

Documentation of a Linked-Population Viability Model (LPVA) to Evaluate Recovery Options for Snake River Fall Chinook Salmon

November, 2013

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**DOCUMENTATION OF A LINKED-POPULATION VIABILITY MODEL
(LPVA) TO EVALUATE RECOVERY OPTIONS FOR SNAKE RIVER
FALL CHINOOK SALMON**

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November 2013

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EXECUTIVE SUMMARY

We developed an age- and life-history based population viability analysis model for linked populations of fall Chinook salmon (LPVA). LPVA was designed to quantify the costs and benefits of re-establishing access to an upstream spawning area using managed reconnection options such as hatchery stocking and translocation. The model incorporates stochasticity in the age at which salmon return to spawn, sex ratio, juvenile life history, and survival rates. Response variables include the proportion of replicate populations that persisted for 80 y (roughly 20 generations), the linked population's growth rate, λ , time to extinction and summaries of population sizes including average female spawner abundance, final female spawner abundance, and total female abundance. This report attempts to provide a complete model description, including simulation of management options and options for simulating forward with a joint distribution of parameters based on their likelihoods with respect to historical data. Intermediate results illustrating the Bayesian approach to identifying poorly-known parameters are reported here. LPVA simulates reconnection of linked populations by representing management processes such as trapping of adults migrating upstream at two dams and juveniles migrating downstream, and hatchery operations for one or two hatcheries. The purpose of the model is to support efforts to recover the threatened Snake River fall Chinook salmon ESU by evaluating population viability using existing spawning areas with and without a hatchery and to assess the potential costs and benefits of programs to re-establish an upstream spawning area.

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1 LPVA MODEL DESCRIPTION

We developed an age- and life-history based PVA model for linked populations (LPVA) designed to quantify the costs and benefits of re-establishing access to an upstream spawning area using managed reconnection options such as hatchery stocking and translocation. The model incorporated stochasticity in age-at-return, sex ratio, juvenile life history, and survival rates. The population viability model described here consists of groups defined by four attributes: 1) spawning area (population), 2) age in years, 3) juvenile life history, and 4) markings indicating trapping or release history. Scalar parameters for the LPVA model are listed in Table 1.

1.1 RESPONSE VARIABLES

Population viability was estimated by two measures, the proportion of replicate populations that persisted for 80 y (roughly 20 generations), and the spatially structured population's (SSP) growth rate, λ . Because females destined to spawn in different upstream reaches are counted at Lower Granite Dam, persistence is defined for the linked-population as a whole. We estimated persistence as the fraction of 200 replicate simulated populations that persisted for twenty generations (80 y). We estimated the intrinsic rate of increase, r by fitting the equation to the simulated time-series of female spawner counts at Lower Granite Dam, $N(t) = N(t_0) e^{r(t-t_0)}$, for r and defined $\lambda = e^r$, with the first five years removed to reduce the effects of initial conditions.

1.2 JUVENILE LIFE HISTORY

In the Snake River, a proportion, P_y , of juveniles remain in the river during their first year and migrate to sea during their second spring when they are yearlings (reservoir-type, $k = 1$). The remainder emigrate as sub-yearlings (ocean-type, $k = 0$) (Connor et al. 2002). Connor et al. found that a higher proportion of juveniles emigrated as yearlings in cooler tributaries such as the Clearwater River than emigrated as yearlings from the warmer mainstem Snake River. Overall, Connor et al. (2005) estimated that 46.5% of females returning to spawn and captured at Lower Granite Dam between 1998 and 2003 had emigrated as yearlings.

The initial proportion of fish of each life history was determined as follows. First, we estimated proportions for each of four spawning areas for historical years between 1991 and 2005. We used Connor et al.'s field estimates when they were available and imputed missing values using temperature data and growth thresholds identified by Perkins and Jager (2011). To simulate proportions in each future year, we selected an historical year at uniform random and adopted its yearling proportion, whether imputed or measured. Thereafter, the model tracked how many female spawners belong to each strategy and allocated their female eggs proportionally, where the count was drawn from a beta-binomial distribution using P_y as the mean. Overdispersion was estimated from the four spawning areas (P_{yev} in Table 2).

Table 1. Parameters in the Snake River fall Chinook metapopulation model. Acronyms include Hells Canyon (HC) population and dam, Lower Granite (LG),

Parameter	Value	Description
<i>Num_iter</i>	200	Number of iterations (populations) for each scenario
<i>Nvary</i>	0	Number of parameters to vary, generating scenarios
<i>Begin_yr</i>	1990	Start year
<i>End_yr</i>	2070	End year
<i>N0</i>	20,000	Initial numbers of females in population
<i>Nsub</i>	4	Number of subpopulations (spawning areas)
<i>Oc_last</i>	0.75	Proportion of year (fall-fall) spent in ocean before up-migration to spawn
<i>Oc-0</i>	0.1	Proportion of year spent in ocean after out-migration for sub-yearling outmigrants
<i>Oc-1</i>	0.7	Proportion of year spent in ocean after out-migration for yearling outmigrants
<i>SR_model</i>	0	0=Beverton-Holt, 1=Hierarchical Bayesian Ricker, 2=Shepherd, 3=Hill-Ricker model
∞	0.0045	Maximum per-capita recruitment in the absence of density-dependent effects (millions); Based on SR fitting to (Milks et al. 2009)
<i>Fec_avg</i>	3,688	Average per-capita fecundity, used in hatchery simulation (Milks et al. 2009)
<i>K_{pop}</i>	5,000	Habitat capacity (number of female spawners) fitted to LG returns
<i>L_{max}</i>	86.331	Maximum size – for age 6 (cm) in fitted logistic growth curve, Equation 5
<i>xs</i>	0.5557	Standard deviation of age in logistic growth curve, Equation 5
<i>x0</i>	1.5302	Age at inflection point in logistic growth curve, Equation 5
<i>Stochastic</i>	1	Simulate stochastic survival and proportions
<i>Scv</i>	0.25	Default coefficient of variation on beta-binomial survival for those lacking estimates (<i>Struck_LG</i> , <i>Sriver_LG</i> , <i>Shatch0</i> , <i>Shatch1</i> in Table 2); MCMC analysis result, 0.2373.
<i>NoPy</i>	0	Flag to “turn off” yearling juvenile life history
<i>Bool_trapmark</i>	1	<i>Trap1_mark</i> and <i>Trap2_mark</i> (see definitions below and in Table 5) are 0/1 values if this is one.
<i>Struck_up</i>	0.91	Survival of translocation is assumed to be similar to pre-spawning mortality, <i>Spre</i>
<i>Sfact</i>	Varied	Ratio of egg-smolt survival in the new habitat above Brownlee Dam vs. the downstream HCC habitat, multiplies <i>S_{EGG}</i>
<i>Kfact</i>	Varied	Ratio of carrying capacity in new habitat above Brownlee Dam vs. the downstream HCC habitat, multiplies <i>K_{pop}</i>
<i>Tdown</i>	0.80	Proportion of juveniles trapped upstream of Brownlee Reservoir while moving downstream. (Chandler and Chapman 2001)
<i>Trans_mark</i>	Table 5	Vector indicating whether or not excess fish with this mark are translocated, values are 0/1
<i>Yr_newpop1</i>	2020	Initial year of introducing new population
<i>Yr_newpop2</i>	2080	Final year of supplementing new population

<i>Fhatch0</i>	0.0	Fraction of spawners taken to hatchery, offspring released as sub-yearlings (age 0)
<i>Fhatch1</i>	0.0	Fraction of spawners taken to hatchery, offspring released as yearlings (age 1)
<i>Ktrap_min</i>	MCMC (Table 4)	Fraction of current trapping rate at start of historical stocking (linear increase)
<i>Up1_quota, Up2_quota</i>	1,600, 1,600	Quota for broodstock removed at each of two traps. Females removed at Lyons Ferry, (Milks et al. 2009)
<i>Qjuv1_below</i>	450,000	Quota on yearling releases below HCC, (Milks et al. 2009)
<i>Qjuv1_above</i>	0	Quota on yearling releases above HCC
<i>Trap1_year, Trap2_year</i>	1985, 2005	First year of trap operation for traps below LG and HC Dams.
<i>Trap1_mark & Trap2_mark</i>	Table 5	Vector indicating adults with this mark used as broodstock, see <i>Bool_TrapMark</i> , or proportion taken from fish with this mark; 0/1
<i>Grid_start</i>	Varied	Vector of initial values of gridded parameter search
<i>Grid_end</i>	Varied	Vector of final values of gridded parameter search
<i>Grid_step</i>	Varied	Vector of step sizes (positive) or multiplier (negative)
<i>MCdata</i>	Varied	Name of csv file with MCMC parameter chain
<i>Parm_name</i>	Varied	Vector of parameter names, of size <i>Nvary</i>
<i>Parm_min</i>	Varied	Vector of minimum values of prior distribution
<i>Parm_max</i>	Varied	Vector of maximum values of prior distribution
<i>Prior_dist</i>	Varied	Vector of prior distributions (beta, Gaussian, Poisson)
<i>Prior_mu, Prior_sd</i>	Varied	Vector of mean, sd of prior distributions
<i>SA_init</i>	Varied	Vector of starting parameter values in search (alternative to drawing from priors)
<i>SAR_target0</i>	0.004	Target value for subyearling smolt-to-adult survival, from historical data
<i>SAR_target1</i>	0.006	Target value for yearling smolt-to-adult survival, from historical data

Table 2. Summary of stochastic models for demographic rates in the LPVA.

Rate or percentage	Parameter	Mean	CV = SE / mean	Varies by	Distribution	Reference
Upmigration survival to LGR	S_{UPI}, S_{UPI_cv}	0.646	0.015		Beta-binomial	Upmigration survival from ocean to above LG Dam from adult pit tags, 2002-2007 average wild and hatchery, SE from digitized graph 1986-2006 and appendix in (NOAA Fisheries 2008); Includes in-river harvest.
Upmigration survival LGR to Snake	S_{UP2}, S_{UP2_cv}	0.710	Same as above		Beta-binomial	Adult survival of upmigration from LG to spawning grounds in the Snake River (Chapman et al. 1994); Includes in-river harvest.
Percent female	$P_{female}, P_{female_cv}$	0.4314	0.0113		Beta-binomial	Proportion of adult spawners that are female (eggs assumed to be 50:50); Lyons Ferry Hatchery data 1990-2002, adult broodstock
Egg sex ratio	Egg_ratio, P_{female_cv}	0.5	0.0113		Beta-binomial	Lyons Ferry Hatchery data 1990-2002, offspring
Spawner-recruit error	$0, SR_cv$	0.0	0.0003		Normal for log(R/S)	Analysis of return data, millions of recruits
Early survival from egg to spring when sub-yearlings become smolt and yearlings remain residualized	S_{EGG}, Env_cv	0.125	0.0	Population	Beta-binomial	MCMC (Table 4); Estimates: 0.105 in (Groves and Chandler 2003) & 0.292 in (McMichael et al. 2005)
Percent yearling type	$P_y(t), P_{ycv}(t)$		Annual SE calculated based on mean,	Population	Beta-binomial	Mean P_y drawn annually based on historical proportions (Perkins and Jager 2011); Each year's CV calculated based on deviations from mean.
Percent of yearlings above LG over winter	P_{yLGRes}	0.50	0.0		Poisson	Proportion of yearling type that overwinter above Lower Granite Dam, influences yearling SAR. Calibrated to smolt-to-adult return ratio for yearling-outmigrant-type
Survival sub-yearling smolts from Snake	$S_{LG,0}, S_{LG,0_cv}$	0.6297	0.0236		Beta-binomial	Pittsburg Landing trap to LG Dam tailrace (Connor et al. 2004)

River to LG tailrace						
Survival yearling smolts from Snake River to LG tailrace	$S_{LG,1}, S_{LG,1_{cv}}$	0.9344	0.0083		Beta-binomial	Pittsburg Landing trap to LG Dam tailrace (Connor et al. 2004)
Survival sub-yearling smolts from LG tailrace to below Bonneville Dam	$S_{BON,0}, S_{BON,0_{cv}}$	0.3685	0.1205		Beta-binomial	See section 1.5.1; DART analysis, Connor pc. 2006; SE from (Muir et al. 2006) for spring Chinook;
Survival yearling smolts from LG tailrace to below Bonneville Dam	$S_{BON,1}, S_{BON,1_{cv}}$	0.538	0.112		Beta-binomial	(Williams et al. 2005, Faulkner et al. 2007)
Estuary survival, sub-yearling	$S_{EST,0}, S_{EST,0_{cv}}$	0.588	0.0		Beta-binomial	Bonneville Dam tailrace through estuary (McMichael et al. 2007)
Estuary survival, yearling	$S_{EST,1}, S_{EST,1_{cv}}$	0.653	0.0		Beta-binomial	Bonneville Dam tailrace through estuary (McMichael et al. 2007)
Ocean survival	$S_{OC,min}, S_{OC,max}, S_{OC_{cv}}$	0.0100, 0.8415	0.0256		Beta-binomial	Equation 5; Lower bound varied (MCMC); Upper estimates: 0.8, (Ricker 1976); 0.885 in nineties (Myers et al. 1998); Max 1986-2006 was 0.797 (NOAA Fisheries 2008)
Ratio of yearling age-0 survival in reservoirs to sub-yearlings survival during the same time	$S_{RES,OC}$	Table 4 (MCMC)	0.0		Poisson	Survival while migrating to the ocean and spending time in the ocean, respectively. Estimates of reservoir survival are 0.13-0.22 over summer; 0.65 over winter. (Muir et al. 1999, Connor et al. 2003)
Proportion trapped, up	$Trap1_{up}, Trap2_{up}$	0.2, Varied	0.0, 0.0	Trap	Poisson	20% of hr, 24h/d, (Milks et al. 2009)
Survival to release for hatchery juveniles released as sub-yearlings, yearlings	$Shatch_0, Shatch_1$	0.893, 0.816	Scv		Beta-binomial	Lyons Ferry Hatchery averages 1990-2003 (Milks et al. 2009)
Survival of juveniles migrating in-river from above Brownlee Dam to	S_{river_LG}	0.3	S_{CV}		Beta-binomial	(Chandler and Chapman 2001)

below LGR						
Survival of juveniles trucked downstream to below LG Dam	<i>Struck_LG</i>	0.8	<i>S_CV</i>		Beta-binomial	(Chandler and Chapman 2001)
Proportion stocked in new population	<i>Pnew</i>	0.0, 0.0	0.0, 0.0		Poisson	No current plans to stock upstream population
Proportion marked	<i>Pmarked, Pmarked_cv</i>	0.76	0.06	Same for age-0 and 1	Beta-binomial	W. Connor personal communication
Broodstock pre-spawn survival	<i>Spre</i>	0.91	0.0		Beta-binomial	Lyons Ferry Hatchery (Milks et al. 2009)

1.3 POPULATION DYNAMICS

The number of female fall Chinook salmon, $n_{k,x}$ in age class x belonging to life history type k includes females from age x to $x+1$ in year t (Equation 1). The LPVA model increments salmon ages from the time of spawning in fall and measures survival from one fall to the next (post-census). Survival from age x to $x+1$ is denoted s_x , and a second subscript is added to indicate life history type, where $s =$ sub-yearling ($k = 0$) and $y =$ yearling life history ($k = 1$) (Equation 1).

$$n_{k,1}(t+1) = n_{k,0}(t) \times \begin{cases} (1 - p_y) s_{0s}, & k = 0 \\ p_y s_{0y} & , k = 1 \end{cases} \quad (1)$$

$$n_{k,2}(t+1) = n_{k,1}(t) \times \begin{cases} (1 - p_y) s_{1s}, & k = 0 \\ p_y s_{1y} & , k = 1 \end{cases}$$

For adults ages 2 and older, we assume that the two life-history types ($k = 0$ and 1) experience the same survival rates (Equation 2). Survival for these ages includes post-spawning mortality. Of those adults that were spawned 3-years previously, proportion b_3 migrate to spawn in the following fall, and fraction $S_{up} = S_{up1} \times S_{up2}$, survive upstream migration. The N_s surviving females age 2 to 5 are counted as they swim upstream past Lower Granite Dam.

$$n_{k,x+1}(t+1) = s_x n_x(t), \text{ age } x = 2 \text{ to } 5 \quad (2)$$

$$n_{k,x}(0) = \begin{cases} (1 - P_y) P_x N(0), & k = 0 \\ (P_y) P_x N(0), & k = 1 \end{cases}$$

$$N_{s_k}(t) = S_{up} \sum_{x=3}^6 b_i n_{k,x}(t) \quad (3)$$

Spawning females collectively produce offspring ($n_{k,0}$ in Equation 4), apportioned among the two life history types, k . Density dependence in recruitment is simulated using a stock-recruitment relationship that applies to offspring from both hatchery and wild spawners. Two approaches can be used to represent density dependence. One relies on fitted data to returns and assumes that recruits are age-1 fish in fall. The second approach, used here, begins with an assumed fecundity, α (maximum recruitment) and then applies density dependence as one source of mortality among others that occur during the first year of life. Either a Ricker model (centered to reduce correlation between parameters) or a Beverton-Holt model is permitted. Initial comparisons of alternative models for density dependence showed little ability to discriminate among models when fit to back-calculated data. We chose the Beverton-Holt relationship instead of the Ricker form for three reasons: First, it avoids the possibility of ‘‘crossing-over’’ when varying the upstream carrying capacity (lower recruits with a higher capacity) because the recruits from two capacities are additive. Second, there has been little evidence of over-compensation through the period of high spawner returns 2009 to 2012. Third, predictions from the Beverton-Holt model (Equation 4) are more conservative. The carrying capacity, K_{pop} , was estimated from previous efforts to fit Equation 4 to back-calculated $S(t)$ (Table 1). The capacity of the upstream, new spawning habitat is obtained by multiplying K_{pop} by parameter, K_{fact} . Note that the number of recruits in Equation 4 accounts for all density dependence during the first year of life.

$$\begin{aligned}
\text{Let } S(t) &= \sum_{k=0}^1 \left[N_{S_{k,wild}}(t) + N_{S_{k,hatchery}}(t) \right] \quad (\text{total female spawners}) \\
n_{k,0}(t+1) &= \frac{\alpha S(t)}{\left(1 + \frac{S(t)}{\widehat{K}_{pop}} \right)} \quad (\text{Spawner – recruit relationship}) \quad (4)
\end{aligned}$$

Let $N(t)$ denote the total abundance of the Snake River population at time t , with initial value, $N(0)$. We adopted the stable age distribution as our initial age distribution, *Pinit_age* (Table 3) and assigned an initial juvenile life history based on vector Py , drawn from a list of historical annual values.

Table 3. Input parameters by age include the initial allocation of individuals by age, and the cumulative proportion of female spawners returning to the mainstem Snake River. Stable age distribution was used to estimate *Pinit_age*. The likelihood of spawning at age $x+1$, given survival to age x is obtained from *Cmature* (mean) and *Cmat_CV* (CV). Values are based on adult returns to Lyon’s Hatchery between 1990 and 2006 (excluding 1995-7, 2001) (Milks et al. 2009).

Parameter	Age 1	Age 2	Age 3	Age 4	Age 5	Age 6
<i>Pinit_age</i>	0.7453	0.2034	0.0416	0.0076	0.0018	0.0030
<i>Cmature</i>		0.05	0.2932	0.7474	0.9913	1.000
<i>Cmat_CV</i>		1.808	0.7615	0.2219	0.0126	0.0009

1.4 VARIATION IN DEMOGRAPHIC RATES

Demographic stochasticity can be important for forecasts of future viability. For example, Zabel and Levin (2002) highlighted the sensitivity of PVA results to age structure. Many stochastic features of our PVA model involve drawing counts from a beta-binomial distribution to account for heterogeneity in probabilities among individuals, leading to over-dispersion (i.e., variance > mean), see Teerapabolarn and Boondirek (2010). Mean rates were drawn from a beta distribution on the interval between zero and one. These rates were then used to draw a count of individuals (those that belong to a given gender or age category or that survive a threat) from a binomial distribution. We obtained estimates of means and CV = standard error (SE)/mean from the literature or from data when possible, as described below. When no estimate of the CV was available, we used a Poisson distribution (i.e., no over-dispersion). Assumptions about stochastic elements are summarized in Table 2.

Demographic stochasticity due to fluctuation in sex-ratio was represented by assuming that no recruitment occurs in years when, by chance, males are absent. Each year a random number of male spawners was drawn from a binomial distribution with proportion male, $P_m \sim \text{beta}(\alpha, \beta)$. In our data, the proportion of female returns over eleven years showed low variation (SE = 0.005, CV = 0.011). We determined the number of female eggs following reproduction using a Poisson distribution with mean 0.5 (Jensen and Hyde 1971), and similar variability to that observed later in life.

Stochasticity in survival was represented by drawing $n_{k,i}(t+1)$ from a negative binomial distribution with a quadratic mean-variance relationship (LeCam 1960, Linden and Mantyniemi 2011) with mean $\lambda = \#$ female spawners x $(1 - Pfemale)$ and coefficient of variation, *Pfemale_cv*. Our efforts to relate environmental stochasticity to ocean conditions revealed a weak relationship with ocean climate, in contrast to previous analyses for spring Chinook salmon (Zabel et al. 2006). Consequently we did not include ocean influences, but the model can represent climate influence on incubation survival if such an effect is detected.

1.5 JUVENILE SURVIVAL

We assume that first-year survival differs for sub-yearling emigrants and juveniles that exit as yearlings (Equation 1). We distinguish five time periods through which juveniles must survive: (1) the period from egg to emergence as fry and development into smolts (rearing), (2) downstream migration survival from above Lower Granite Dam (LG) in the Snake River to below LG, (3) survival from the LG Dam tailrace to the Bonneville Dam tailrace, (4) survival through the unimpounded Lower Columbia River and estuary before reaching the ocean, and (5) ocean survival during the remainder of the year.

For both juvenile life histories, first-year survival includes the rearing period from egg to smolt. Survival of the rearing period ranges from 6 to 15% below Hells Canyon Dam, with 46.5% survival to emergence (Groves and Chandler 2003) and the remaining mortality after emergence and before emigration of sub-yearlings in late-spring.

1.5.1 SUB-YEARLING LIFE HISTORY

Jolly-Seber-Cormack survival estimates for juveniles migrating downstream rely on release and recapture data from PIT-tagged juveniles released upstream and tracked using detectors at each of eight downstream dams. Unfortunately, detection probabilities are not high enough to permit estimates of survival all the way from the Snake River to below Bonneville Dam. This problem is circumvented by multiplying average survival from the Snake River to LG and from juveniles released below LG to below McNary Dam, and from below McNary Dam to below Bonneville Dam. According to Williams et al. (2008), sub-yearling survival through the eight-dam hydrosystem lies between 0.05 and 0.25. A more-recent estimate by Rechisky et al. (2009) found 40% survival for larger (>140 mm) smolts released at Kooskia National Fish Hatchery above Dworshak Dam in the Clearwater River.

Snake-LG—Survival of marked juveniles to LG has been shown to increase with size (Connor et al. 2004) and decrease with temperature (Connor et al. 2003). Survival has been shown to be lower for later outmigrants (0.20 in September) than for earlier emigrants (0.45-0.76 in May-June) (Smith et al. 2003). We take our estimate of SE from Muir et al. (2006), who estimated migration survival of spring Chinook smolts in six years (1997-2002) as 0.4702 (SE = 0.0444). For fall Chinook, we calculated a weighted average of $S_{LGR,0} = 0.6297$ based on a 1997-1998 study of hatchery juveniles PIT-tagged and released from Pittsburg Landing and detected passing LG Dam (Connor et al. 2004). Connor (personal communication) estimated survival of surrogate juvenile fall Chinook in 2006 as 0.4146.

LG-Bonneville—Two recent Jolly-Seber-Cormack estimates of survival from LG Dam to below Bonneville Dam, averaged $S_{BON,0} = 0.3685$. We estimated survival from LG Dam to below Bonneville based on detection data from a transportation study in 2004 as 0.3224. Marked yearling individuals that remain in reservoirs until winter and are detected the following year were removed from the estimates, but concerns about violating the assumption of constant likelihood of detection remain.

Estuary—Estimates of estuary survival of sub-yearling fall Chinook, $S_{EST,0}$ from the Bonneville Dam tailrace to the mouth of the Columbia River, a distance of 226 km traveled in 4-5 days, ranged from 0.15 to 1.0 [average 0.588 ± 0.083 ; (McMichael et al. 2007)]. A later study of survival in the Columbia River below Bonneville indicated that survival was quite variable (Clemens et al. 2009). Sub-yearlings arrive in the estuary during spring and summer, after which we apply ocean survival, $S_{OC,0}$ from summer to fall.

Total first-year survival is simulated as the product of survival through four periods: egg-to-smolt, outmigration from the Snake River to LG, LG to Bonneville, estuary-to-ocean by August, followed by a final quarter year in the ocean ($S_{OC,0}$)^{OC-0}. During their second year of life, we assume that sub-yearling emigrants are exposed to a full year of ocean mortality, $S_{OC,1}$.

We did not consider different routes of downstream transportation of juveniles to the estuary. Downstream transportation of juveniles is a controversial management tool that could have an important effect on overall survival during the second year of life. However, evidence that transportation has a significant effect, delayed or otherwise, seems to be evaporating under continued scrutiny. Juvenile survival estimates were similar for spring Chinook migrating through the six of the dams in the hydrosystem (mean = 0.486, range 0.279 to 0.578) and for transported juveniles (mean = 0.553, range 0.336 to 0.683, including delayed mortality) (Williams et al. 2005). Delayed mortality was not significantly greater than one in any year between 1994 and 2004 (Schaller and Petrosky 2007) and was not consistent with results of a survival study tracking large fall Chinook smolts released in the Clearwater River and monitored by an offshore ocean array (Rechisky et al. 2009).

1.5.2 YEARLING LIFE HISTORY

Yearling-type fish remain in the river through the fall of their first year and exit during late winter. They then traverse the estuary, and spend the remainder of their second year in the ocean. For the remainder of the first year, between spring emigration of sub-yearlings and fall birth date, we represent reservoir survival as a multiplier of ocean survival contemporaneously experienced by sub-yearlings, $S_{RES} = S_{RES_OC} S_{OC,0}$. We calibrated S_{RES_OC} , along with the proportion remaining above Lower Granite Dam, P , against the yearling smolt-to-adult return ratio. Our best estimate of survival during the second year (from fall) is the product of (1) survival of fall Chinook salmon during downstream migration from above LG Dam in the Snake River to below LG Dam, $S_{LGR,I}$, (2) survival while migrating downstream from the LG tailrace to the Bonneville Dam tailrace, $S_{BON,I}$, (3) estuary survival, $S_{EST,I}$, and (4) ocean survival during the remaining quarter-year to the following fall, $(S_{OC,I})^{OC-1}$.

Faulkner et al. (2007) estimated survival of yearlings through the eight-dam hydrosystem from the Snake River trap (located at rkm 224.6 near the Clearwater R. confluence) to the Bonneville Dam tailrace for each year from 1999 and 2006 (average 0.4804). This is within the range of other published survival estimates (0.3102 to 0.5232), obtained by combining releases at rkm 341 on the Snake River detected at Lower Granite Dam with releases from the LG tailrace detected in the Bonneville Dam tailrace (see below).

Snake-LG.—Average survival of hatchery fall Chinook released as yearlings from Pittsburg Landing (rkm 341) in 1997 and 1998 was 0.9079 (standard error, SE = 0.015; (Connor et al. 2004)). Estimated survival between 2001 and 2006 of wild yearlings from the Snake River trap at the head of LG (rkm 224.6) to the LG Dam tailrace averaged 0.9438 (SE = 0.034; (Williams et al. 2005, Faulkner et al. 2007)). We use the weighted average of these two estimates, $S_{LGR,I} = 0.9344$ for this period. The reported survival of wild yearlings from the Salmon River trap to the LG tailrace was lower, 0.862 (Williams et al. 2005).

LG-Bonneville.—Survival of out-migrating yearling fall Chinook is not known at the time of this study. We therefore assume that survival is the same as survival of yearling spring Chinook, which has increased over time, possibly in response to improvements at the dams and in flow regimes (Williams et al. 2005). An early estimate of out-migration survival during the period 1977-1979 was 0.095 (Marmorek et al. 1998, cited by Kareiva et al. (2000)). Recent survival estimates, derived from PIT-tag data for wild and hatchery yearling spring Chinook salmon migrating downstream from above Lower Granite Reservoir to below Bonneville Dam, are higher. Smith et al. (2010) reported an average hydro-system survival of 0.332 between 1993 and 2004. Williams et al. (2005) reported a somewhat higher estimate, 0.464 (SE = 0.052), for the period from 1997-2003. Ferguson (2007) estimated 2007 yearling survival through all 8 reservoirs and dams as 0.56. We estimated $S_{BON,I} = 0.5142 (= 0.4804 \div S_{LGR,I})$ to be consistent with Faulkner et al.'s (2007) estimate, which includes the whole river starting from the Snake River down.

Estuary—Survival of yearlings from below Bonneville Dam to the mouth of the Columbia River estuary,

a distance of 226 km travelled, on average, over 4.1 days, ranged from 0.57 to 0.66 [avg. 0.615; (Ferguson 2007)]. This estimate is considerably higher than an earlier one using an inverse method ($S_{EST,I} = 0.017$) (Kareiva et al. 2000)(Wilson 2003). McMichael et al. (2007) reported twelve estimates of estuary survival for yearlings during 2005 and 2006, averaging $S_{EST,I} = 0.653 \pm 0.046$ (range 0.564 to 0.873).

1.6 ADULT SURVIVAL

Adult fall Chinook migrate farther north along the North Pacific coast with age, where they are exposed to fisheries from the coast of Oregon and Washington up to West Vancouver Island, Central British Columbia, and Alaska (Norris et al. 2000). Snake River fall Chinook Columbia River apparently do not move as far north as stocks that spawn farther downstream (Norris et al. 2000). Most individuals marked at Lyons Ferry Hatchery (30% of age-3 adults, 27% of age-4 adults, and 24% of age-5 adults) migrated to the area west of Vancouver Island and the Queen Charlotte Islands, but sizable fractions of adults age 4 (24%) and 5 (41%) continued on to the coast of Alaska (Norris et al. 2000).

Ocean survival has varied over time: The ocean exploitation rate, S_{OC} , for fall Chinook decreased from 34.9% between 1982 and 1989 [PSC 1994 in Myers et al. (1998)], to 11.5% in 1995 and 23% in 1996 (Myers et al. 1998). In our model, we assume that females of age x in the ocean survive at rate $S_{OC,x}$ (Tables 1, 3). We simulate size-dependent predation by piscivores and other marine predators, $S_{oc,x}$ (Equation 5; Figure 1), where a logistic equation for average fork length was fitted to length data for sub-yearlings and yearlings passing Bonneville Dam for ages 1 and 2 (Connor personal communication via 2008 presentation) and to average sizes of female spawners for ages 3 to 6 (Milks et al. 2009). In Equation 5, $S_{oc,max}$ is the maximum survival and L_{max} the average size of age-6 female spawners (Table 2).

$$S_{oc,x} = S_{oc,min} + (S_{oc,max} - S_{oc,min}) \left(\frac{(L_x - L_0)}{L_{max} - L_0} \right), \quad (5)$$

$$\text{where } L_x = \frac{L_{max}}{1 + \exp \left[\frac{-(x - x_0)}{xs} \right]}.$$

We estimated maximum ocean survival from exploitation rates, Z , for wild Snake River fall Chinook salmon for 1986-2006 (NOAA Fisheries 2008) as $S_{oc,max} = \exp(-Z)$. Because the lower bound, $S_{oc,min}$, is the only component of survival with no measured estimate, we estimated the posterior distribution of parameters using the MCMC procedure described in section 3.

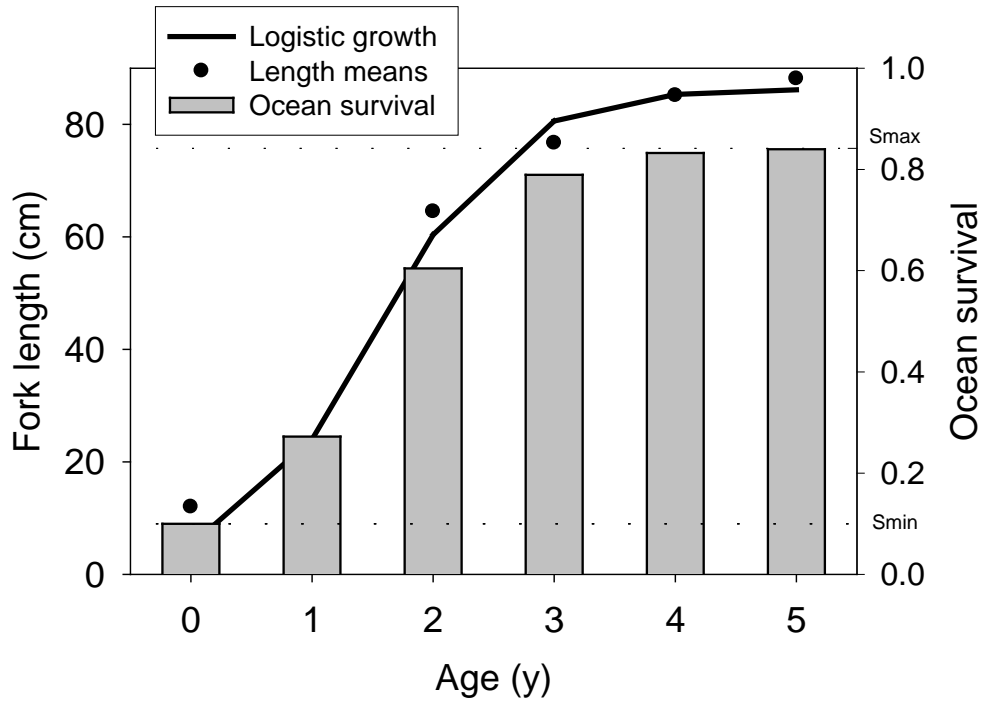


Figure 1. Size-dependent model of ocean survival between limits $S_{oc, min}$ and $S_{oc, max}$.

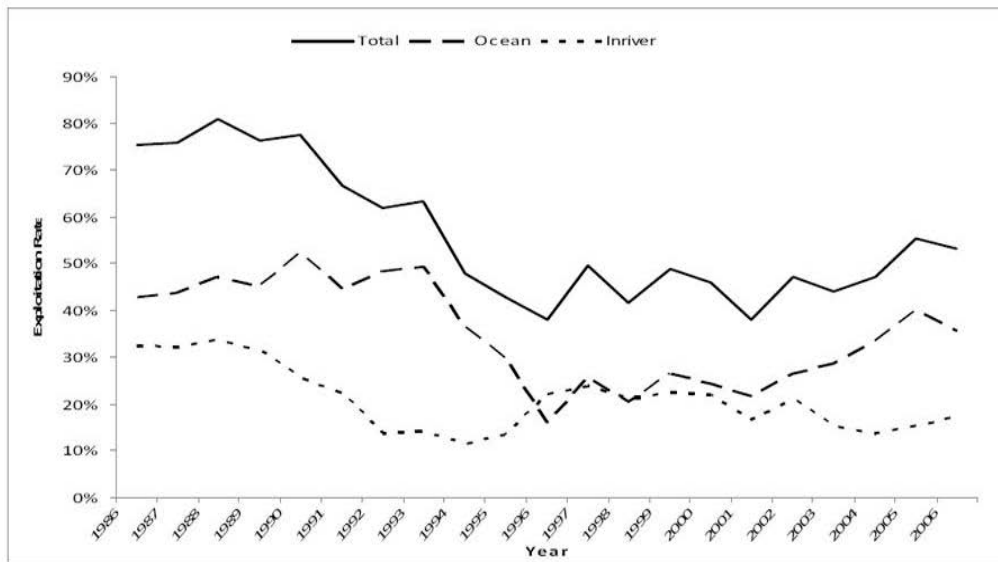


Figure 2. Ocean and in-river exploitation rates (percent of upmigrating spawners counted at Bonneville Dam) for Snake River fall Chinook. Source: (NOAA Fisheries 2008).

LPVA assumes that all females that attempt a spawning migration die within the same year. However, to back-calculate the number of females at each reproductive age in winter from counts the following fall, we require an estimate of survival from winter to fall of the year of spawning. We assume that females of age i intending to spawn during the next year spend $Oc_last = \frac{3}{4}$ of the year (December to August) in the ocean, with survival $S_{OC,i}$. Not all females that attempt migration are counted at Lower Granite Dam because a sizable fraction dies during migration up river, represented by S_{UP1} . During the 1990's, upmigration survival to LG estimated based on pit-tagged adults observed above LG was 0.55 (Peters et al. 2001). This estimate did not separate males from females, but jacks were excluded. We used a more recent estimate, the unadjusted Bonneville-to-LG conversion rate, $S_{UP1} = 0.645$, which was reported in a Biological Opinion by NOAA Fisheries (2008). Approximately half of mortality during upmigration is caused by harvest within the Lower Columbia River; Survival of in-river harvest alone averaged 0.79 between 1987 and 2006 (NOAA Fisheries 2008) (Figure 2). The exploitation rate within the Lower Columbia River decreased since the mid-1980's [Table 1, Pacific Salmon Commission 1994 in (Myers et al. 1998)], but has more-recently increased (Figure 2).

Tribal harvest in the Snake River between Lower Granite pool and their spawning destinations is believed to be low. We estimated survival through this final, pre-spawning period as $S_{UP2} = 0.71$ based on comparing counts of upmigrating adults with redd counts. Chandler and Chapman (2001) used a fallback estimate of 35% to adjust escapement data for 1993 and 2000. Fish-per-redd estimates ranged from 2.0 to 3.6, suggesting an average mortality between passing LG Dam and spawning in the Snake River of 0.29 for adults passing LG. Upon reaching the spawning ground, most, but not all, females survive to spawn, S_{pre} (Table 1).

1.7 REPRODUCTION

Spawner-recruitment (SR) relationships are typically used to model reproduction. In the simulations reported here, we used a mechanistic approach to simulating recruitment to age 1. Female offspring that survive to age 1 were estimated from females surviving to reach the spawning grounds based on fecundity, density dependence, and estimates of juvenile survival. Most females spawn between the ages of three and five. We allocated ocean females among ages at return using $P_{init_age}(x)$, the proportion surviving to age x that spawn before reaching age $x+1$ (Table 3). This number of females was reduced by removing females used for translocation or broodstock at the two traps, and estimating the female spawners surviving upstream migration to LG, S_{UP1} and from LG to the Snake River below Hells Canyon, S_{UP2} .

Egg production in the new population was calculated by applying mortality to females that were translocated upstream (presumably with males). The model provides for different egg-to-smolt survival in the new population. We simulated density dependence with a habitat capacity of 5,000 females below Hell's Canyon Dam based on peak returns to LG observed during 2009-2012. Maximum fecundity was based on hatchery estimates. We then applied mechanistic sources of first-year mortality described earlier. Finally, we estimated and reported the model-simulated spawner recruitment parameters for comparison against empirically-derived values, which are currently being constructed.

The model provides for an alternative empirical approach that estimates a spawner-recruitment relationship for age-1 females empirically by back-calculating from census counts of female adults returning to LG Dam. When this approach is used, mechanistic sources of mortality during the first year are not applied.

2 BAYESIAN MULTI-PARAMETER MODELING & SENSITIVITY ANALYSIS

We implemented a Bayesian approach to estimate the posterior distributions of poorly-known parameters, $\bar{\theta}$, given historical data (\mathbf{D} = spawner returns to Lower Granite Dam, 1961-2011), as shown in Equation 6. The LPVA compares with data from two sources, historical spawner abundances and average smolt-to-adult return ratios (SAR) at LG for the two juvenile life histories. Between 1990 and 2001, averages based on studies of coded-wire tag juveniles detected upon returning to spawn indicate that roughly 0.4% of juveniles released as sub-yearlings and 0.615% of juveniles released from Lyons Ferry hatchery as yearlings returned to Lower Granite Dam as adults. Likelihoods are estimated separately for the two types of data, as described below, and combined by multiplying.

The posterior distribution is the stationary distribution of the chain (Marjoram et al. 2003), as shown in Equation 6.

$$P(\bar{\theta} | \bar{\mathbf{D}}) = \frac{\pi(\bar{\theta}) P(\mathbf{D} | \bar{\theta})}{P(\mathbf{D})} \quad (6)$$

Following Piou et al. (2009), we began by assigning prior distributions, π_j (Table 4). Two survival parameters (S_{EGG} and $S_{OC,min}$) and $K_{trap,min}$ were assigned beta-distributed priors; The ratio $S_{RES,OC}$ was assigned a Gaussian prior distribution (Table 4).

Table 4. Parameters of prior distributions and hyper-parameters used in estimating the posterior distribution of four poorly known LPVA parameter consistent with available historical data for spawner returns.

Parameter	Distribution	Mean	SD	Minimum	Maximum
$K_{trap,min}$	Beta	0.10	0.01	0.00	0.8
S_{EGG}	Beta	0.15	0.01	0.0	0.7
$S_{OC,min}$	Beta	0.05	0.005	0.0	0.5
$S_{RES,OC}$	Gaussian	2.0	0.1	0.0	3.0

We simulated a Monte Carlo Markov chain of length 100,000. For each iteration, a new parameter vector, $\bar{\theta}$, was independently drawn from a joint, independent prior distribution, π . For each multivariate draw, we estimated the negative log-likelihood, $POM = -2 \sum_i \log(L(D_i | \bar{\theta}))$ using a kernel-density estimation approach that can be used for black-box models (Marjoram et al. 2003, Piou et al. 2009). We used a Metropolis-Hastings algorithm to simulate a Markov chain to estimate the posterior distribution. Each parameter's jump distribution was $\mathbb{N}(\mathbf{0}, \mathbf{V})$, where $v_{ii} = \sigma$; $v_{ij} = 0$. The jump distribution can be optionally adapted by varying σ (Roberts and Casella 2010) (Shaby and Wells 2011), as part of the Langevin adaptive procedure, where

$$\sigma_t = \sqrt{\sigma_{t-1}^2 e^{\frac{1}{2}(r_t - r_{opt})}}, \quad (7)$$

r_t is the acceptance rate at step t and $r_{opt} = 0.234$ is the optimal acceptance rate. Proposed vectors $\bar{\theta}$, falling outside the specified parameter domain were rejected, as recommended (Gelman et al. 2004, Roberts and Casella 2010). Parameter sets within the specified domain and leading to higher likelihoods $L(\bar{\theta} | \mathbf{D})$ were accepted and those within the domain with lower likelihoods were accepted with

$$\text{probability, } r = \frac{P(\theta' | D)}{P(\theta | D)} = \frac{\pi(\theta') L(D | \theta')}{\pi(\theta) L(D | \theta)}.$$

We characterized the posterior distribution of four parameters (Figure 3). The historical data was able to resolve these four parameters fairly well, as evidenced by the well-defined peaks (Figure 3).

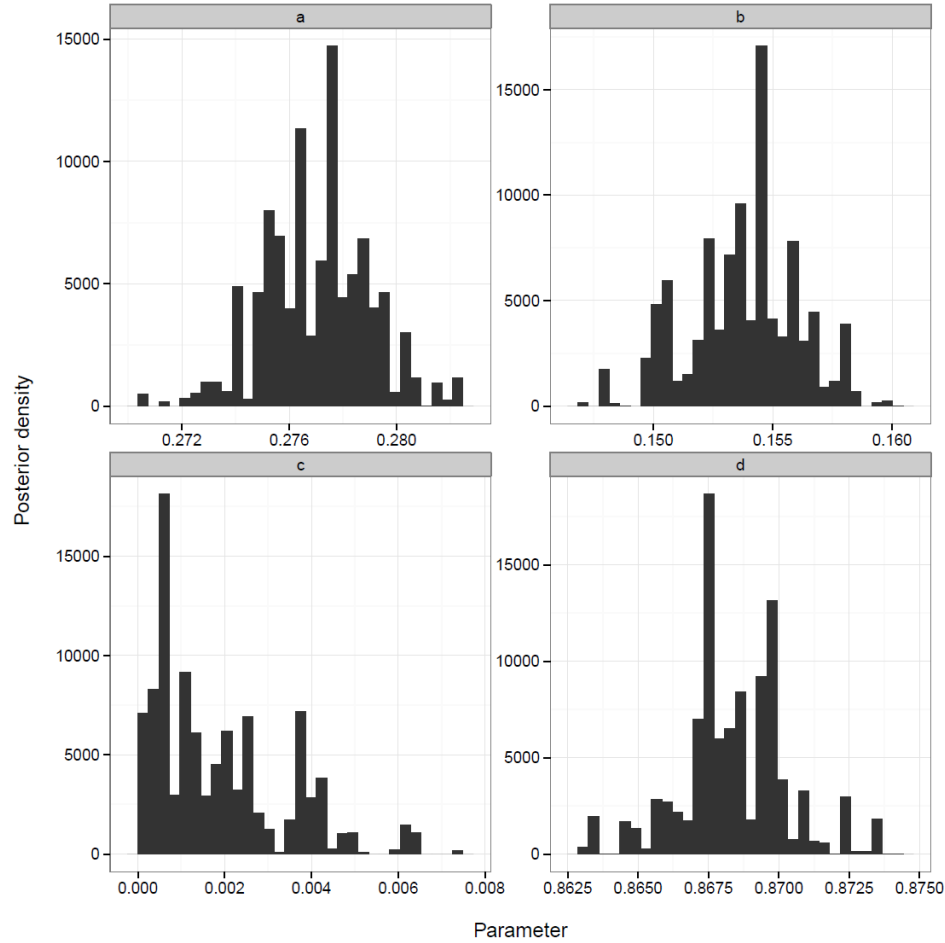


Figure 3. MCMC-estimated posterior distributions of four poorly-known parameters, a) K_{trap_min} , b) S_{EGG} , c) $S_{OC,min}$, and d) S_{RES_OC} .

We conducted ensemble modeling of future persistence under different reconnection scenarios. This was accomplished by simulating from the posterior chain of parameters. We sampled this distribution by retaining the final 10,000 vectors. The following options are provided for running the LPVA with more than one parameter set, selected through parameter switch *MC_method*:

- 1) Generate a grid of values for an arbitrary number of parameters, specifying minimum, maximum, and step size, where a negative step size is used to indicate a multiplicative change.
- 2) Use Gibbs sampling to estimate the joint posterior distribution of parameters (rejection sampling).
- 3) Use the Metropolis-Hastings algorithm described earlier, updating all parameters as a single block, with either adaptive or non-adaptive sampling.
- 4) Conduct simulated annealing to find the maximum likelihood parameter set.

- 5) Read-in a previously generated list of parameters.
- 6) Read-in a previously generated list of parameters and combine with all possible combinations of a grid. This method is used to project alternative reconnection scenarios for a chain of equally-likely parameter alternatives.

After following this procedure, we used regression tree analysis to explore the importance of management variables, including up and downstream trapping rates, spawning the ratio of habitat capacity above Brownlee to that below Hells Canyon, and survival of early life stages in Brownlee Reservoir relative to that below Hells Canyon.

To assess sensitivity, a sensitivity program was developed in R. This program calculates partial correlations between model-simulated results (historical population trends) for each parameter vector and the individual parameter values.

3 SIMULATING REINTRODUCTION OPTIONS

The purpose of the LPVA model was to assess the benefits to the overall fall Chinook salmon ESU of introducing a new upstream population. LPVA represents supplementation options and to evaluate their effectiveness in supporting the Hells Canyon fall Chinook salmon ESU. LPVA tracks cohorts defined by four attributes: 1) population, 2) age in y, 3) juvenile list history type, and 4) mark type. One option for introducing a “new” population of fall Chinook salmon above the Hells Canyon Complex (HCC) is to use hatchery supplementation of the Brownlee reach. The approach is general, allowing two hatcheries, one drawing from adult returns below Lower Granite Dam (LG) and one drawing from adult returns below Hell’s Canyon Dam (HC). Processes simulated for each hatchery include i) trapping of adults for broodstock, ii) survival of broodstock, iii) egg production and survival, iv) division into release groups by destination (below HC and above Brownlee) and by age at release (age-0 and age-1), v) division into cohorts with different marks, and vi) simulation of downstream migration through two routes, as depicted by Figure 4.

At each node, demographic stochasticity is simulated via binomial decisions (i.e., for individuals within an age class-). Individual variation in probabilities is simulated using a beta-binomial distribution as described by Link and Hahn (1996), which makes use of coefficients of variation, such as *Scv*. These parameters are described in Table 2.

Adult trapping.—Adult trapping begins at a specified year for each trap, *Trap1_year* and *Trap2_year* (Table 1). During years of operation, the hatchery module removes broodstock by capturing upmigrating females that return to LG with rate, *Trap1_up*. This rate was estimated from operational data from traps at LG. This rate was estimated from operational data from traps at Lyons Ferry Hatchery. The rate of upstream trapping, λ , is assumed to increase over time, *t*, mirroring historical trends in juvenile releases of hatchery fish.

$$\lambda(t) = \text{Trap_rate_up} \frac{(1 - K_{\text{trap_min}})(t - \text{Trap1_year})}{(\text{Trap_yr_historic2} - \text{Trap1_year})} \quad (8)$$

In future simulations, those reaching the upstream trap were removed at rate, *Trap2_up*.

Efforts to maintain a new, distinct population above the HCC depends on the ability to determine adult origin and prevent introgression. The main tool for doing this is selective removal of adults with different marks indicating origin at the two traps. Six possible marks distinguish salmon with different histories (Table 5).

Table 5. Marks distinguishing Snake River fall Chinook salmon caught and released at different locations.

Mark id	Previous mark	Trap	Origin	Site or event of last marking	Marks	Translocate excess fish?	Disposition upon return as adult
0 (none)	none	Unknown origin	Unknown	Unknown	none	no	Downstream trap
1	none	LG dam trap	Below HCC	LF hatchery (ponded fry)	adipose fin clip	no	Downstream trap; Upstream trap only during transition.
2	none	HC dam trap	Below HCC	BR hatchery (ponded fry)	mandible clip	yes	Upstream trap only
3	none	HC dam trap	Above HCC	BR hatchery (ponded fry)	mandible + adipose clip	yes	Upstream trap only
4	none	Brownlee (natural) juvenile trap	Below HCC	Translocation release site; Brownlee trap	mandible + left ventral (translocated parents)	yes	Upstream trap only
5	3	Brownlee (hatchery) juvenile trap	Below HCC	BR hatchery; Brownlee trap	mandible + adipose + left ventral	yes	Upstream trap only

Although trap rates are indiscriminate, our trap quotas discriminate among returning females with different origins. The idea is that the trap catches all returning females with a given rate, but only those selected are removed either for use as broodstock or to be transported upstream. When parameter *Bool_trapmark* = 1, *Trap1_mark* and *Trap2_mark* are zero-one vectors indicating whether or not females of a certain origin, indicated by marks in Table 5, should be removed. We also defined a transition period between the year of establishment for a new spawning population, *Yr_newpop1* and operation of the upstream trap below HC Dam. Negative values of *Trap2_mark* indicate that operations can be seeded using adults with these marks, but only during the transition period.

In our analyses, we assumed that the lower LG trap removed unmarked adults and those indicating origin below HCC, i.e., Mark id's 0, 1, and 2 (Table 5). We assumed that the upper trap (HC) removed females with marks 3, 4, and 5, (origin above the HCC). During the transition period, we permitted females with mark 1 (LF hatchery origin) to be removed at the upstream, HC trap.

Alternatively, *Trap_mark* vectors can be proportions summing to one, and thereby apportion the specified *Up1_quota* or *Up2_quota* among returning females with different marks. At the upper, HC trap, we translocated females captured beyond this quota above the HCC (Figure 4) if this was indicated by vector *Trans_mark*. We assumed that adults trapped at the lower LG trap would not be used to supplement the new, upstream spawning population.

Egg production.—Each year, the number of broodstock surviving pre-spawn mortality was drawn from a beta-binomial distribution with mean, *Spre*. On average, 50% of eggs are assumed to be female, drawn using a binomial distribution. The number of green eggs surviving to release at ages zero and one are drawn from beta-binomial distributions with mean *Shatch1* and *Shatch2*, respectively. Parameter values were estimated from data in reports from Lyons Ferry Hatchery (Milks et al. 2009).

At this point, surviving eggs are divided between juveniles to be released at age 1 and at age-0. We specify a quota of age-1 releases and this quota is met before releasing age-0 eggs below, *Qjuv1_below*, or above, *Qjuv1_above* the HCC. Age-0 releases are added to the age-1 cohort, whereas eggs slated for release at age-1 are stored until the following year and subsequently added to the age-2 cohort. All surviving hatchery-reared juveniles are ultimately released.

The user specifies start and end years for implementation of a new population. Prior to the start year, hatchery offspring are added to the population below HCC. After the start year, hatchery offspring are divided between the habitat above and below HCC using a proportion *Pnew* specified for each trap. Different levels of age-0 survival can be simulated. However, we expect that the poor water quality above HCC would actually lead to much lower survival.

Density dependence.—An important aspect of simulating hatchery supplementation is to represent the effects of adding juveniles on habitat capacity. To address this, the model now separates the non-density-dependent portion of reproduction and the density-dependent portion. After simulating maximum egg production, both wild and hatchery-produced, these are combined by population prior to estimating the reduction due to density-dependent effects. Because we already have eggs at this point, the model back-estimates females and applies a Beverton-Holt relationship. Differences in habitat capacity for the two populations (*Kr* = ratio of capacity above to below HCC) come into play here. The natural (translocated) and hatchery component are separated proportionally after recruitment to age-1 has been estimated based on total density for each population.

Marking.—Evaluating population models against data is greatly facilitated when the model simulates the observation process, including sources of uncertainty. This is because nearly all observations rely on tracking of marked individuals. We assumed that a proportion of adults and juveniles is marked whenever captured in a trap, regardless of ultimate disposition. The number of hatchery juveniles that are marked was drawn with parameters mean proportion, *Pmark*, and CV, *Pmark_cv*.

Downstream migration.— Juveniles above HCC travel downstream to LG via two routes. First, trapping

is simulated by specifying a downstream trapping rate, *Tdown*. This is done separately for cohorts with different marks. For age-0 releases, a Poisson count is drawn from both natural offspring of translocated females (if any) and age-0 hatchery releases. Migration survival from above HCC to LG is simulated for juvenile cohorts trapped and transported (average = *Struck_LG*) and those migrating in-river (*Sriver_LG*) using beta-binomial distributions (Table 1, 2).

4 CONCLUSIONS

This report documents the methods to be used in evaluating the persistence of the Snake River fall Chinook salmon ESU under different management scenarios, including hatchery operations and trap-and-transport to spawning habitat above Brownlee Reservoir. The results of the simulations of these scenarios are reported elsewhere.

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