

Appendix A. Life-cycle modeling to estimate the reponse of Columbia River salmonid populations to improvements in survival in the freshwater and estuarine life stages.

INTRODUCTION

Objectives

The objective of this analysis is to assess the likelihood that necessary improvements outside the hydropower system (i.e. the “gap” between hydrosystem survival under the proposed action and the total estimated impact of the hydrosystem) fall within a biologically realistic range. To do this, we first developed life-cycle models for each of the listed salmonid ESUs impacted by the Federal Columbia River Power System (FCRPS). We then performed sensitivity analyses by varying survival and other demographic rates associated with freshwater and estuarine habitats and examined their impact on modeled population trajectories. We varied survival rates within a range of rates actually observed in wild populations of chinook and steelhead (see main document) to assess the likely magnitude of population response to these changes.

Types of life-cycle models

While many types of life-cycle models exist, we based our analyses on age-structured Leslie matrices (Leslie 1945). This type of analysis is also referred to as a demographic Population Viability Analysis (PVA, Caswell 2001, Morris and Doak 2002) and has been an integral part of recovery efforts for a broad range of at-risk species including loggerhead sea turtles (Crouse et al. 1987), northern spotted owl (Lande 1988), dessert tortoise (Doak et al. 1994). In addition, several studies have applied demographic PVAs to Pacific salmon (Ratner et al. 1997, Kareiva et al. 2000, CRI 2000, McClure et al. 2001, Cooney et al. 2002, Ellner and Fieberg 2002, Wilson 2003, Greene and Beechie 2004).

Demographic PVAs are based on demographic rates and parameters (survival rates, carrying capacity, and fecundity) that govern the transition of individuals from one age class to the next. These rates and parameters are based, as much as possible, on data derived from the particular ESU. Each analysis is accompanied by a data table describing all the sources of information. Thus, demographic PVAs are data-based, relatively transparent and easily repeatable.

Demographic PVAs are either *deterministic* or *stochastic* (Caswell 2001, Morris and Doak 2002). Deterministic models assume that demographic rates (e.g., life stage specific survival rates and fecundity) do not vary with respect to time. In contrast, stochastic models allow at least some of the demographic rates to vary with respect time. Stochastic models are more realistic but require substantially more data than deterministic models.

Thus, if we had sufficient data for an ESU, we developed a stochastic model. Otherwise, we developed a deterministic model. In the analyses presented here, we developed stochastic life cycle models for Snake River spring/summer chinook and Snake River steelhead, and we developed deterministic life-cycle models for Snake River fall chinook and upper Columbia River spring chinook and steelhead. Lower Columbia River chum have virtually no demographic data (WLC-TRT 2003), so we did not construct a life cycle for this ESU. Similarly, little demographic data exist to construct a life-cycle model for the mid-Columbia River steelhead; we therefore use results from other steelhead to inform conclusions about this ESU.

Population metrics

Our analyses involved relating changes in population performance metrics to improvements in freshwater and estuarine habitats. We used the following metrics to gauge population performance:

- mean annual population growth rate, λ (applicable to both deterministic and stochastic models). This metric provides an estimate of the likely population trajectory in the short term.
- mean population abundance (spawners) measured over the simulation time period (applicable only to stochastic models).
- probability of a population falling below some pre-determined abundance threshold during the simulation time period (applicable only to stochastic models).

Methods

Overview

The form of each ESU's life cycle model is based on its life history. Thus the first step in the model development process is to characterize each ESU's life history in terms of life span and ages of smolting and breeding. The time step for the models is a year. Thus annual demographic rates are often expressed as sub-models reflecting that individuals may occupy several habitats in a year and may be exposed to multiple hazards such as harvest and natural mortality.

Each ESU-wide model is based, as much as possible, on data specific to the ESU. Thus availability of data determines the complexity of the model and its sub-models. In order to create a stochastic model, we need data to characterize the variability of a demographic rate in response to factors such as climatic conditions or population density.

Life Cycle Model Structure

In all cases, the models are *age-structured*; that is, the model keeps track of the number of individuals in each age class. Population abundance by age class is denoted by the vector $\mathbf{n}(t)$, which with 5 age classes is of the form:

$$\mathbf{n}(t) = \begin{bmatrix} n_1(t) \\ n_2(t) \\ n_3(t) \\ n_4(t) \\ n_5(t) \end{bmatrix} \quad (1)$$

Thus for example, $n_3(t)$ is the number of three-year olds alive at the end of time period t .

The model converts age-structured abundances in the current time step t to the abundances in time step $t+1$ using a population projection matrix. For the deterministic model, this matrix is invariant through time and is denoted \mathbf{A} . With the stochastic model, the matrix changes with each time step, and is thus designated $\mathbf{A}(t)$. In terms of linear algebra, the deterministic model is expressed as

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

and the stochastic model is expressed as

$$\mathbf{n}(t+1) = \mathbf{A}(t) \cdot \mathbf{n}(t). \quad (2)$$

If we assume fish breed at ages 3, 4, and 5, $\mathbf{A}(t)$ takes on the form:

$$\mathbf{A} = \begin{array}{c|ccccc} & 1 & 2 & 3 & 4 & 5 \\ \hline 1 & & & & & \\ 2 & s_2 & & & & \\ 3 & & s_3 & & & \\ 4 & & & (1-b_3) \cdot s_4 & & \\ 5 & & & & (1-b_4) \cdot s_5 & \\ \hline & & & b_3 \cdot F_3 & b_4 \cdot F_4 & F_5 \end{array} \quad (3)$$

Note that blank elements contain zeros. Each element of the matrix represents the transition of i year-olds (columns) to j year-olds (rows) during a yearly time step. In the simplest case a matrix element is just a survival rate, such as s_2 and s_3 , which are the survival rate during the second and third years, respectively. The terms b_3 and b_4 are the propensity for adults to breed as three and four year-olds, respectively. Thus, for example, b_4 of the four year-olds spawn and then die, while $(1-b_4)$ of the females remain in the ocean. Note that all fish that survive to age 5 and have not yet bred will do so as 5-year olds. Finally, F_3 , F_4 , and F_5 are the fertilities of three, four and five year-olds, respectively. Fertility is the number of one year-olds produced per spawning female and

thus represents both fecundity of females and survival through the first year. All the vital rates can be functions of time, and most have sub-models to account for all the sources of mortality encountered in a given year.

The models project a population from time t to $t+1$ using simple linear algebra. As an example, using the matrix \mathbf{A} above, we compute age structured abundances in time $t+1$ as:

$$\begin{aligned}
 n_1(t+1) &= b_3 \cdot F_3 \cdot n_3(t) + b_4 \cdot F_4 \cdot n_4(t) + b_5 \cdot F_5 \cdot n_5(t) \\
 n_2(t+1) &= s_2 \cdot n_1(t) \\
 n_3(t+1) &= s_3 \cdot n_2(t) \\
 n_4(t+1) &= s_4 \cdot (1 - b_3) \cdot n_3(t) \\
 n_5(t+1) &= s_5 \cdot (1 - b_4) \cdot n_4(t)
 \end{aligned} \tag{4}$$

Snake River spring/summer chinook salmon and steelhead

We developed stochastic LCMs for Snake River spring/summer chinook and steelhead. We used similar methods for both, so we will present them together. These two ESUs have distinctly different life histories (Figure 1). In particular, Snake River spring/summer chinook always smolt at age 2, and females typically breed after 2 or 3 years in the ocean. Snake River steelhead smolt at ages 2 or 3, and females typically breed after 1 or 2 years in the ocean. Because of this variability in smolt age, it is difficult to assign ages to returning adults. Thus, we refer to returning adults as 1-ocean or 2-ocean fish, depending on the number of years they spent in the ocean.

The two stochastic elements in the life cycle model are 1) density dependent survival in the freshwater stage, and 2) estuary/early ocean conditions related to variability in monthly Pacific Decadal Oscillation indices (PDO, Mantua et al. 1997).

It is this freshwater spawning/rearing phase that we address first. In this stage, we related production of smolts (abundances estimated at Lower Granite Dam) to the abundance of spawners (also based on counts of adults at Lower Granite Dam). The adult counts were modified to account for harvest above Lower Granite Dam. Since older fish are more fecund, and since steelhead smolts are two or three years old, we converted adult counts to *effective spawners*¹.

¹ For spring/summer chinook, *effective spawners* are obtained by multiplying the number of (post-harvest) 5 year olds by a fecundity factor, f , that accounts for their higher fecundity and adding this to the number of (post-harvest) 4 year olds. For steelhead, we multiply 2-ocean fish by f to account for their increased

We tested several forms of density dependence: the Ricker model (Ricker 1954), a Beverton-Holt (1957) relationship, the hockey stick and quadratic hockey stick models (Myers et al. 2000), and a linear model (no density dependence) We selected the Beverton-Holt model based on AIC values, to relate smolts to effective spawners:

$$smolts(t) = \frac{a \cdot spawners(t)}{1 + b \cdot spawners(t)} \quad (6)$$

The parameter a determines smolts per spawner at low spawner density, and a/b is the carrying capacity of the system.

A primary goal of this analysis was to produce sub-models that we could then incorporate into a simulation model. Thus, in addition to estimating the functional form the model, we also need to describe the error. In particular, we hoped to use transformations such that the resulting errors were independently identically distributed as normal deviates. In the case of equation (6), the residual terms were clearly not normally distributed. The standard transformation for the Beverton-Holt model is a log-normal transformation. This also produced residuals that were not normally distributed, based on visual inspection of the resulting normal probability plot. We then used a Box-Cox transformation (Box and Cox 1964, Sokal and Rohlf 1981, Seber and Wild 1989), which is essentially a weighted least-squares approach for nonlinear regressions. The goal of this approach is to chose a parameter ϕ such that the residuals, ε_t , of the nonlinear regression equation

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

are distributed independently as $N(0, \sigma^2 \cdot f(x_t | \theta)^\phi)$. The model parameters and transformation parameter are estimated simultaneously by minimizing the centralized log-likelihood function (Seber and Wild 1989). Thus in addition to estimating the Beverton-Holt parameters, we also estimated the parameters σ^2 and ϕ , which are associated with the error about the relationship. This transformation resulted in residuals that were homogeneous (based on a lack of relationship between the residuals and spawners), normally distributed (based on visual inspection of the normal probability plot), and lacking in significant autocorrelation at any time lag (Figure 2).

The Beverton-Holt relationship covers the entire period from spawners to smolts, which lasts for 2 to 3 years. Thus in order to incorporate this into the life cycle model,

fecundity compared to 1-ocean fish. The proportion of 1- and 2- ocean fish was based on analysis of scales (C. Petrosky, pers. comm.). We must also account for the fact that 2 year old smolts arose from a different brood year than 3 year old smolts. We assumed an equal proportion of 2 and 3 year old smolts (C. Petrosky, pers. comm.), and thus half the (post-harvest) adults in a given year were assigned as *effective spawners* for 2 year old smolts, and the other half as *effective spawners* for 3 year old smolts.

which is based on yearly time steps, we needed to partition the relationship into yearly increments. Our approach was to partition the density dependence and stochasticity into the fertility term, which is the number of one-year olds produced per spawner. The remaining freshwater terms were assumed to be density independent and deterministic. This preserved the overall relationship between smolts and spawners.

Estuary/early-ocean survival

We related estuary/early ocean survival ($s_3(t)$ for Snake River spring/summer chinook, $s_{01}(t)$ for Snake River steelhead) to ocean indices based on the Pacific Decadal Oscillation (PDO, Mantua et al. 1997). In the presentation of methods that follows, we use notation for spring/summer chinook. The derivations for steelhead are analogous but with slightly different notation.

To estimate $s_3(t)$, we began with the smolt-to-adult survival rate $SAR(t)$, which is based on smolt and adult counts at Lower Granite Dam (data derived from Raymond 1988, Marmorek et al. 1998, Petrosky et al. 2001, and updated by C. Petrosky, IDFG, pers. comm. and Williams et al. 2004). Smolt-to-adult survival overlaps over several years, so we needed to partition out $s_3(t)$. First, we note that $s_3(t) = n_3(t+1)/n_2(t)$. $n_2(t)$ is derived from the number of smolts at Lower Granite Dam as follows:

$$\begin{aligned} n_2(t) &= s_d(t) \cdot \text{smolts}(t) \\ s_d(t) &= p_T(t) \cdot s_T + (1 - p_T(t)) \cdot s_I(t) \end{aligned}$$

where $s_d(t)$ is survival of downstream migrants through the hydrosystem. Since a portion of fish arriving at Lower Granite Dam are transported (denoted $p_T(t)$ and derived from Marmorek et al. 1998 and Williams et al. 2004), downstream survival must be portioned between transported and inriver migrants. The survival of inriver migrants is denoted $s_I(t)$ and is based on Williams et al. 2001, and the survival of transported fish is denoted s_T . Note that s_T includes “delayed differential mortality” of transported fish (denoted D and obtained from Williams et al. 2004).

To determine $n_3(t+1)$, we back-calculated from the number of returning adults partitioned into the number of years they spent in the ocean. In this manner, we estimated $n_3(t+1)$ as

$$n_3(t+1) = \frac{1}{s_u} \cdot \left[\frac{n_{A3}(t+1)}{1 - h_r(t+1)} + \frac{n_{A4}(t+2)}{s_o \cdot (1 - h_r(t+2))} + \frac{n_{A5}(t+3)}{s_o^2 \cdot (1 - h_r(t+3))} \right] \quad (8)$$

In equation (8) $n_{A3}(t)$, $n_{A4}(t)$, and $n_{A5}(t)$ refer to the numbers of 3, 4, and 5 year old adults counted at Lower Granite Dam in year t , s_o is ocean survival, and $h_r(t)$ is the year harvest rate in the mainstem Columbia River (obtained primarily from Petrosky et al. 2001). We assumed that $s_o = 0.8$ (Kareiva et al. 2000, Ricker 1976). Adult ocean survival rates are not well-known. This method produces modeled SAR values consistent with observed SAR rates.

Before we related $s_3(t)$ to PDO indices, we first used a logistic transformation. This 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:

$$\frac{\ln(s_3(t))}{\ln(1 + s_3(t))} = \beta_0 + \beta_{APR} \cdot PDO_{APR}(t) + \dots + \beta_{MAR} \cdot PDO_{MAR}(t+1) + \varepsilon_t \quad (9)$$

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 at the $\alpha = 0.05$ level. We always eliminated the term with the highest P -value and then re-ran the regression with the remaining terms. We did this until all terms in the regression model were significant. Plots (Figure 3).

We used the resulting coefficients from the regression equation above to generate predicted estuary/early ocean survival over the 100+ year period during which PDO was measured (Figure 4). We determined the 95% confidence interval about the predictions by applying the variance associated with the error term in the regression. For the spring chinook, we also ran simulations with “bad” ocean conditions, which were the ocean conditions during the years 1977-1998. We replicated these years to produce a time series of equivalent length to the historic time series.

Other model terms

In order to complete the life cycle model, we needed to estimate several other parameters. We estimated propensity to breed by age based on the age composition (by migration year) of returning adults (counted at Lower Granite Dam), upstream survival and harvest, and an estimate of ocean survival (0.8, Kareiva et al. 2000, Ricker 1976). All parameters, with data sources and descriptions are provided in Tables 1 and 2.

Simulations

We began the simulations with spawner numbers reflecting the most recent return year. To populate the remaining age classes, we applied deterministic survival rates to the spawner numbers to back-calculate abundances in the younger age classes, which would reflect a long-term, stable age-class distribution. We began the simulations using the first year, 1900, of available PDO data. We then ran simulation for 102 years, through to PDO year 2002. For each year, we estimated estuary/early ocean survival based on the historical PDO indices and stochastic term from a normal distribution.

For each year of the simulation, parr-per-spawner numbers were obtained by applying the Beverton-Holt equation to the number of spawners to determine the number of parr. This was modified by the error term obtained by back-calculation from the Box-Cox transformation.

By applying these two stochastic terms and the deterministic terms to the yearly age-class distribution, we simulated 102 year population trajectories (Figures 5 and 6, top plots). For each simulation, we also calculated a “running λ ”, which, for a given simulation year, is λ calculated over the previous 20 years of the simulation. Thus,

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

Clearly, $\lambda(t)$ is quite variable over the simulation period (Figs. 5 and 6, bottom plots).

Ocean conditions strongly influenced the results of the simulations for spring chinook (Figure 5). The number of spawners decreased substantially under simulated “bad” ocean conditions.

Sensitivity Analyses

The purpose of this analysis was to provide a general sense of how population performance metrics responded to changes in demographic rates corresponding to freshwater and estuarine habitats. For the freshwater habitat, we varied the parameters of the Beverton-Holt relationship. We varied the density-independent slope term, the ceiling or carrying capacity term or both ceiling and slope together. Figure 7 demonstrates the effects of increasing these parameters by 20 percent. For the saltwater habitat, we varied estuary/early ocean survival. In all cases, we varied model parameters over a range of percentage increases (0 to 100 percent) and observed the corresponding responses of mean abundance, λ , and probability of falling below threshold values.

All three performance metrics of Snake River spring/summer chinook were responsive to increases in both freshwater and saltwater survival Snake River spring/summer chinook (Figure 8). Mean abundance and λ generally increased linearly with increases in survival rates and freshwater carrying capacity. They were most responsive to increases in estuarine/early ocean survival and to factors that increased both the slope and ceiling of the Beverton-Holt relationship. Increases in freshwater carrying capacity conferred greater responses in mean abundance and λ than did increases in the Beverton-Holt slope term. The probability of population abundance falling below 5000 individuals decreased strongly with increasing survival and carrying capacity. Increases in estuarine/early ocean survival and to both the slope and ceiling of the Beverton-Holt relationship conferred the strongest response in this metric. Increases in the freshwater slope or carrying capacity terms resulted in similar decreases in the probability of falling below the threshold.

Results for Snake River steelhead were similar to those of Snake River spring/summer chinook with a few exceptions (Figure 9). Increases in the fresh water carrying capacity conferred responses similar to those conferred by increases in estuarine/early ocean survival and to both the slope and carrying capacity of the Beverton-Holt relationship. Also, increase in the Beverton-Holt slope term did little to decrease the probability of steelhead abundances falling below 5000.

One caveat for potential gains due to increases in estuarine/early ocean survival (Figure 10) is that we cannot empirically partition this survival into mortality that occurs in the estuary (which we can potentially reduce due to habitat actions) and that which occurs in the ocean (which we can have little effect on). Thus we partitioned the estuary/early ocean mortality across a range of values from all occurring in the estuary to none occurring in the estuary, and examined the change in λ sensitivity in response (Figure 10). As expected, when little mortality occurs in the estuary, λ increases little in response to a 5% increase in estuarine survival.

Upper Columbia River spring chinook and steelhead and Snake River fall chinook

The models for these ESUs were based primarily on previous analyses. Models for the Upper Columbia River ESUs were developed by Cooney et al. (2002), and a model for the Snake River fall chinook was developed by CRI (2000). All three of these models are deterministic and density independent (Tables 3-5, Figs. 11 and 12).

Since these life cycle models are deterministic, we could only use λ as a population performance metric. Further, proportional increases in either first year survival or estuarine survival produce identical results in terms of proportional increases in λ . For all three ESUs, λ is very responsive to increases in the life-stage specific survivals (Figure 13). In all three cases, a 50 percent increase in either first-year or estuarine survival produced a 10-12 percent increase in λ .

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Table A-1. Model parameters for Snake River spring/summer chinook salmon simulations.

Parameter	Value	Description
<u>Freshwater Productivity</u>		
a	179.2	
b	0.0000454	Beverton-Holt parameters, fit to smolt and spawner data
s ₁	0.00618	
f	0.6	
f	1.26	Fecundity of 5-year olds relative to 4-year olds [*]
s _{p-s}	0.186	Parr-to-smolt survival [†]
<u>Downstream Migration</u>		
s _i	0.39	Downstream inriver survival (mean of last 5 years) [†]
s _T	0.58	Survival of transported fish, included delayed effects [‡]
p _T	0.729	Proportion of fish transported [†]
<u>Estuary/Early Ocean</u>		
b ₀	-2.601	
b _{APR}	0.442	Parameters used to derive third-year ocean survival from monthly PDO indices
b _{MAY}	-1.053	
b _{JUN}	0.334	
b _{AUG}	-0.291	
s ₃	0.284	Variance associated with third year survival
<u>Ocean</u>		
s _o	0.8	Ocean survival [§]
b ₃	0.0345	Propensity to breed as a 3- and 4-year old, respectively; based on age composition data and ocean and upstream migration survival
b ₄	0.4592	
<u>Adult Migration</u>		
s _u	0.794	Upstream migration survival [†]
H _r	0.10	Inriver harvest (mean of last 5 years) [¶]

Sources:

* Kareiva et al. (2000)

† Levin et al. (2002)

‡ Williams et al. (2004)

§ Ricker (1976)

¶ Petrosky et al. (2001)

Table A-2. Model parameters for Snake River steelhead.

Parameter	Value	Description
<u>Freshwater Productivity</u>		
a	216.0	Beverton-Holt parameters, fit to smolt and spawner data
b	0.00018	
s ₁	2.943	Parameters used to generate variability about the Beverton-Holt relationship with Box-Cox transformation
f	1.0	
fecund_fac	1.26	Fecundity of 2-ocean fish relative to 1-ocean fish
P _{smolt2}	0.33	Probability of smolting as 2-year old; based age composition of smolts (Charlie Petrosky, pers. comm.) and overwintering survival of parr
S _{ow}	0.50	Overwintering survival, based on (Kiefer et al. 2002)
S _{p-s}	0.186	Parr-to-smolt survival, assumed same as spring/summer chinook
<u>Downstream Migration</u>		
S _d	0.30	Survival through the hydrosystem, mean from last 5 years
D	0.58	Differential mortality of transported fish
p _T	0.729	Assumed same as spring/summer chinook
<u>Estuary/Early Ocean</u>		
PDO ₀	-1.7569	Parameters used to derive estuary/early ocean survival from monthly PDO indices
PDO _{APR}	0.9963	
PDO _{2MAY}	-1.4384	
PDO _{3OCT}	0.4195	
S ₃	0.211	Variance associated with third year survival
<u>Ocean</u>		
S _o	0.8	Ocean survival, assumed same as spring/summer chinook
b _{o1}	0.4405	Propensity to breed as a 1-ocean fish; based on age composition data and ocean and upstream migration survival
<u>Adult Migration</u>		
S _{up}	0.794	Upstream migration survival
H _r	0.05	Mean of recent years

Table A-3. Model parameters for Snake River fall chinook salmon. Parameters based on CRI (2000) and Peters et al (1998).

Parameter	Value	Description
<u>Freshwater</u>		
s_1	0.0041	First-year survival
<u>Ocean</u>		
s_2, s_3, s_4, s_5, s_6	0.8	Ocean survival
H_{o2}	0.013	Ocean harvest rates, by age
H_{o3}	0.046	
H_{o4}	0.137	
H_{o5}	0.184	
H_{o6}	0.195	
b_3	0.055	
b_4	0.633	
b_5	0.872	
<u>Adult Migration</u>		
h_{MS}	0.174	Mainstem harvest rate
s_{MS}	0.471	Survival during upstream migration through the mainstem
s_{SB}	0.9	Subbasin survival
<u>Fecundity</u>		
m_3	2885	Fecundity of females, by age
m_4	3133	
m_5	3251	
m_6	3251	
pf_3	0.097	Proportion females, by age
pf_4	0.613	
pf_5	0.638	
pf_6	0.617	

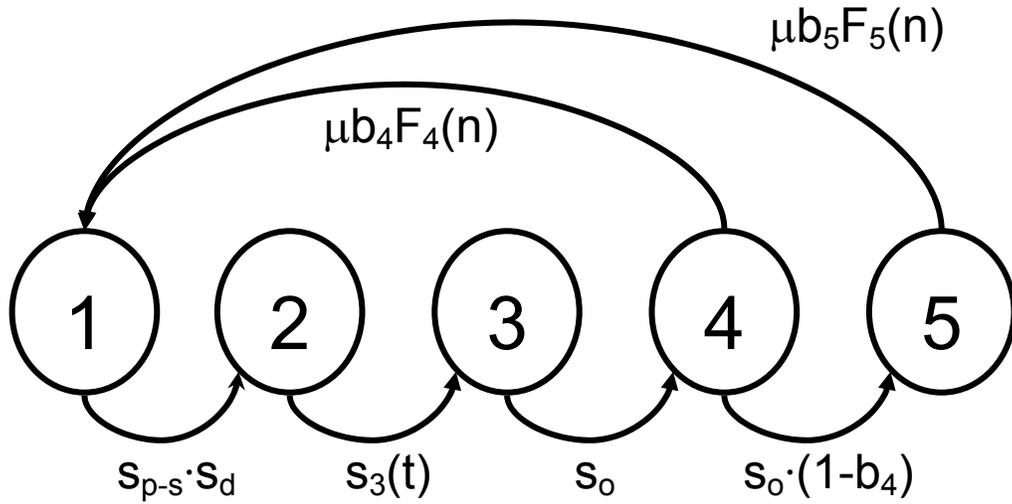
Table A-4. Model parameters for Upper Columbia spring chinook. Parameters based on Cooney (2002).

Parameter	Value	Description
<u>freshwater</u>		
s_1	0.095	First-year survival (modified based on T. Cooney, pers. comm.)
s_d	0.39	Downstream migration survival
<u>estuary/early ocean</u>		
s_e	0.043	Estuary/Early Ocean survival
s_3	0.7	Ocean survival by age
s_4	0.8	
s_5, s_6	0.9	
b_4	0.54	Propensity to breed by age
b_5	0.997	
<u>upstream migration</u>		
s_{MS}	0.58	Upstream migration survival
H_{MS}	0.14	Mainstem harvest rate
<u>fecundity</u>		
m_4	4300	Fecundity by age
m_5, m_6	5400	

Table A-5. Model parameters for Upper Columbia steelhead. Based on Cooney et al. (2002).

Parameter	Value	Description
<u>freshwater</u>		
s_1	0.038	First-year survival
s_d	0.38	Downstream migration survival
<u>estuary/early ocean</u>		
s_e	0.045	Estuary/Early Ocean survival
s_3, s_4, s_5, s_6	0.8	Ocean survival
b_3	0.330	Propensity to breed by age
b_4	0.693	
b_5	0.923	
<u>upstream migration</u>		
s_{MS}	0.76	Upstream migration survival
H_{MS}	0.11	Mainstem harvest rate
H_{SB}	0.05	Subbasin harvest rate
<u>fecundity</u>		
m_3, m_4, m_5, m_6	5000	Fecundity by age

Snake River spring summer chinook



Snake River steelhead

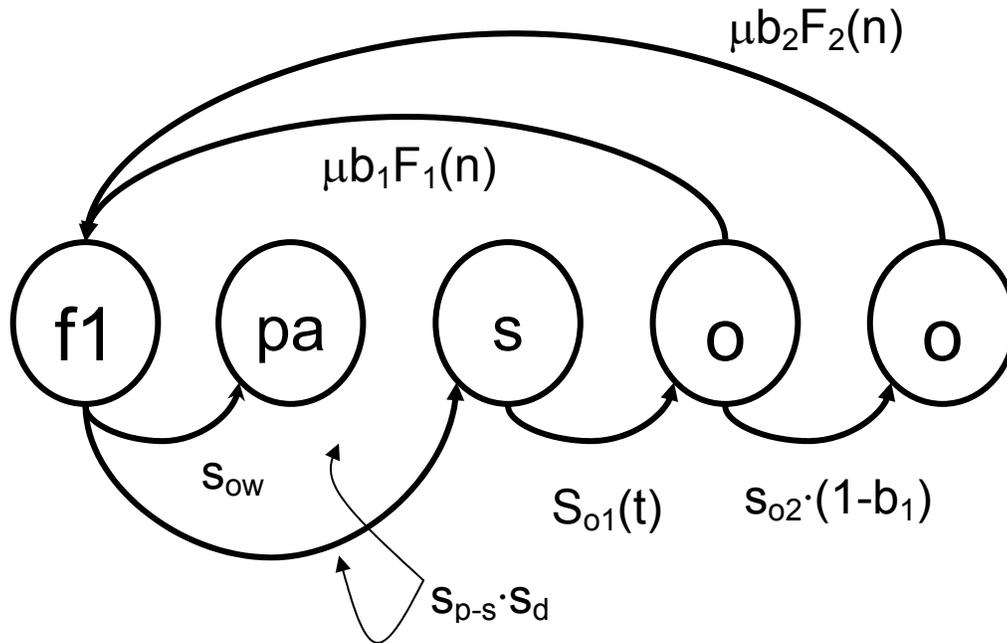


Figure A-1. Schematic diagram of the life histories of Snake River spring/summer chinook (top plot) and steelhead (bottom plot). s_d (downstream migration survival) is equal to $p_T(t) \cdot s_T + (1 - p_T(t)) \cdot s_I(t)$. μ (upstream survival) is equal to $su \cdot (1 - h_r(t))$. See text and Tables A-1 and A-2 for definitions of symbols.

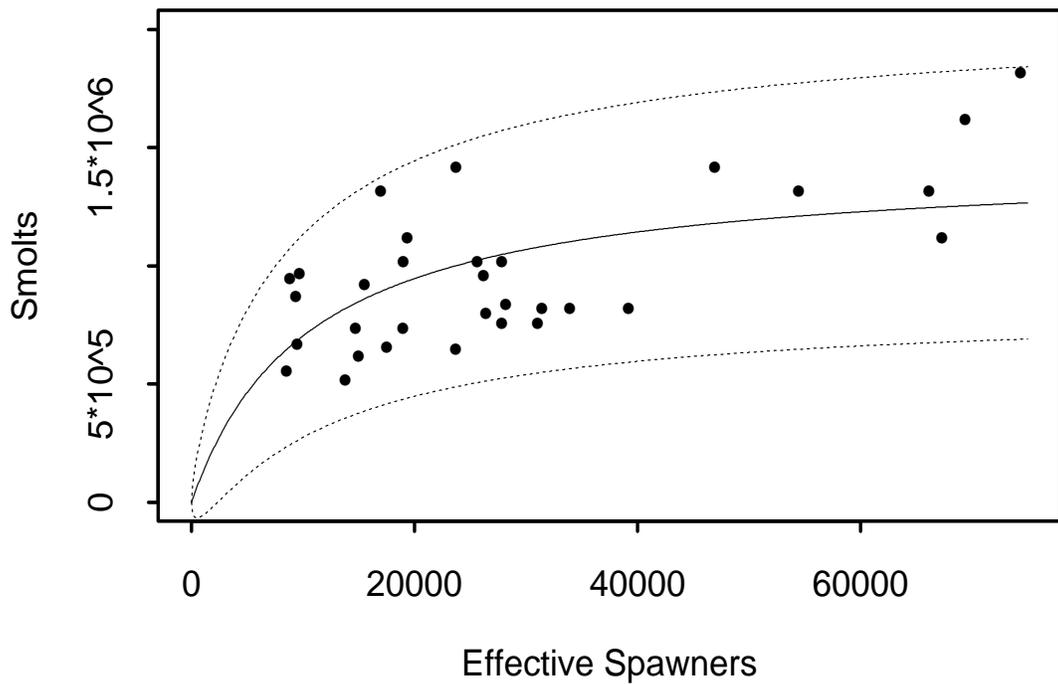
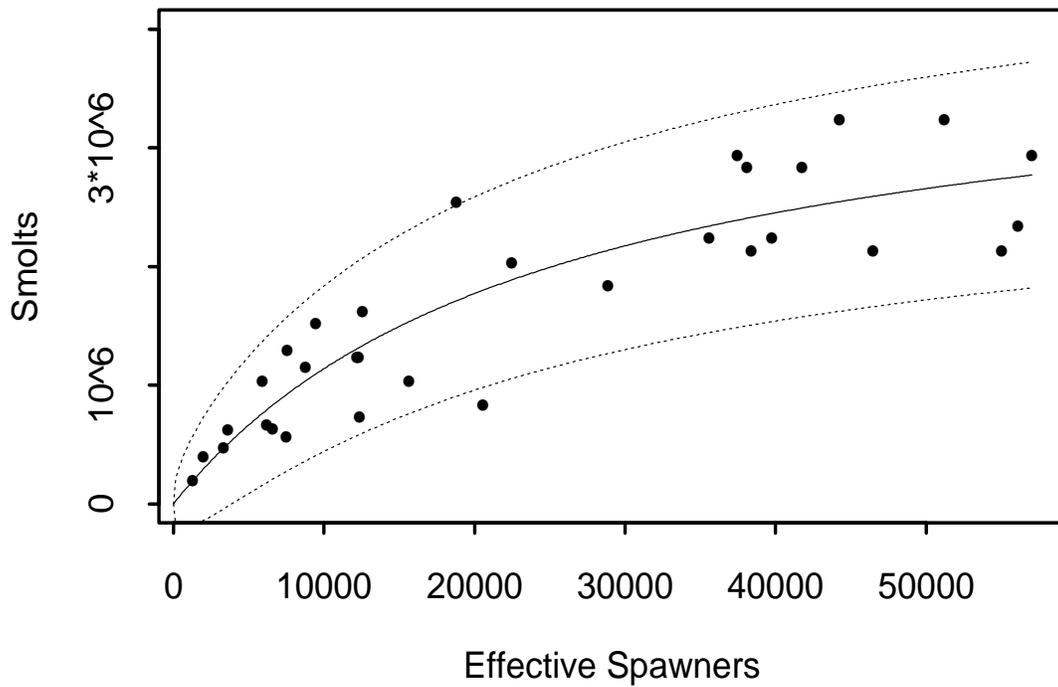


Figure A-2. The relationship between smolts and effective spawners (defined in text) for Snake River spring/summer chinook salmon (top plot) and steelhead (bottom plot). The solid line is the best-fit Beverton-Holt curve (see text), and the dashed lines represent 95% confidence intervals about the predicted relationship.

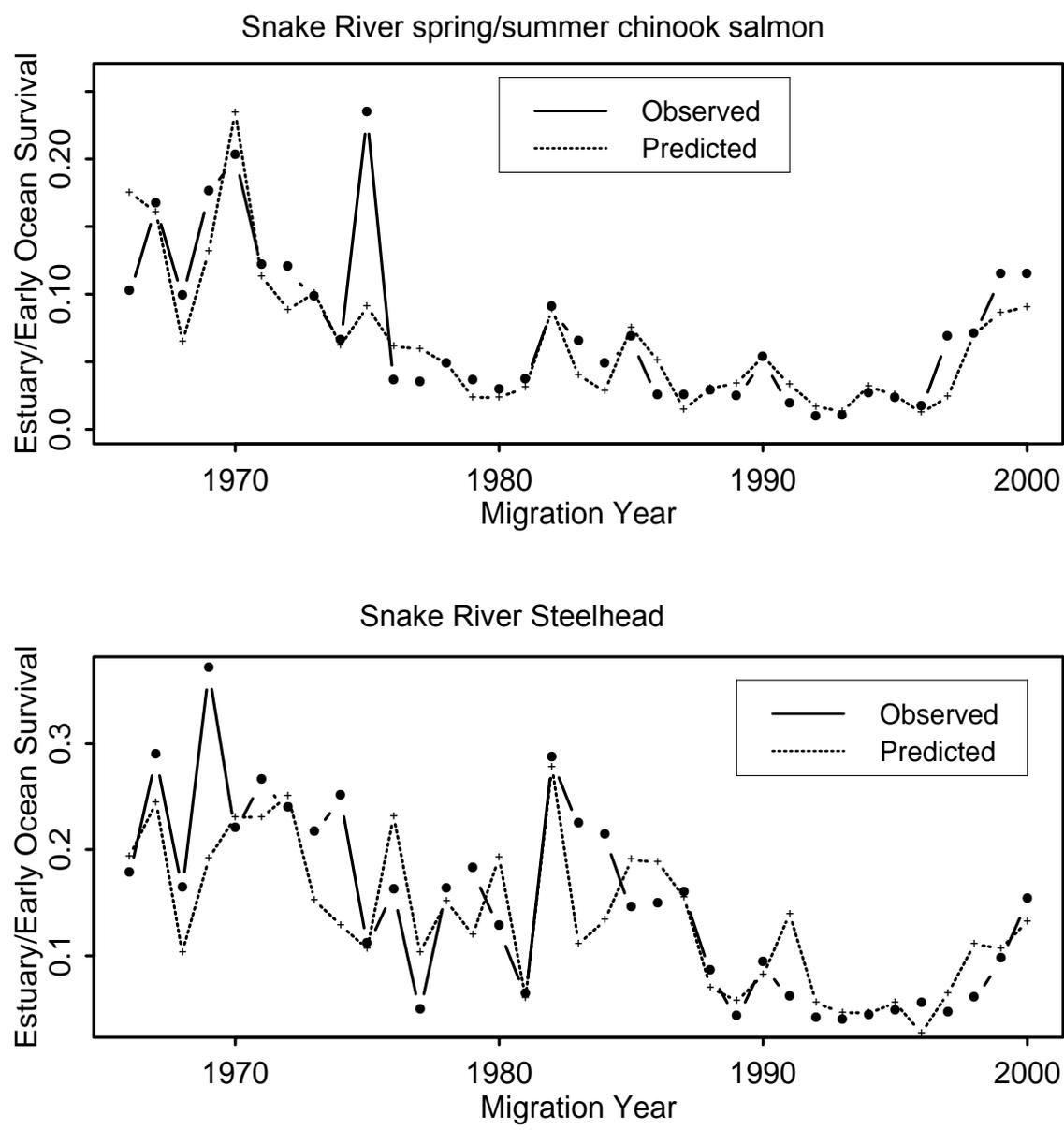


Figure A-3. Predicted and observed estuary/early ocean survival for Snake River spring/summer chinook salmon (top plot) and steelhead (bottom plot).

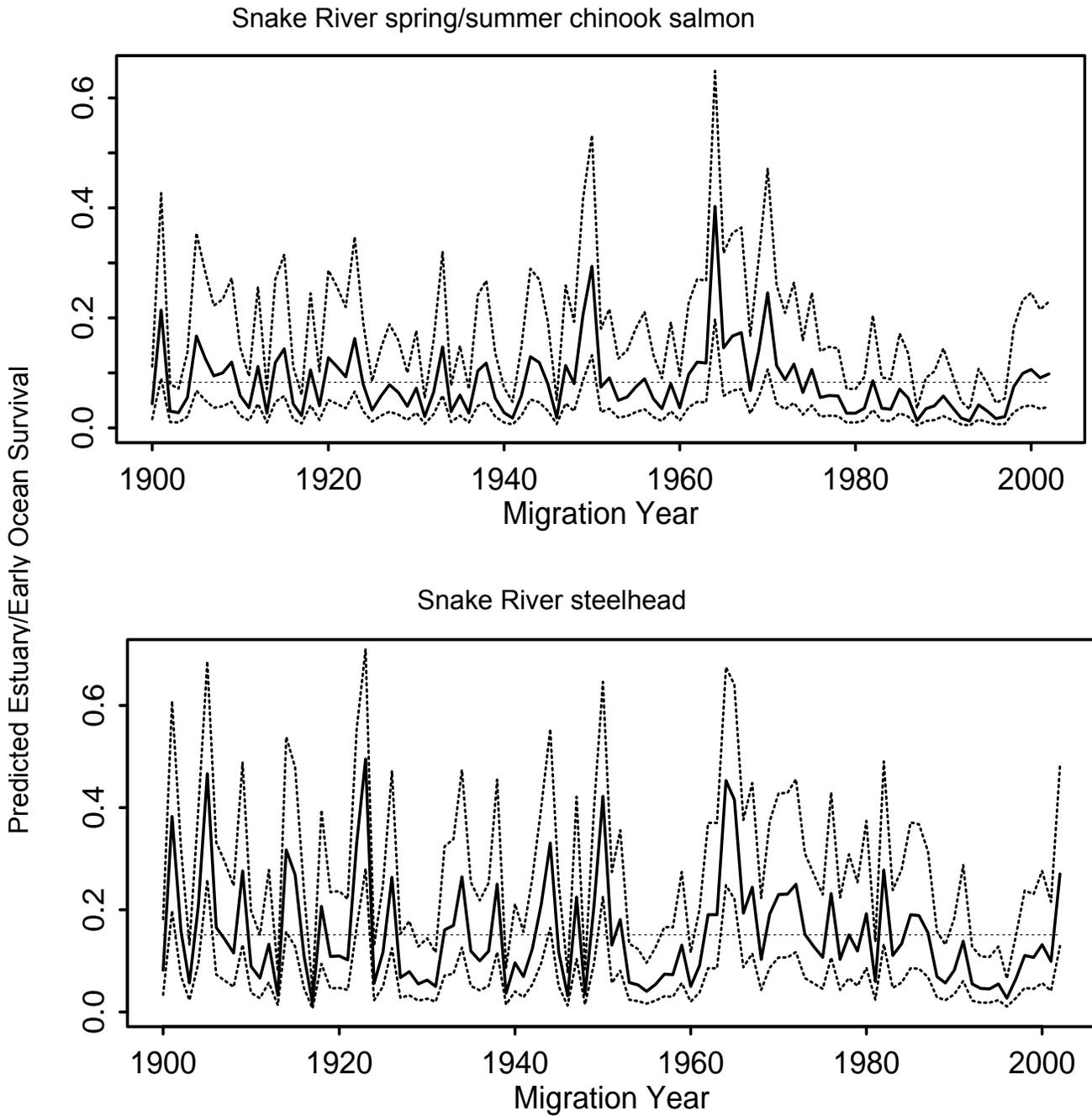


Figure A-4. Predicted estuary/early ocean survival (solid line) by year for Snake River spring/summer chinook salmon (top plot) and steelhead (bottom plot). The dashed lines represent the 95% confidence interval about the predictions.

Snake River spring/summer chinook

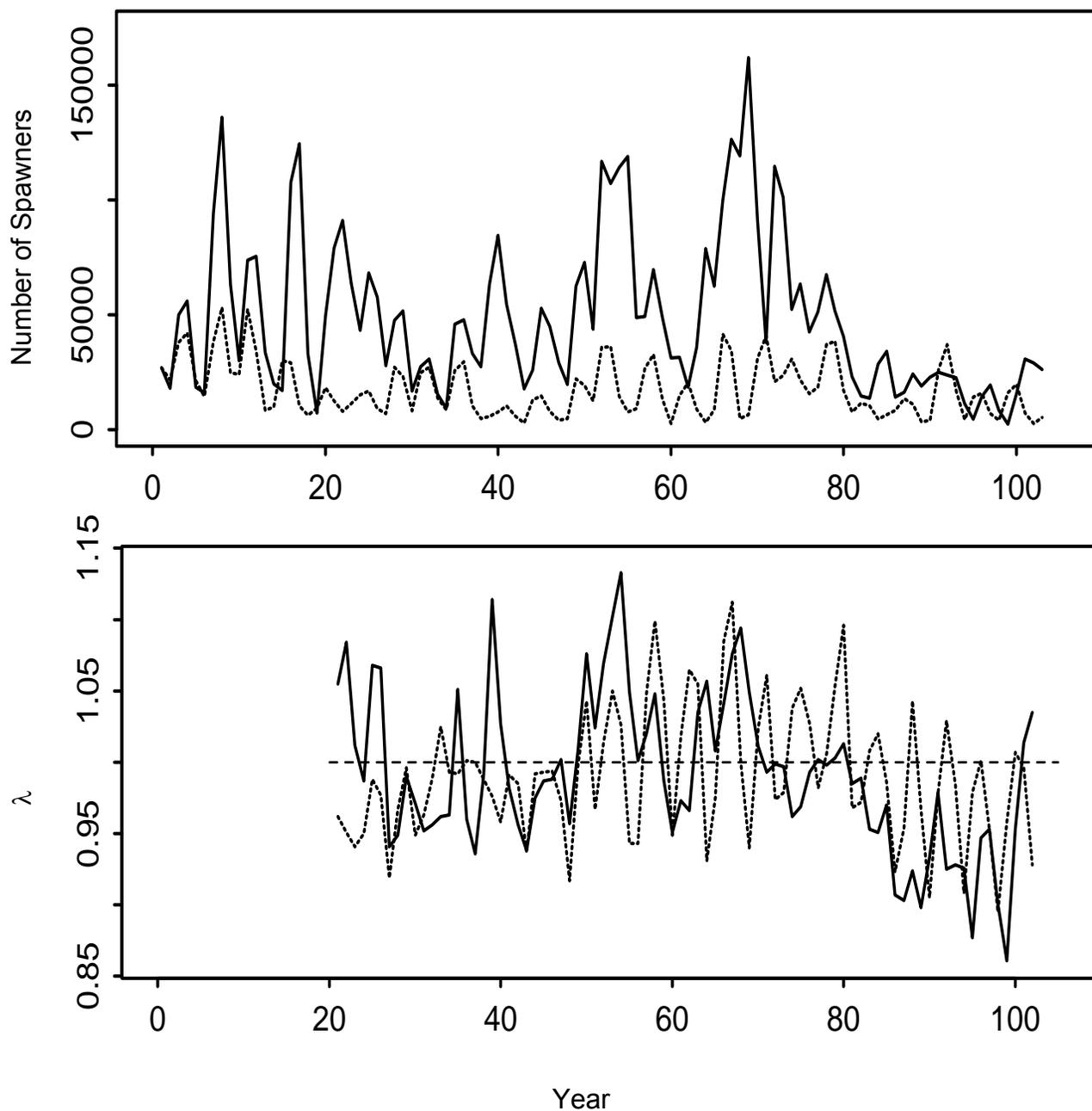


Figure A-5. Examples of simulated output for Snake River spring/summer chinook salmon. The solid line represents historic ocean conditions, and the dotted line represents “bad” ocean conditions.

Snake River steelhead

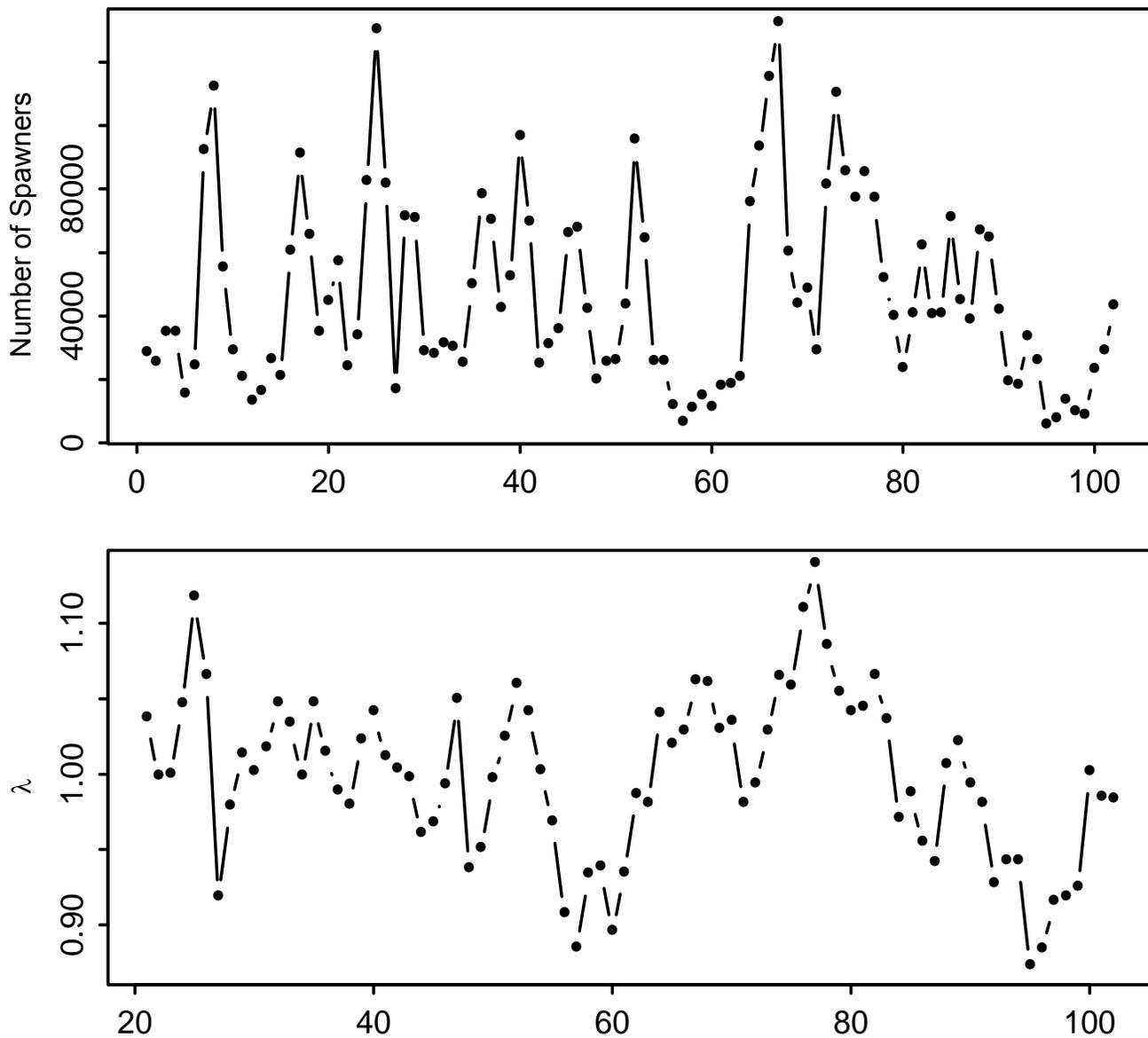


Figure A-6. Example of simulated output for Snake River steelhead.

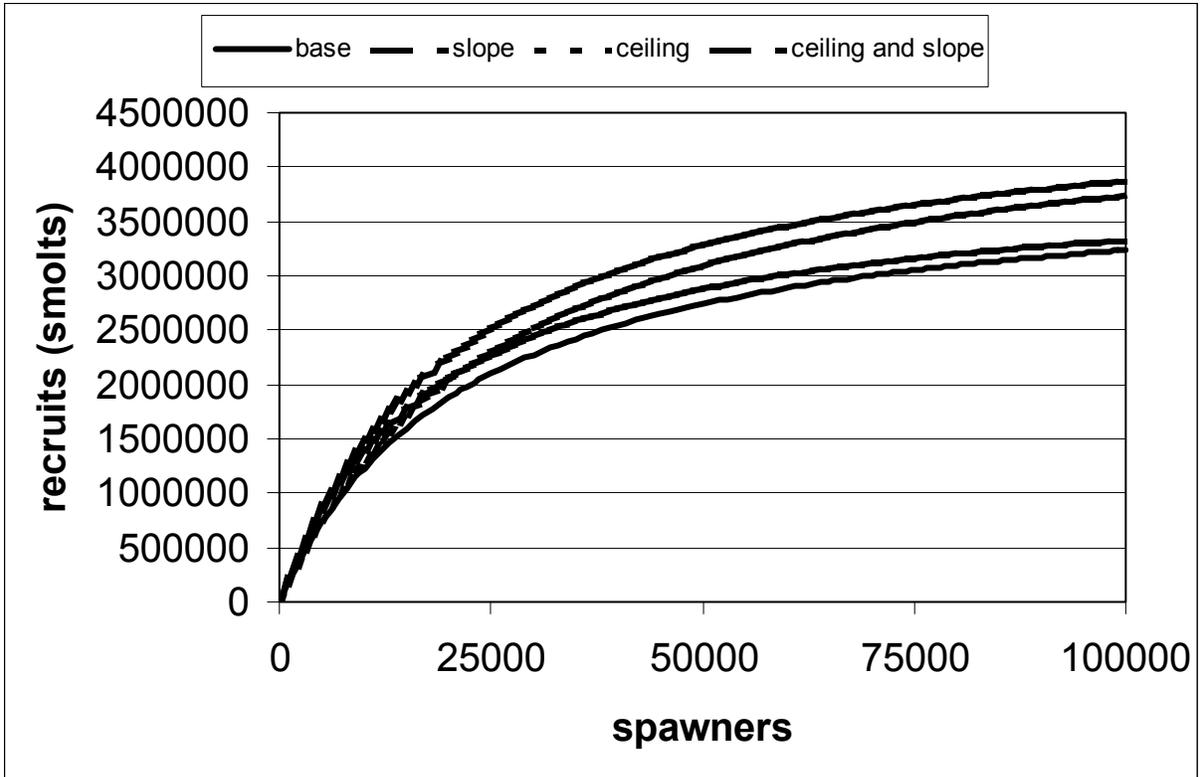


Figure A-7. Beverton-Holt relationship, based on parameters for Snake River spring/summer chinook salmon. The base curve is colored black. The alternative curves result from increasing parameters by 20%.

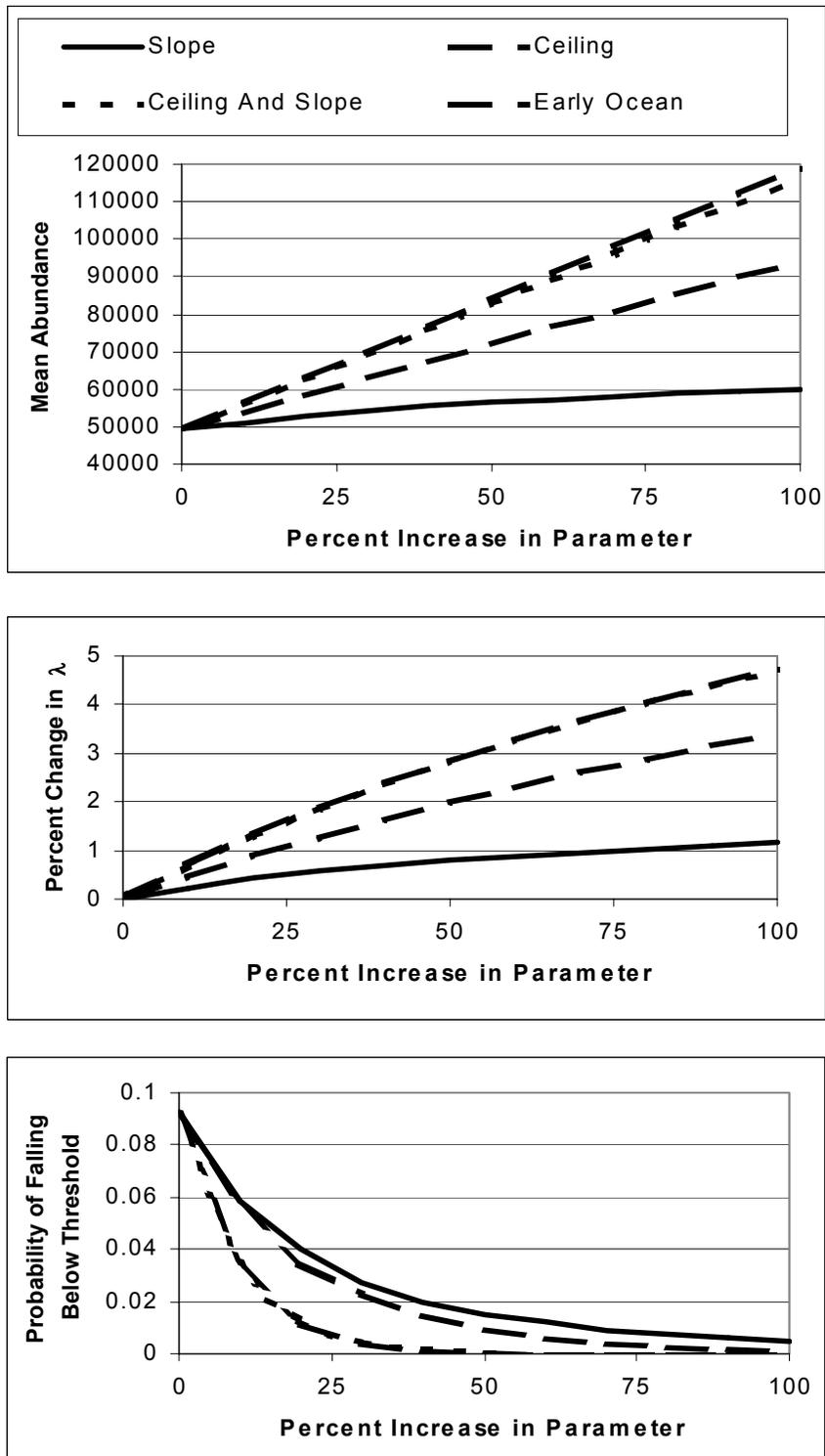


Figure A-8. Results of sensitivity analyses for Snake River spring/summer chinook salmon. See text for details. In the plots, the curves for “Ceiling And Slope” and “Early Ocean” are superimposed.

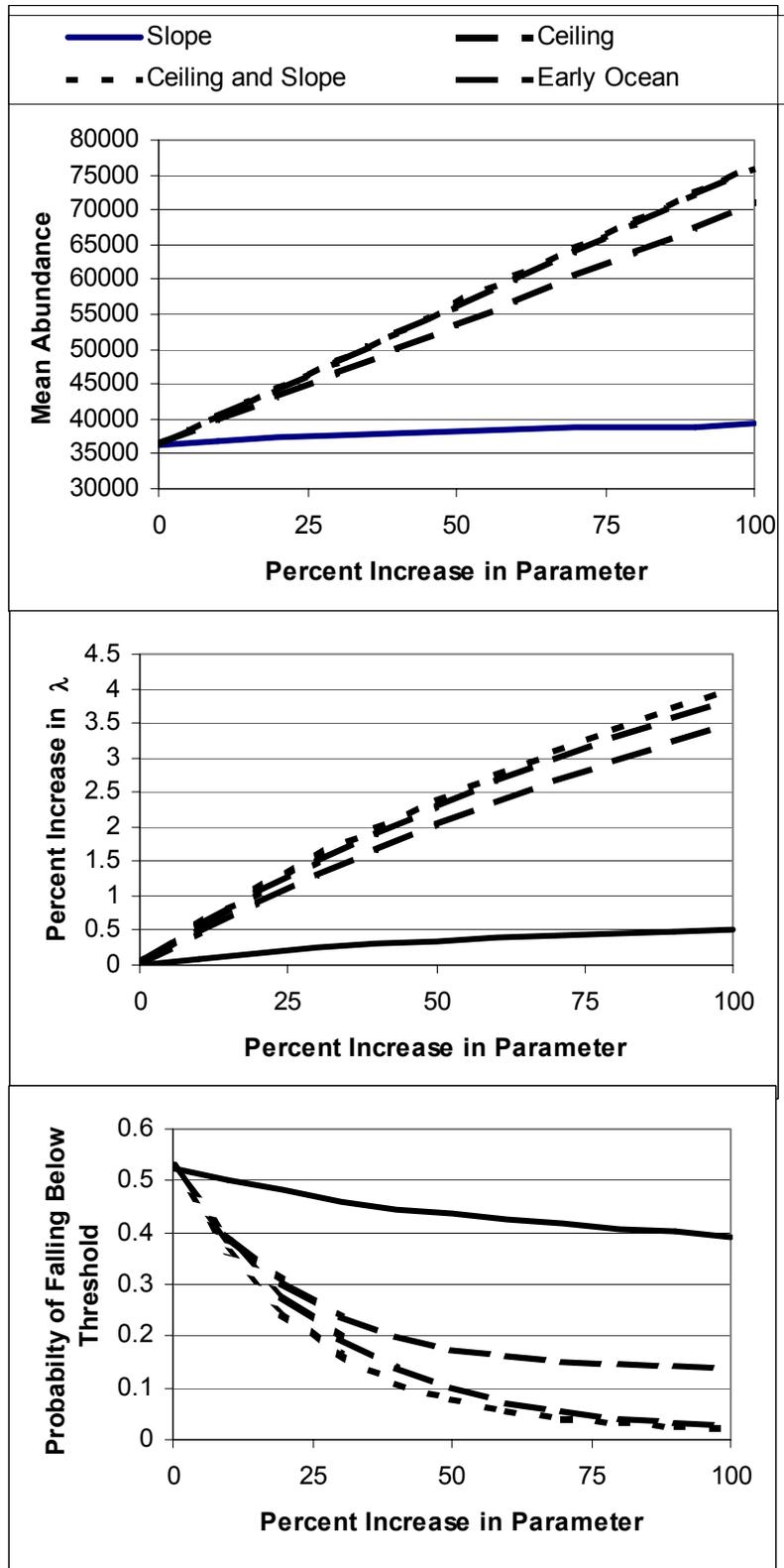


Figure A-9. Sensitivity analyses for Snake River steelhead. See text for details. In the top two plots, the “Ceiling and Slope” and “Early Ocean” curves are superimposed.

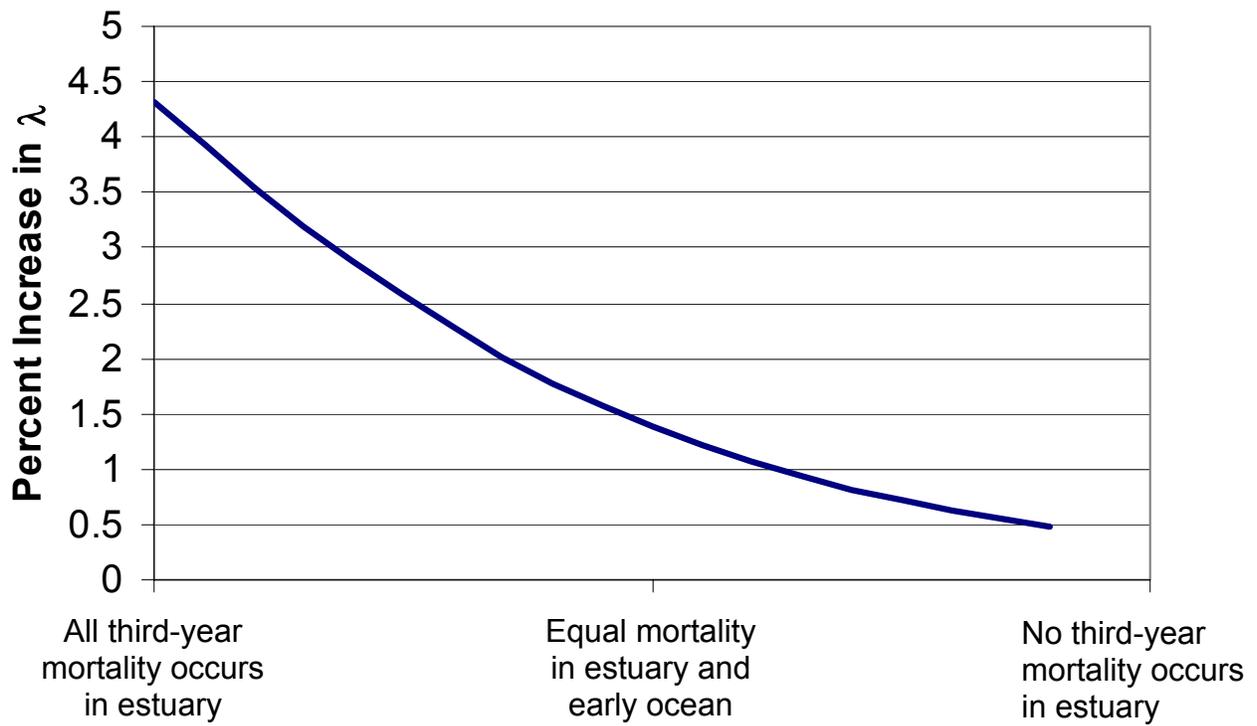


Figure A-10. Percent increase in λ after an absolute increase in estuarine survival of 5% for Snake River spring/summer chinook salmon. The x axis presents ranges of the proportion of third-year mortality occurring in the estuary from all (far left) to none (far right).

Snake River fall chinook

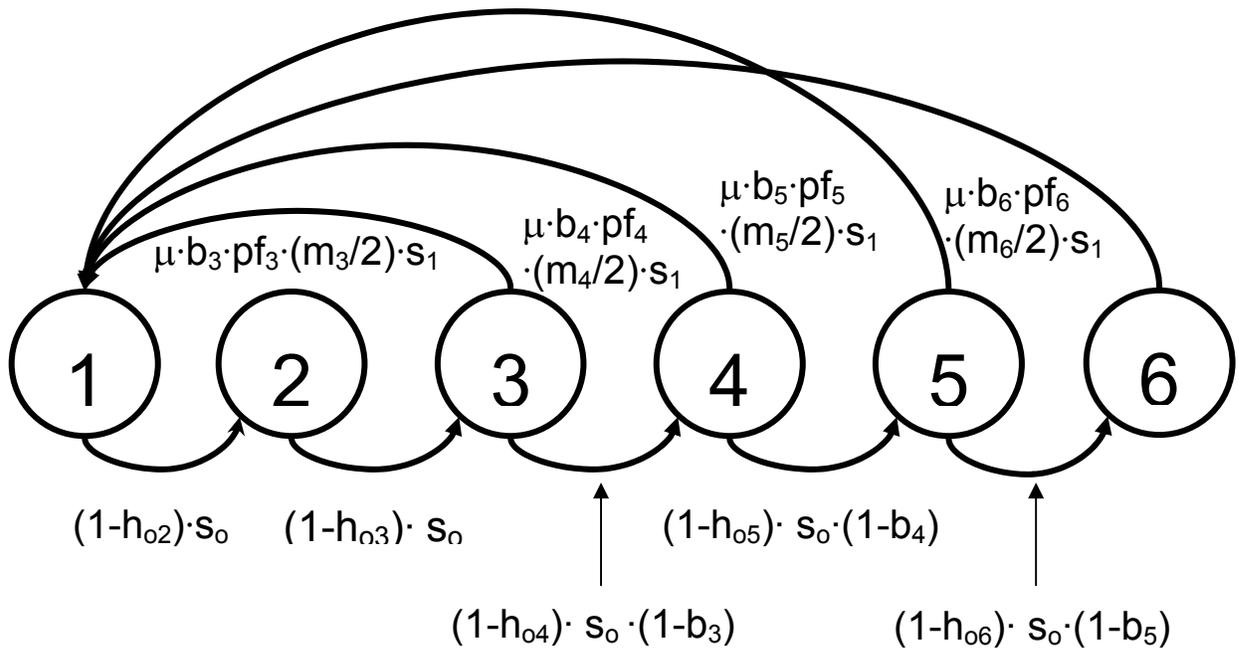
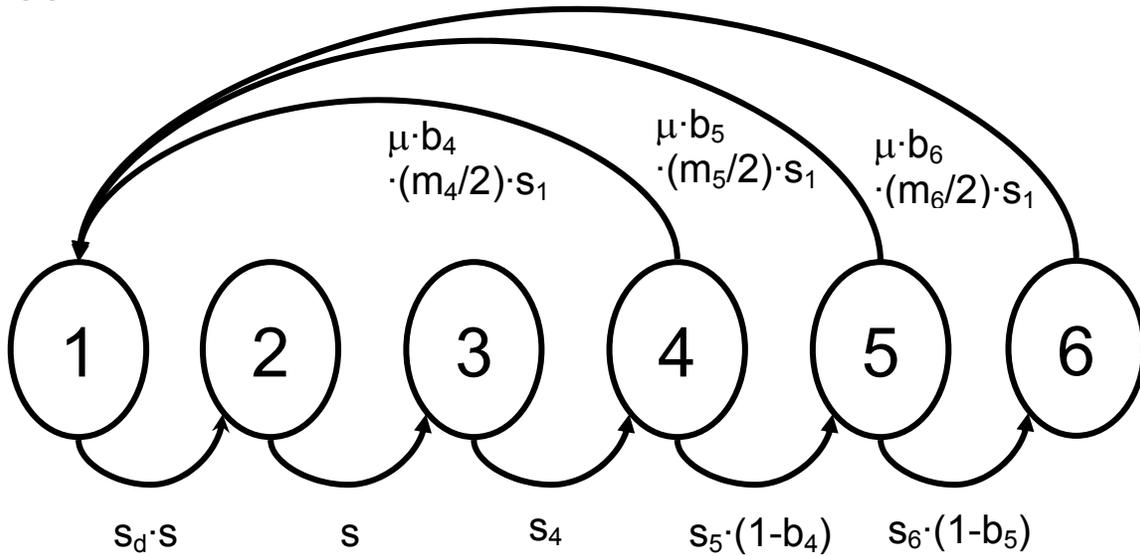


Figure A-11. Schematic diagram for Snake River fall chinook

Upper Columbia River



Upper Columbia River

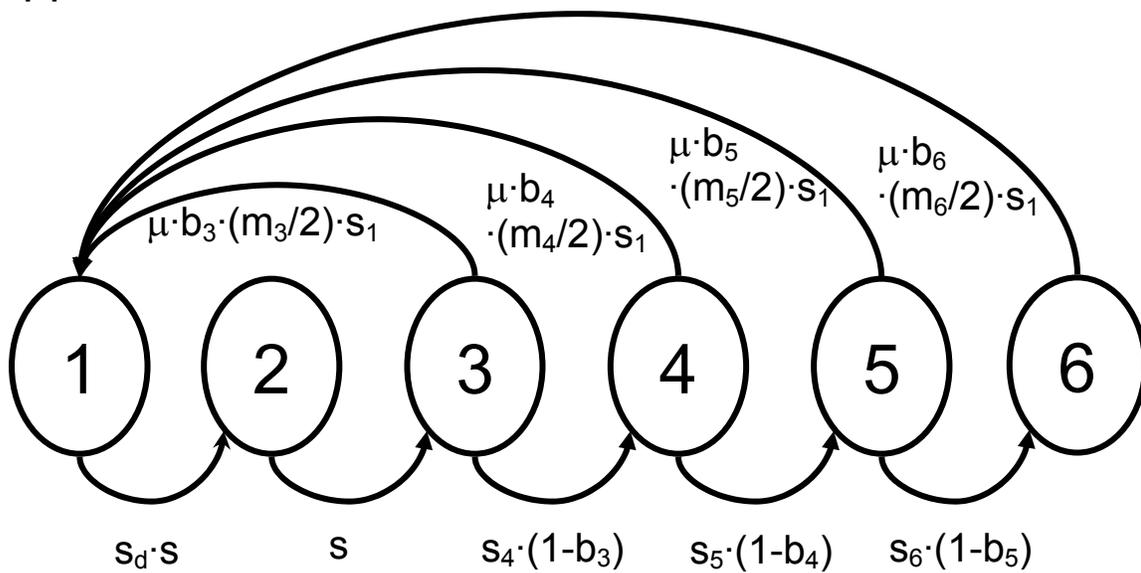


Figure A-12. Schematic diagrams of the life histories of Upper Columbia River spring chinook (top figure) and steelhead (bottom figure).

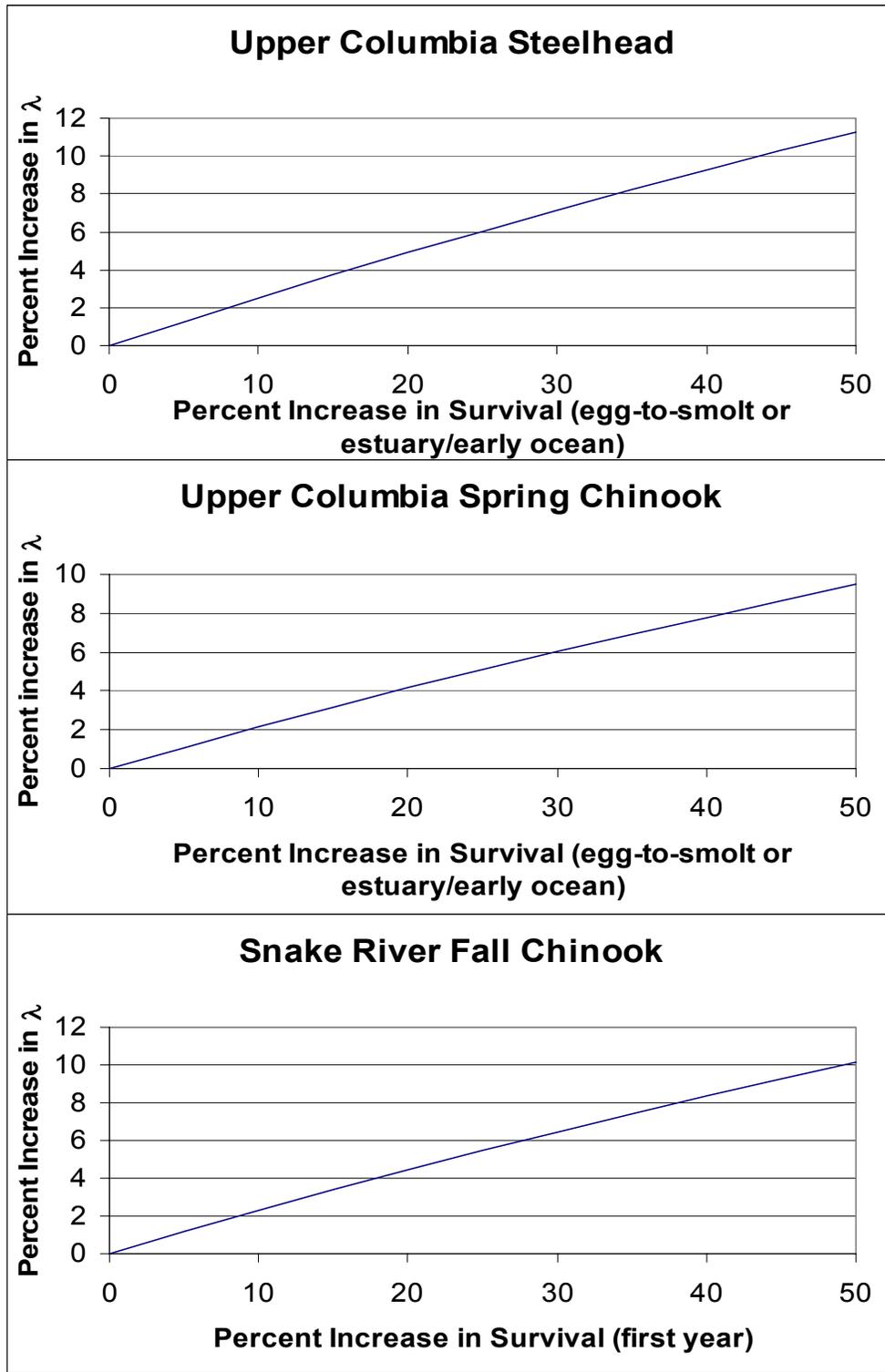


Figure A-13. Sensitivity analyses for Upper Columbia steelhead (top plot), Upper Columbia chinook (middle plot), and Snake River fall chinook (bottom plot).