 1996; Regetz 2003). Furthermore, severe declines in the number of returning adults from the 1970s through the 1990s most likely resulted in a loss of marine-derived nutrients, which are important to sustaining the proper functioning of freshwater and terrestrial ecosystems and salmon production in particular (Gresh et al. 2000; Schindler et al. 2003). The importance of the b parameter (density-dependent parameter in juvenile productivity) for preventing the population from falling below the quasi-extinction level and for increasing mean abundance suggests that increasing the freshwater carrying capacity for juveniles is most likely important for recovery. This may include improving the quality of existing habitats and making areas currently unoccupied accessible or suitable. In addition, competition

among conspecifics or with other species, in particular nonindigenous brook trout (*Salvelinus fontinalis*, Levin et al. 2002), leads to decreases in overall juvenile productivity. Thus, understanding these interactions is important to assessing potential for decreasing the b parameter. Currently, few ecological studies in the Snake River basin are directed at these questions.

One caveat in interpreting our results is that the smolt and adult data reflect a large spatial scale (the entire Snake River basin). Juvenile survival varies across populations (Zabel & Achord 2004), and it is highly likely that each population will respond differently to habitation restoration (McHugh et al. 2004). Thus, we suggest that future PVA studies focus on the variability among populations within the ESU.

Our results concerning hydrosystem-related parameters also suggest that a change in emphasis might benefit the ESU. Currently, a great deal of effort is directed toward increasing the survival of in-river migrants (National Research Council 1996). Our sensitivity analyses, however, indicated that improvements in this life stage might have little effect on population viability. In contrast, the survival of transported fish was deemed far more important for population viability but far fewer resources are directed at addressing how to improve this survival.

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