Model Description for the Sacramento River Winter-run Chinook Salmon Life Cycle Model

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I. Background and Model Structure

Given the goals of improving the reliability of water supply and improving the ecosystem health in California's Central Valley, NMFS-SWFSC is developing simulation models to evaluate the potential effects of water project operations and habitat restoration on the dynamics of Chinook salmon populations in the Central Valley. These life cycle models (LCMs) couple water planning models (CALSIM II), physical models (HEC-RAS, DSM2, DSM2-PTM, USBR river temperature model, etc.) and Chinook salmon life cycle models to predict how various salmon populations will respond to suites of management actions, including changes to flow and export regimes, modification of water extraction facilities, and large-scale habitat restoration. In this document, we describe a winter-run Chinook salmon life cycle model (WRLCM). In the following sections, we provide the general model structure, the transition equations that define the movement and survival throughout the life cycle, the life cycle model inputs that are calculated by external models for capacity and smolt survival, and the steps to calibrate the WRLCM.

Winter-run Life Cycle Model (WRLCM)

The WRLCM is structured spatially to include several habitats for each of the life history stages of spawning, rearing, smoltification (physiological and behavioral process of preparing for seaward migration as a smolt), outmigration, and ocean residency. We use discrete geographic regions of Upper River, Lower River, Floodplain, Delta, Bay, and Ocean (Figure 1). The temporal structure of winter-run Chinook is somewhat unique, with spawning occurring in the late spring and summer, the eggs incubating over the summer, emerging in the fall, rearing through the winter and outmigrating in the following spring (Figure 2). We capture these life-history stages within the WRLCM by using developmental stages of eggs, fry, smolts, ocean sub-adults, and mature adults (spawners). The goal of the WRLCM is consistent with that of Hendrix et al. (2014); that is, to quantitatively evaluate how Federal Central Valley Project (CVP) and California State Water Project (SWP) management actions affect Central Valley Chinook salmon populations.

In 2015, the WRLCM was reviewed by the Center for Independent Experts (CIE). In response to recommendations from the CIE, the following modifications were implemented in the WRLCM: 1) divided the River habitat to encompass above Red Bluff Diversion Dam (Upper River) and below Red Bluff Diversion Dam (Lower River); 2) incorporated hatchery fish into the WRLCM; 3) used 95% of observed density as an upper bound for calculation of habitat capacity; 4) re-parameterized the Beverton-Holt function; 5) used appropriate spawner sex-ratios for model calibration to account for bias in Keswick trap capture; 6) modified the WRLCM to a state-space form to incorporate measurement error and process noise; and 7) designed metrics and simulation studies to evaluate model performance. Hendrix et al. (2014) indicated that future work would use DSM2's enhanced particle tracking model to track salmon survival, which is currently being developed yet is not ready to incorporate into this version of the model.

Additional comments received in the CIE review that have not been incorporated yet include: 1) expanding spatial structure for spring and fall-run; 2) tracking additional categories of juveniles (e.g., yearling) for applying an LCM to spring-run Chinook; 3) implementing shared capacity for fall and

spring-run Chinook; 5) tracking monthly cohorts through the model; and 6) evaluating multiple model structural forms. We are actively working on improving the WRLCM and developing the spring-run LCM (SRLCM) and fall-run LCM (FRLCM). Many of the CIE recommendations will be implemented with subsequent versions of these models.
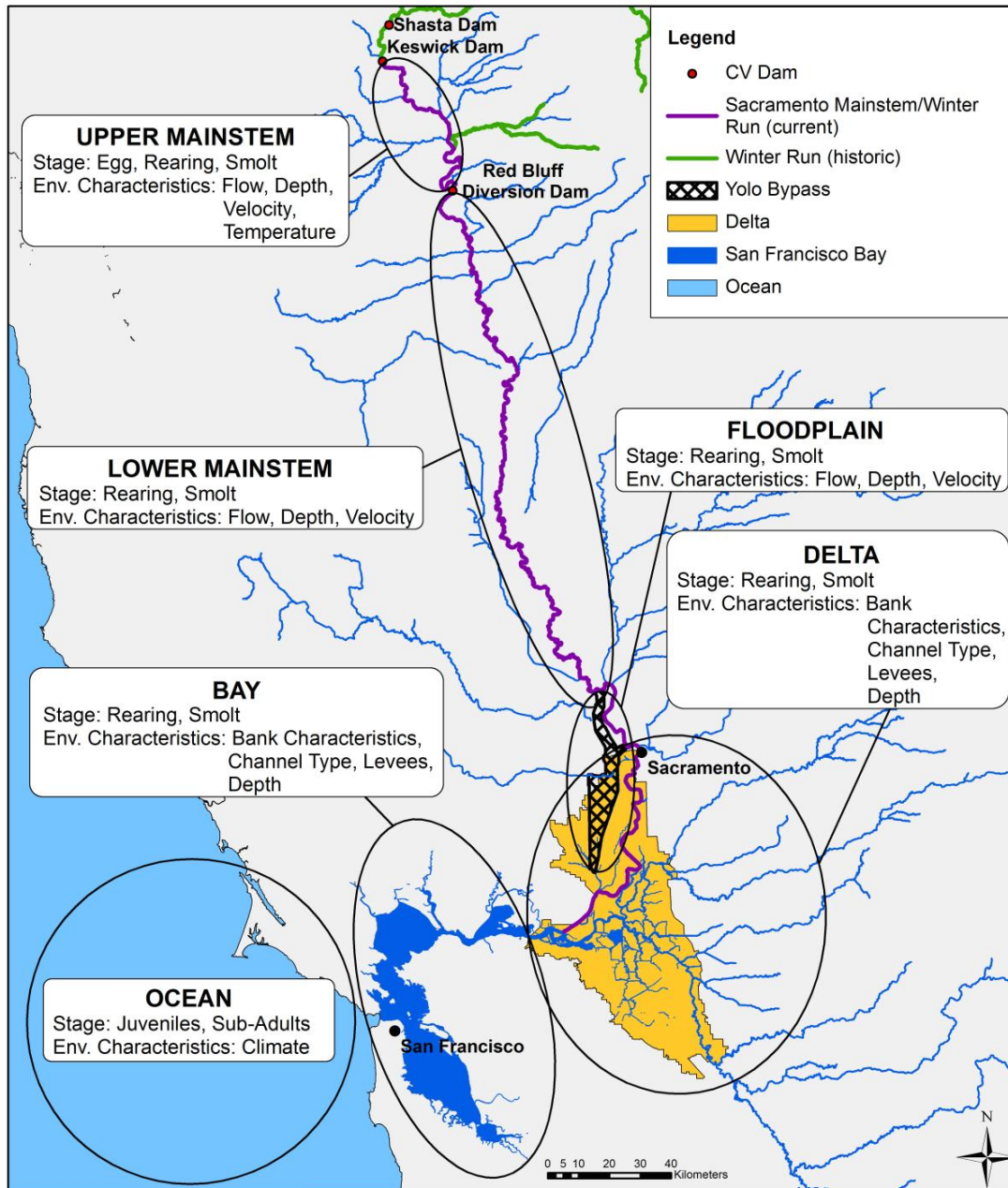

Figure 1. Geographic distribution of Chinook life stages and examples of environmental characteristics that influence survival.

The quantity and quality of rearing and migratory habitat are viewed as key drivers of reproduction, survival, and migration of freshwater life stages. Various life stages have velocity, depth, and temperature preferences and tolerances, and these factors are influenced by water project operations and climate.
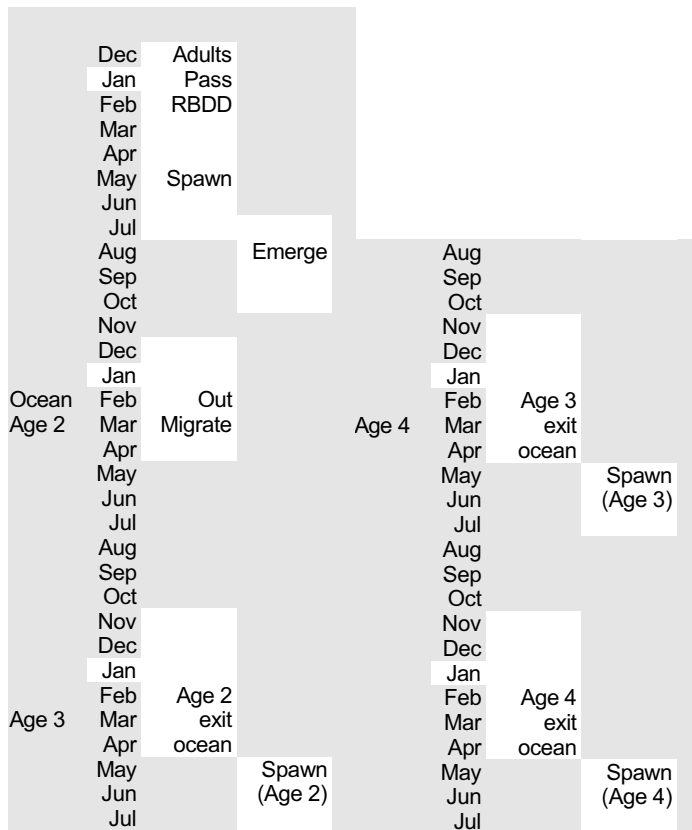
	Month	Stage		Month	Stage		Stage
	Dec	Adults					
	Jan	Pass					
	Feb	RBDD					
	Mar						
	Apr						
	May	Spawn					
	Jun						
	Jul						
	Aug	Emerge		Aug			
	Sep			Sep			
	Oct			Oct			
	Nov			Nov			
	Dec			Dec			
	Jan			Jan			
Ocean	Feb	Out		Feb	Age 3		
Age 2	Mar	Migrate	Age 4	Mar	exit		
	Apr			Apr	ocean		
	May			May			Spawn
	Jun			Jun			(Age 3)
	Jul			Jul			
	Aug			Aug			
	Sep			Sep			
	Oct			Oct			
	Nov			Nov			
	Dec			Dec			
	Jan			Jan			
	Feb	Age 2		Feb	Age 4		
Age 3	Mar	exit		Mar	exit		
	Apr	ocean		Apr	ocean		
	May	Spawn		May			Spawn
	Jun	(Age 2)		Jun			(Age 4)
	Jul			Jul			

Figure 2. Temporal structure of the winter-run Chinook salmon, each cohort begins in March of the brood year. Figure from Grover et al. (2004).

Hydrology (the amount and timing of flows) is modeled with the California Simulation Model II (CALSIM II). Hydraulics (depth and velocity) and water quality is modeled with the Delta Simulation Model II (DSM2) and its water quality sub-model QUAL, the Hydrologic Engineering Centers River Analysis System (HEC-RAS), the U.S. Bureau of Reclamation's (USBR) Sacramento River Water Quality Model (SRWQM), and other temperature models. Many of the stage transition equations describing the salmon life cycle are directly or indirectly functions of water quality, depth, or velocity, thereby linking management actions to the salmon life cycle. The combination of models and the linkages among them form a framework for analyzing alternative management scenarios (Figure 3).
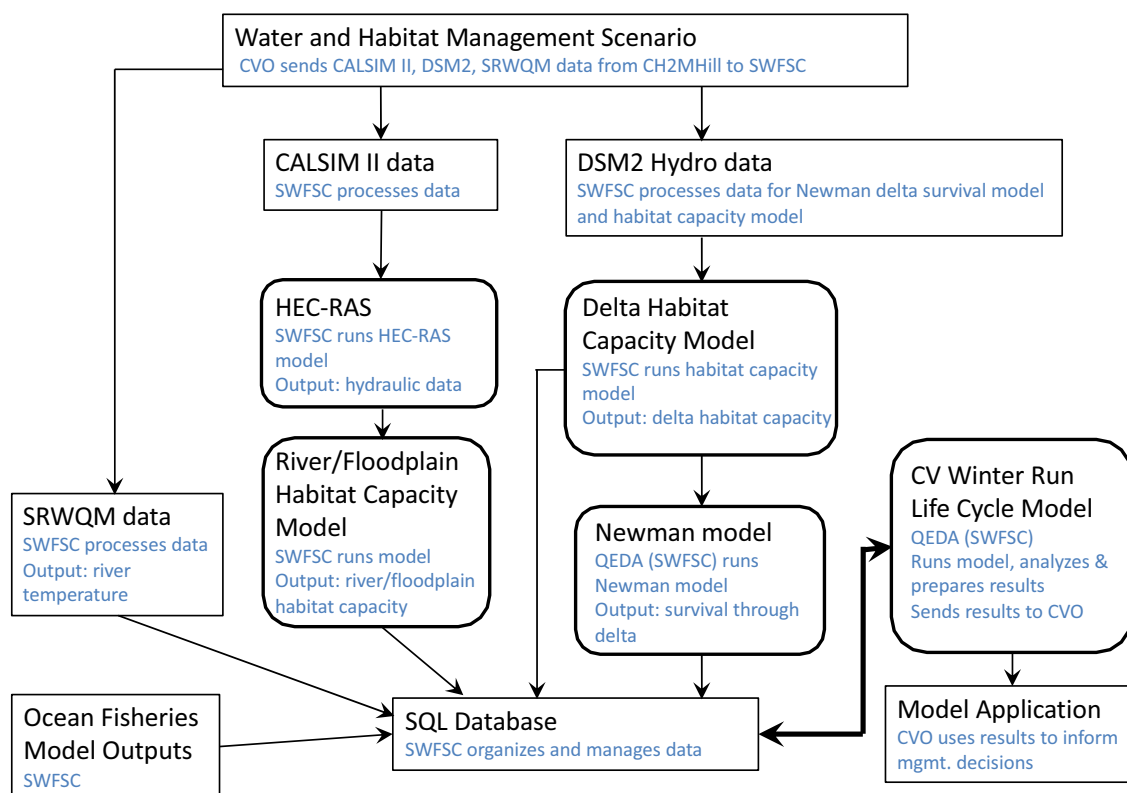
Central Valley Winter Run LCM Model Linkages

Figure 3. Submodels that support and provide parameter inputs that feed into the life cycle model.

The life cycle model is a stage-structured, stochastic life cycle model. Stages are defined by development and geography (Figure 1), and each stage transition is assigned a unique number (Figure 4).

II. Model Transition Equations

This section is divided into two parts. In the first part, we explain each of the transitions for the natural origin winter-run Chinook, which are described by the life cycle diagram (Figure 4). In the second part, we explain the transitions for hatchery origin fish. The transitions are described for an annual cohort; however, in most cases we have not included a subscript for the cohort brood year to simplify the equations. For those transitions in which there are multiple cohorts, such as the production of eggs in transition 22, a subscript to distinguish cohort is included in the equation. Note that all parameters used in the model are defined in Appendix B.
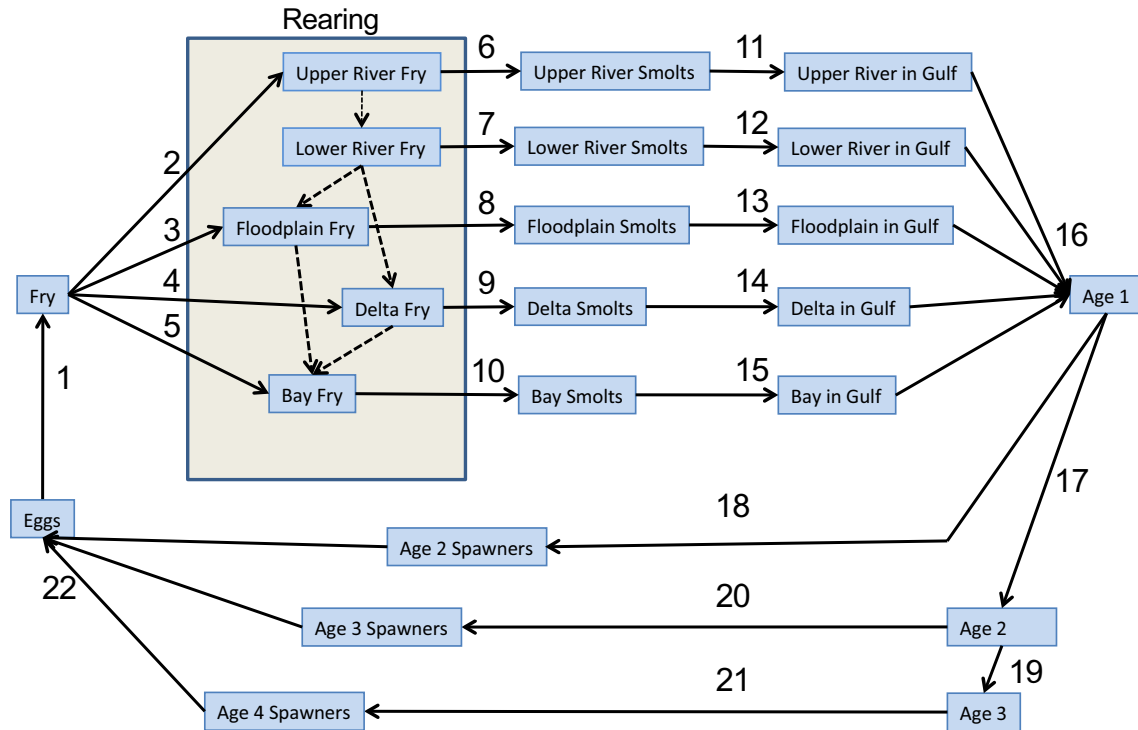
Figure 4. Central Valley Chinook transition stages. Each number represents a transition equation through which we can compute the survival probability of Chinook salmon moving from one life stage in a particular geographic area to another life stage in another geographic area.

Natural Origin Chinook

Transition 1
Definition: Survival from Egg to Fry

$Fry_{m+2} = Eggs_m * S_{eggs,\ m}$

$$logit(S_{eggs,m}) = \begin{cases} B0_1, & TEMP \le t.crit \\ B0_1 + B1_1(TEMP_m - t.crit), & TEMP > t.crit \end{cases}$$

where $S_{eggs,m}$ is the survival rate of fry as a function of the coefficients $B0_1$, $B1_1$ and $t.crit$ (model parameter representing the critical temperature at which egg survival begins to be decline), the covariate $TEMP_m$ (the average of the month of spawning m and the following 2 months), logit(x) = log(x/[1-x]) is a function that ensures that the survival rate is within the interval [0,1], for months m = (2, …, 6) corresponding to April to August.

Transition 2
Definition: Fry emerged in a given month either remain in the Upper River (UR) as Rear Fry ($RearFry_{UR,m}$) or disperse downstream as Tidal Fry ($TidalFry_m$) to the h habitats = Floodplain (FP), Delta (DE), and Bay (BA) in months m = (4, …, 8) corresponding to June to October.

$TidalFry_{m,} = P_{TF,}* Fry_m$

$RearFry_{UR,m} = (1 - P_{TF}) * Fry_m$

where P_{TF} is the proportion of fry moving out of the Upper River as tidal fry, and $RearFry_{UR,m}$ are the number remaining in the Upper River habitat (UR) as rearing fry.

Transitions 3 - 5

Definition: Dispersal of tidal fry to the h habitats = Lower River (LR), Floodplain (FP), Delta (DE), and Bay (BA) arriving in the month following emergence m = (5, …, 9) corresponding to July to December.

Floodplain Tidal Fry (Transition 3)

Whenever there are flows into the Yolo Bypass, a proportion of the Tidal Fry move into the floodplain habitat:

$TidalFry_{FP,m} = S_{TF,FP} * TidalFry_m * P_{FP,m}$

where $P_{FP,m}$ is the proportion of fry (including tidal fry) that move into the Floodplain habitat, and $S_{TF,FP}$ is the monthly survival of tidal fry in the floodplain. The $P_{FP,m}$ is modeled as a function of the expected flow onto the Floodplain habitat due to proposed modifications of the Fremont Weir.

$$P_{FP,m} = \begin{cases} min.p, & y.flow_m < 100 \\ min.p + \dfrac{(y.flow_m - 100)*(0.5 - min.p)}{5900}, & 100 \leq y.flow_m \leq 6000 \\ inv.logit\left(\dfrac{p.rate*(y.flow_m - 6000)}{1000}\right), & y.flow_m > 6000 \end{cases}$$

where $P_{FP,m}$ is the proportion of fry moving into the Floodplain as a function of the coefficients *min.p* and *p.rate*, and the covariate *y.flow_m*. The function inv.logit(x) = e^x/(1+ e^x) ensures that the proportion of fry moving into the Floodplain is within the interval [0,1]. The covariate *y.flow_m* represents the monthly average flow rate (cfs) at the entrance to Yolo Bypass (CALSIM node D160). The relationship between $P_{FP,m}$ and flow is depicted in Figure 5.
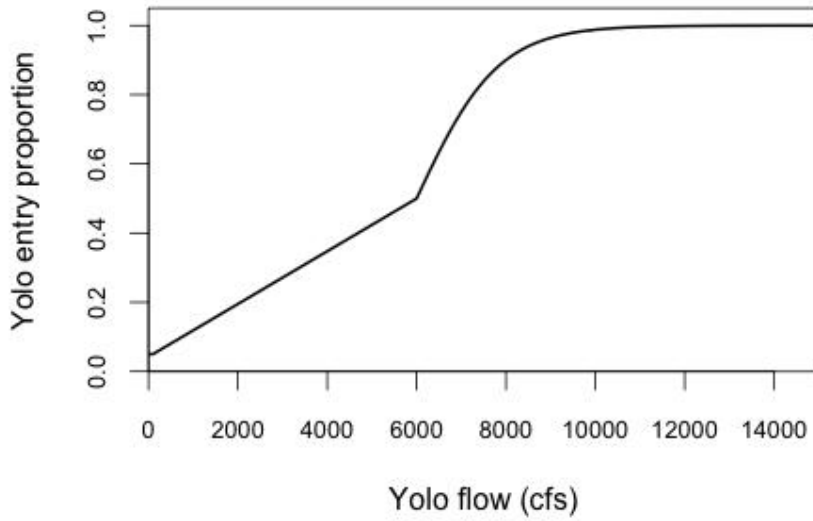
Figure 5. The relationship of Floodplain entry (Yolo bypass) entry proportion (P_{FP}) as a function of Yolo flow.

Delta and Bay Tidal Fry (Transition 4 and 5)

$TidalFry_{DE,m} = TidalFry_m * (1 - P_{FP,m}) * (1 - P_{TF,BA,m}) * S_{TF,DE,m}$

$TidalFry_{BA,m} = TidalFry_m * (1 - P_{FP,m}) * P_{TF,BA,m} * S_{TF,DE,m} * S_{TF,DE-BA}$

where $S_{TF,DE,m}$ is the survival to the Delta by Tidal Fry.

$logit(S_{TF,DE,m}) = B0_4 + B1_4 * DCC_m$

where $B0_4$ and $B1_4$ are model parameters, and DCC_m is the proportion of the transition month that the DCC gate is open.

$P_{TF,Bay,m}$ is the proportion of fish moving to the Bay from the Delta

$logit(P_{TF,Bay,m}) = B0_5 + B1_5 * Q_{RioVista,m}$

where $B0_5$ and $B1_5$ are model parameters, and $Q_{RioVista,m}$ is the flow anomaly (subtract mean and divide by standard deviation). The mean and standard deviation were calculated from 1970-2014 data at Rio Vista, which was the period of model calibration.

Rearing
Definition: Fry rear among Upper River, Lower River, Floodplain, Delta, and Bay habitats according to a density dependent movement function in months $m = (5, …, 17)$ corresponding to July to the following July (brood year + 1).
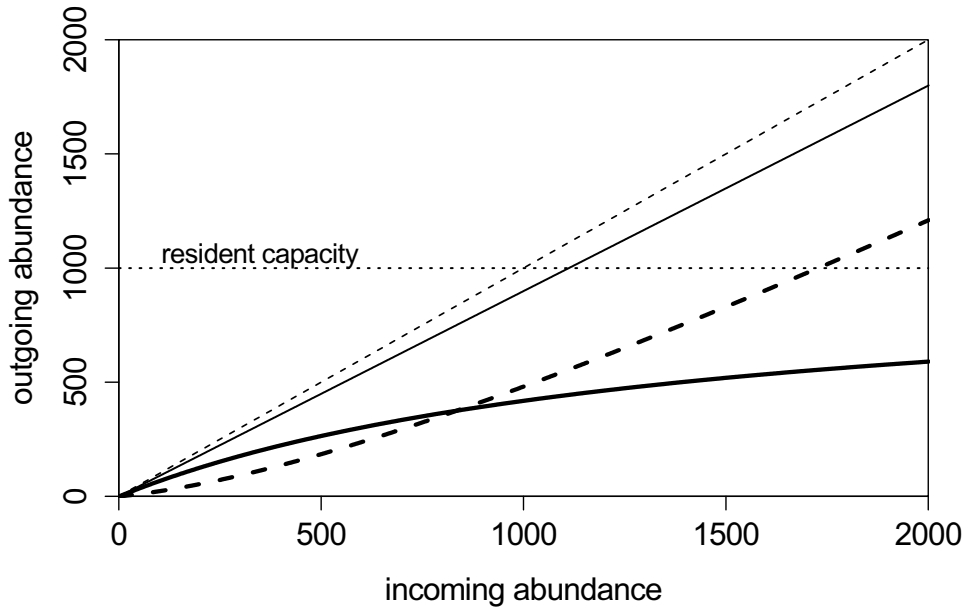
Figure 6. Example of the Beverton-Holt movement function in which the outgoing abundance (thin solid black line) is split between migrants (thick dashed line) and residents (solid dark line), that are affected by the resident capacity (thin dotted line). The 1:1 line (thin dashed line) is also plotted for reference. Parameter values used in the plotted relationship are survival, S = 0.90; migration, m = 0.2; and capacity, K= 1000.

While Transitions 2-5 calculate the number of fry that seed specific habitats immediately following emergence, the density dependent movement function follows how numbers of fish move downstream through each habitat during the entire fry rearing period. Specifically, the density dependent movement function calculates the total number of fish in a given habitat and month ($Residents_{h,m}$) versus the number of fish that will migrate to downstream habitats ($Migrants_{h,m}$). The number of residents and migrants in the month is calculated from the following equations (Figure 6):

$Residents_{h,m} = S_{FRY,h,m} * (1 - mig_{h,m}) * N_{h,m} / (1 + S_{FRY,h,m} *[1 - mig_{h,m}]* N_{h,m}/K_{h,m})$

$Migrants_{h,m} = S_{FRY,h,m} * N_{h,m} - Residents_{h,m}$

where $S_{FRY,h,m}$ is the survival rate in the absence of density dependence, $N_{h,m}$ is the pre-transition abundance composed of *Migrants* from upstream habitats in *m-1* and *Residents* from the current habitat (Figure 7) in *m-1*, $K_{h,m}$ is the capacity for habitat type h and $mig_{h,m}$ is the migration rate in the absence of density dependence in month m.

The migration rate in the Lower River is modeled as a function of a flow threshold at Wilkins Slough

$logit(mig_{LR,m})= B0_M + B1_M * I(Q_{Wilkins, m} > 400 \; m^3 s^{-1})$

whereas in all other habitats and months the migration rate $mig_{h,m}$ is a constant value. Survival of resident and migrant fry $S_{FRY,h,m}$ are also constant over habitats and months.

Transitions 6 - 10

Definition: Smolting of *Residents* in the Upper River, Lower River, Floodplain, Delta, and Bay habitats in months $m = (11, ... ,17)$ corresponding to January to July in the calendar year after spawning.

$Smolts_{h,m} = P_{SM,m} * Residents_{h,m-1}$

where $P_{SM,m}$ is the probability of smolting in month m which is assumed to be the same across habitats, by the *Residents* from the previous month (m-1) in that habitat.

The probability of smolting is modeled as a proportion ordered logistic regression model of the form:

$\text{logit}(P_{SM, m}) = Z_k$

where $-\infty < Z_1 < Z_2 ... < Z_k < \infty$ are the monthly rates of smoltification based on photoperiod (k = 1, ..., 7 encompassing January to July).

Note that during months where smoltification occurs (in months $m = 11, ... ,17$) smolts are removed from the total number of fish in a given habitat before the movement function is applied. The model performs the following steps during the months in which smoltification occurs:

1. Smoltification of Resident fry
2. Accumulation of the Migrant fry from the upstream habitats and Resident fry from the current habitat remaining from the previous month that did not smolt
3. Survival and movement of the fry calculated in step 2
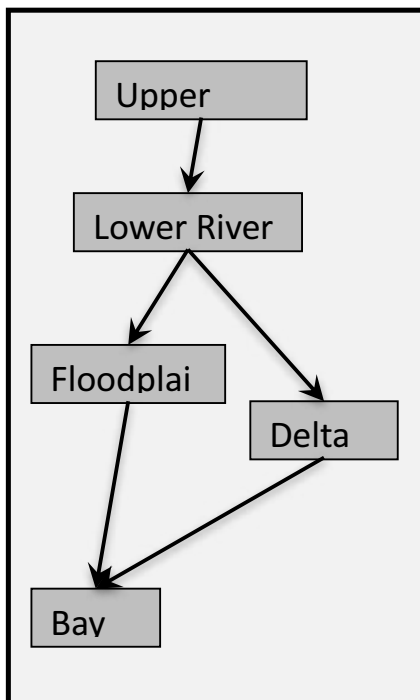

Figure 7. Connectivity among habitats for winter-run Chinook fry. Connections between the Lower River and Floodplain occur due to flooding of the Yolo bypass and are thus ephemeral.

Transitions 11 & 12

Definition: Smolts that reared in the Upper River and Lower River habitats migrate to the Gulf of the Farallones in months $m = (12, ... ,18)$ corresponding to February to August.

Upper River smolt outmigration (Transition 11)

$$Gulf_{UR,m} = S_{11,UR,m-1} * S_{G1} * Smolts_{UR,m-1}*exp(\varepsilon_y - \sigma_\varepsilon^2/2)$$

Lower River smolt outmigration (Transition 12)

$$Gulf_{LR,m} = S_{12,LR,m-1} * S_{G1} * Smolts_{LR,m-1}*exp(\varepsilon_y - \sigma_\varepsilon^2/2)$$

where survival $S_{T,h,m}$ is the smolt survival rate from transition T (11, ..., 15) in habitat h (*UR, LR, FP, DE, BA*) in month m. The rates $S_{11,UR,m}$ and $S_{12,LR,m}$ are composed of three components: A) survival rate from the Upper or Lower River to the Sacramento River near Sacramento; B) survival through the Delta to Chipps Island; and C) survival from Chipps Island to Golden Gate. The survival rate S_{G1} is the survival rate of smolts originating from the Upper River, Lower River, and Floodplain habitats during ocean entry at the Gulf of Farallones. Finally, the transition to the ocean from all habitats includes a random effect term ε_y that is specific to each year y and is distributed as a normal random variable, that is $\varepsilon_y \sim N(0, \sigma_\varepsilon^2)$. The formulation used here is a biased-corrected form so the expected value of the random effects equals 0.

$$S_{11.UR,m} = {}^AS_{11,UR,m} * {}^BS_{12,LR,m} * {}^CS_{11}$$
$$S_{12,LR,m} = {}^AS_{12,LR,m} * {}^BS_{12,LR,m} * {}^CS_{11}$$

The first smolt survival component is modeled as a function of flow at Bend Bridge

$$logit({}^AS_{11,UR,m}) = B0_{11,UR} + B1_{11} * q.bb_m$$
$$logit({}^AS_{12,LR,m}) = B0_{12,LR} + B1_{11} * q.bb_m$$

where $B0_{11,UR}$, $B0_{12,LR}$ and $B1_{11}$ are model parameters, and $q.bb_m$ is monthly flow at Bend Bridge which is the closest station to the Red Bluff Diversion Dam standardized relative to historic Bend Bridge flows from 1970-2014.

$${}^BS_{12.LR,m} = Newman_{LR,m}$$

where $Newman_{LR,m}$ is a mean monthly survival rate for smolts originating from the Sacramento River through the Delta to Chipps Island as calculated by the Newman model. The value $^CS_{11}$ is a model parameter representing survival from Chipps Island to Golden Gate and is applicable to smolts originating from all habitats.

Transition 13

Definition: Smolts that reared in the Floodplain migrate to the Gulf of the Farallones in months m = (12, … ,18) corresponding to February to August.

$$Gulf_{FP,m} = S_{13,FP,m-1} * S_{G1} * Smolts_{FP,m-1} * \exp(\varepsilon_y - \sigma_\varepsilon^2/2)$$

The rate $S_{13,FP,m}$ is composed of three components: A) survival rate from the Floodplain to the Delta; B) survival through the Delta to Chipps Island; and C) survival from Chipps Island to Golden Gate.

$$S_{13,FP,m} = {}^AS_{13,FP,m} * {}^BS_{13,FP,m} * {}^CS_{11}$$

where ${}^AS_{12,FP,m}$ is survival in the Floodplain until the Newman equation is applied for survival through the Delta

$${}^BS_{13.FP,m} = Newman_{FP,m}$$

where $Newman_{FP,m}$ is a mean monthly survival rate for smolts originating from the Floodplain through the Delta to Chipps Island as calculated by the Newman equation.

Transition 14

Definition: Smolts that reared in the Delta migrate to the Gulf of the Farallones in months m = (12, … ,18) corresponding to February to August.

$$Gulf_{DE,m} = S_{14,DE,m-1} * S_{G2} * Smolts_{DE,m-1} * \exp(\varepsilon_y - \sigma_\varepsilon^2/2)$$

The rate $S_{14,DE,m}$ is composed of two components: A) survival through the Delta to Chipps Island; and B) survival from Chipps Island to Golden Gate.

$$S_{14,DE,m} = {}^AS_{14,DE,m} * {}^CS_{11}$$

where ${}^AS_{14,DE,m} = Newman_{DE,m}$

The survival rate S_{G2} is the survival rate of smolts in the nearshore from Delta and Bay habitats relative to the survival rate in the nearshore of Upper River, Lower River, and Yolo habitats.

$$S_{G2} = \text{logit}(\text{inv.logit}(S_{G1}) + D_{G2})$$

Transition 15

Definition: Smolts that reared in the Bay migrate to the Gulf of the Farallones with an associated migration survival in months m = (12, … ,18) corresponding to February to August.

$$Gulf_{BA,m} = S_{15,BA} * S_{G2} * Smolts_{BA,m-1} * \exp(\varepsilon_y - \sigma_\varepsilon^2/2)$$

where $S_{15,BA}$ is the survival from the Bay habitat to the Golden Gate.

Transition 16

The total number of Age 1 fish entering the Gulf of the Farallones from all habitats arriving in a given month can be calculated by summing across each of the individual rearing areas. Furthermore, earlier arriving fish are retained in the Age 1 stage and an ocean survival rate is applied to those fish that were already in the Age 1 stage in the previous month. Fish arrive into the Age 1 stage in months $m = (12, …, 21)$ corresponding to February through October.

$$Age1_m = Gulf_{UR,m} + Gulf_{LR,m} + Gulf_{FP,m} + Gulf_{DE,m} + Gulf_{BA,m} + Age1_{m-1} * S_{17}^{1/4}$$

Transition 17

Definition: Survival in the ocean from Age 1 to Age 2 (for Chinook that remain in the ocean)

$$Age2 = Age1_{m=21} * (1 - M_2) * S_{17}$$

where S_{17} is a model parameter representing the survival rate of Age 1 fish in the ocean to Age 2 and M_2 is a model parameter representing the maturation rate that leads to 2-year old spawners. The model transitions from a monthly time step (used for months 1 through 20) to an annual time step (used for Age 2, Age 3 and Age 4 fish) in this transition, thus the S_{17} survival represents a 4-month survival rate from 21 months to 24 months.

Transition 18

Definition: Maturation and migration for Age 2 males and females that will spawn as 2-year olds

$$Sp_{2,F} = Age1_{m=21} * S_{17} * M_2 * Fem_{Age2} * S_{sp2}$$
$$Sp_{2,M} = Age1_{m=21} * S_{17} * M_2 * (1 - Fem_{Age2}) * S_{sp2}$$

where S_{17} and M_2 are model parameters for maturation and survival as described in Transition 17. Fem_{Age2} is a model parameter representing the proportion of Age 2 spawners that are female, and S_{sp2} is a model parameter representing the natural survival rate of Age 2 spawners from the ocean to the spawning grounds.

Transition 19

Definition: Survival in the ocean from Age 2 to Age 3 (for Chinook that remain in the ocean)

$$Age3 = Age2 * (1 - I_3) * S_{19} * (1 - M_3)$$

where I_3 is the fishery impact rate for Age 3 fish, S_{19} is a model parameter representing natural survival rate for fish between Age 2 and Age 3, and M_3 is a model parameter representing maturation rate of Age 3 fish.

Transition 20

Definition: Maturation and migration for Age 3 males and females that will spawn as 3-year olds

$$Sp_{3,F} = Age2 * (1 - I_3) * S_{19} * M_3 * Fem_{Age3} * S_{sp3}$$
$$Sp_{3,M} = Age2 * (1 - I_3) * S_{19} * M_3 * (1 - Fem_{Age3}) * S_{sp3}$$

where I_3 is the Age 3 fishery impact rate, and M_3 and S_{19} are the Age 3 maturation and survival rates as described in Transition 19. Fem_{Age3} is a model parameter representing the proportion of Age 3 and 4 spawners that are female, and S_{sp3} is a model parameter representing the natural survival rate of Age 3 spawners from the ocean to the spawning grounds.

Transition 21

Definition: Maturation and migration for Age 3 males and females that will spawn as 4 year olds

$$Sp_{4,F} = Age3 * (1 - I_4) * S_{21} * Fem_{Age3} * S_{sp4}$$
$$Sp_{4,M} = Age3 * (1 - I_4) * S_{21} * (1 - Fem_{Age3}) * S_{sp4}$$

where I_4 is the Age 4 fishery impact rate, S_{21} is a model parameter representing survival rate from Age 3 to Age 4, Fem_{Age3} is a model parameter representing the proportion of Age 3 and 4 spawners that are female, and S_{sp4} is a model parameter representing the natural survival rate of Age 4 spawners from the ocean to the spawning grounds.

Transition 22

Definition: Number of eggs produced by spawners of Ages 2 – 4 in months $m = (2, ..., 6)$ corresponding to April to August.

$$Eggs_m = \frac{\sum_{j=2}^{4} TSp_{j,F} * P_{SP,m} * V_{eggs,j}}{1 + \frac{\sum_{j=2}^{4} P_{SP,m} * TSp_{j,F} * V_{eggs,j}}{K_{Sp,m}}}$$

where TSp_j are the total number of female spawners of age $j = 2, 3, 4$ (composed of both natural and hatchery origin), $V_{eggs,j}$ is the number of eggs per spawner of age $j = 2, 3, 4$, $K_{Sp,m}$ is the capacity of eggs in the spawning grounds per month, and $P_{SP,m}$ is the proportion of spawning that occurs in month m and is a function of April average temperature at Keswick Dam. Because the April temperature can vary among years, the monthly distribution varies as well to reflect observed patterns in spawn timing among the years from 1999 to 2012. Please see Appendix A for description of the analysis of historical patterns in spawn timing.

$$TSp_{2,F} = Sp_{2,F} + Sp_{2,F,Hatchery}$$

$$TSp_{3,F} = Sp_{3,F} + Sp_{3,F,Hatchery} - hat.f$$

$$TSp_{4,F} = Sp_{4,F} + Sp_{4,F,Hatchery}$$

$$hat.f = 0.15 * Sp_3 \quad (min = 10; max = 60)$$

where $hat.f$ is the number of spawning females removed for use as hatchery broodstock, and $Sp_{j,Hatchery}$ for $j = (2,3,4)$ is the spawners of age j hatchery origin, which are described below in the *Hatchery Origin Chinook* section.

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Hatchery Origin Chinook

Transition 1H
Definition: Survival of hatchery fish from eggs to Age 2

$Age2_{Hatchery} = hat.f * 3000 * H_{S1}$

$H_{S1} = 2.3 * Age2_{Natural} / Fry_{Natural}$

where H_{S1} is the hatchery-origin survival rate from pre-smolt at release to Age 2 in the ocean, $Age2_{Natural}$ is the number of natural-origin Chinook that survived to Age 2 and remained in the ocean, and $Fry_{Natural}$ is the number of natural origin emerging Fry (see Transition 1 for Natural Origin Chinook). The multiplier of 3000 hatchery smolts per spawner was obtained from Winship et al. (2014). The multiplier of 2.3 was used to equate hatchery origin survival to the end of age 2 to natural origin survival to the end of age 2 as described in Winship et al. (2014). Note this transition includes the total number of Age 2 hatchery fish, including fish that remain in the ocean and Age 2 spawners.

Transition 2H
Definition: Maturation and spawning for hatchery origin Age 2

$Sp_{2,F,Hatchery} = Age2_{Hatchery} * M_2 * Fem_{Age2} * S_{sp2}$
$Sp_{2,M,Hatchery} = Age2_{Hatchery} * M_2 * (1 - Fem_{Age2}) * S_{sp2}$

where the coefficients are described under Transition 18.

Transition 3H
Definition: Survival of hatchery origin fish in the ocean from Age 2 to Age 3 (for Chinook that remain in the ocean)

$Age3_{Hatchery} = Age2_{Hatchery} * (1 - I_3) * S_{19} * (1 - M_3)$

where the coefficients are described under Transition 19.

Transition 4H
Definition: Maturation and spawning for hatchery origin Age 3

$Sp_{3,F, Hatchery} = Age2_{Hatchery} * (1 - I_3) * S_{19} * M_3 * Fem_{Age3} * S_{sp3}$
$Sp_{3,M, Hatchery} = Age2_{Hatchery} * (1 - I_3) * S_{19} * M_3 * (1 - Fem_{Age3}) * S_{sp3}$

where the coefficients are described under Transition 20.

Transition 5H
Definition: Survival and maturation rate for hatchery origin Age 4

$Sp_{4,F, Hatchery} = Age3_{Hatchery} * (1 - I_4) * S_{21} * Fem_{Age3} * S_{sp4}$
$Sp_{4,M, Hatchery} = Age3_{Hatchery} * (1 - I_4) * S_{21} * (1 - Fem_{Age3}) * S_{sp4}$

where the coefficients are described under Transition 21.

Fishery Dynamics

To simulate the winter-run population dynamics under alternative hydrologic scenarios, we include fishery dynamics that are consistent with the current fishery control rule (NMFS 2012) (Figure 8). For each year of the simulation, the impact rate for age 3 (I_3) was calculated from the control rule by obtaining the 3-year trailing geometric average of spawner abundance. The age-4 impact rate (I_4) in that year was calculated as double the instantaneous age-3 impact rate (Winship et al. 2014).
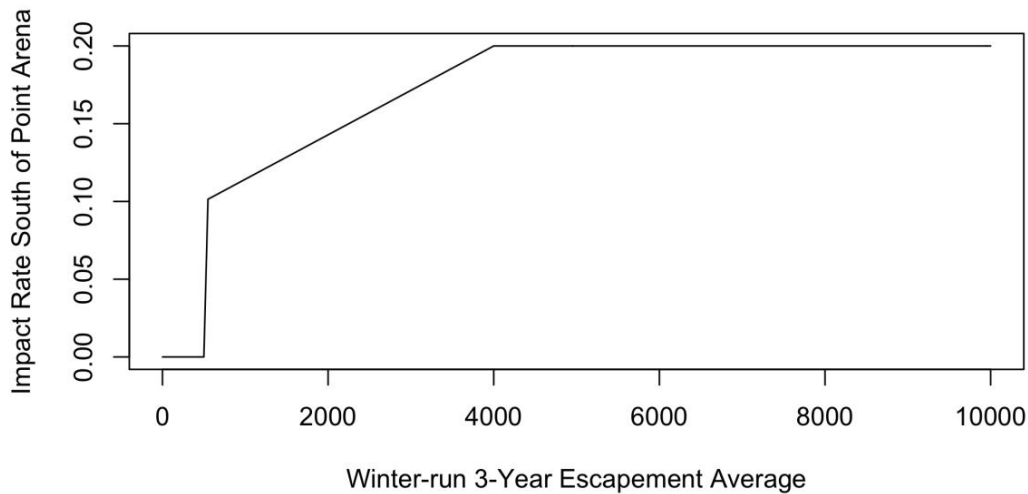

Figure 8. Fishery control rule determining the level of Age 3 impact rate as a function of trailing 3-year geometric mean in winter-run escapement.

III. Inputs to the Winter-run life-cycle model

Water Temperature

The life cycle model (LCM) incorporates monthly average temperature below Keswick Dam into the definition of egg to fry survival. The water temperature can be obtained from water quality gages on the Sacramento River (for model calibration) or from a forecasted water temperature model, such as the as the Sacramento River Water Quality Model (SRWQM).

Fisheries

Estimates of impact rates on vulnerable age classes of Chinook salmon are computed as part of the Pacific Fisheries Management Council (PFMC) annual forecast of harvest rates and review of previous years' observed catch rates. For runs that are not actively targeted, such as winter-run and

spring-run Chinook, analyses of coded wire tag (CWT) groups are used to infer impact rates for these races (e.g., O'Farrell et al. 2012).

Habitat Capacity

Juvenile salmonids rear in the mainstem Sacramento River, delta, floodplain, and bay habitats (Figure 1). The model incorporates the dynamics of rearing fry by using density-dependent movement out of habitats as a function of capacity for juvenile Chinook. The capacities of each of the habitats are calculated in each month using a series of habitat-specific models that relate habitat quality to a spatial capacity estimate for rearing juvenile Chinook salmon. Habitat quality is defined uniquely for each habitat type (mainstem, delta, etc.) with the goal of reflecting the unique habitat attributes in that specific habitat type. For example, the mainstem habitat quality is a function of velocity and depth (Beechie et al. 2005). Higher quality habitats are capable of supporting higher densities of rearing Chinook salmon, with the range of densities being determined from studies in the Central Valley and in river systems in the Pacific Northwest where appropriate.

Defining habitat capacity. For each habitat type (Upper River, Lower River, Floodplain, Delta, and Bay), capacity was calculated each month as:

$$K_i = \sum_{j=1}^{n} A_j d_j$$

where K_i is the capacity for a given habitat type i, n is the total number of categories describing habitat variation, A_j is the total habitat area for a particular category, and d_j is the maximum density attributable to a habitat of a specific category. Three variables were determined for each habitat, the ranges of each were divided into high and low quality, and all combinations were examined, resulting in a total of eight categories (2 x 2 x 2) of habitat quality for each habitat type (Table 1). In the Upper River, Lower River, and Floodplain, there were 4 categories (2x2) of habitat quality. Ranges of high and low habitat quality were based on published studies of habitat use by Chinook salmon fry across their range and examination of data collected by USFWS within the Sacramento-San Joaquin Delta and San Francisco Bay.

Defining maximum densities. Determining maximum densities for each combination of habitat variables is complicated by the fact that most river systems in the Central Valley are now hatchery-dominated with fish primed for outmigration. In addition, the Central Valley river system is at historically low natural abundance levels compared to expected or potential density levels. Because of this deficiency in the Central Valley system, salmon fry density data from the Skagit River system were used, which in contrast has very low hatchery inputs, has been monitored in mainstem, delta, and bay habitats, and exhibits evidence of reaching maximum density in years of high abundance (Greene et al. 2005; Beamer et al. 2005). These data from the Skagit River were compared with Central Valley density estimates calculated by USFWS. For each of these data sets, the upper 90 to 95 percentile levels of density defined a range of maximum density levels, assuming that the highest five percentile of density levels were sampling outliers. The comparison indicated that Skagit River values represented conservative estimates of maximum density (Figure 9).

Table 1. Habitat variables influencing capacity for each habitat type. Mainstem includes Upper River, Lower River and Floodplain habitats.

Habitat type	Variable	Habitat quality	Variable range
Mainstem	Velocity	High	<= 0.15 m/s
		Low	> 0.15 m/s
	Depth	High	> 0.2 m, <= 1 m
		Low	<= 0.2 m, > 1 m
Delta	Channel type	High	Blind channels
		Low	Mainstem, distributaries, open water
	Depth	High	> 0.2 m, <= 1.5 m
		Low	<= 0.2 m, > 1.5 m
	Cover	High	Vegetated
		Low	Not vegetated
Bay	Shoreline type	High	Beaches, marshes, vegetated banks, tidal flats
		Low	Riprap, structures, rocky shores, exposed habitats
	Depth	High	> 0.2 m, <= 1.5 m
		Low	<= 0.2 m, > 1.5 m
	Salinity	High	<= 10 ppt
		Low	> 10 ppt
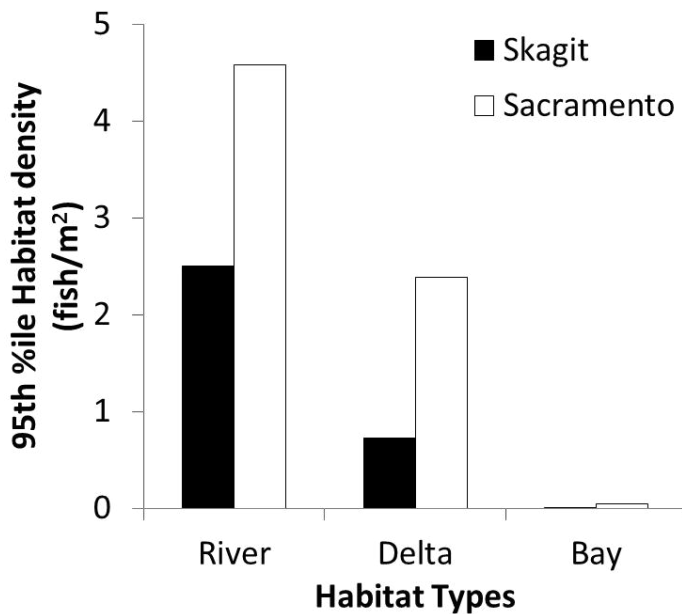
Figure 9. 95th percentile values of densities in river, delta, and bay habitats in the Skagit and Sacramento Rivers. Skagit data are based on electroshocking in mainstems and beach seining in delta and bay habitats (Beamer et al. 2005), while Sacramento data are based on beach seining across all habitat types (USFWS, 2005).

Determining habitat areas. Two approaches were used to map the spatial extents of different combinations of habitat variables. In the mainstem and floodplain, the HEC-RAS model divides the

river into units based on multiple cross-sections defining depth ranges (Figure 10). Each unit defined by the cross-sections has velocity parameters associated with it. Different levels of flow in a given month or year change the distribution of velocity and depth. Total habitat area in each of the eight classes is calculated by integrating over the river channels modeled by HEC-RAS.
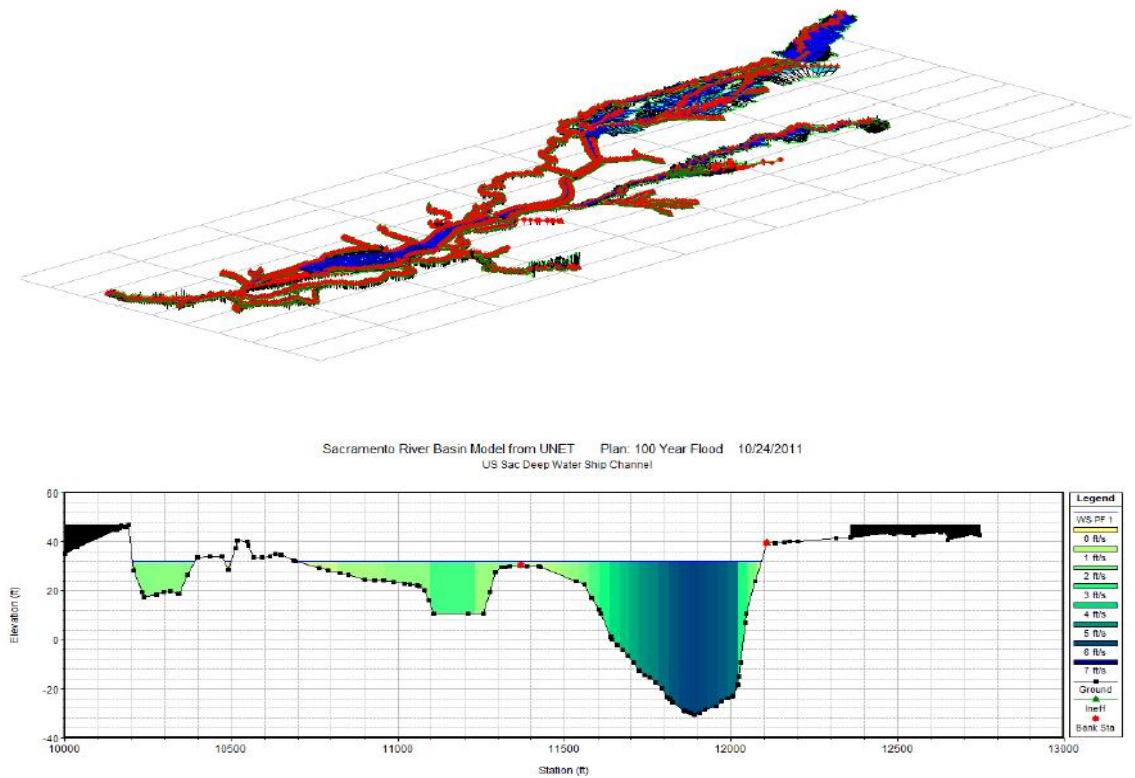

Figure 10. HEC-RAS model cross sections of the Sacramento River mainstem and floodplain (upper panel), and a visualization of a single cross-section, showing depth and velocity differences (lower panel).

For the delta and bay, channel type, depth, cover, salinity, and shoreline type were mapped from existing delta and bay Geographic Information Systems (GIS) products (Figure 11). Delta and bay polygons[1] were classified into high quality habitat types (blind tidal channels) and low quality habitat types (mainstem, distributaries, large water bodies, and bay). For the channel typing, several datasets comprised the base GIS layers, including National Wetlands Inventory (NWI) wetland polygons, San Francisco Estuary Institute's Bay Area Aquatic Resource Inventory's (BAARI) stream lines and polygons, Hydro24ca channel polygons (USBR 2006, Mid-Pacific Region GIS Service Center), aerial photos and Google Earth. The Hydro24ca channel data included channel types such as major river, slough, lake and several other types. When channel type could not be defined for a given reach, aerial photos and attributes from surrounding channels were used to estimate channel type. National Wetland Inventory (NWI) GIS data served as base channel and wetland data. NWI data provides comprehensive data coverage as well as detailed wetland categories that were required. However, NWI data did not have enough information to distinguish accessibility for juveniles. Thus,

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[1] A closed shape used in GIS mapping that is defined by a connected sequence of x, y coordinate pairs, where the first and last coordinate pair are the same and all other pairs are unique.

Bay Area Aquatic Resource Inventory (BAARI) data were used as a reference to identify accessible wetlands from NWI polygons. For the areas that BAARI data did not cover, levee GIS layers were overlain to estimate accessible wetland habitat.
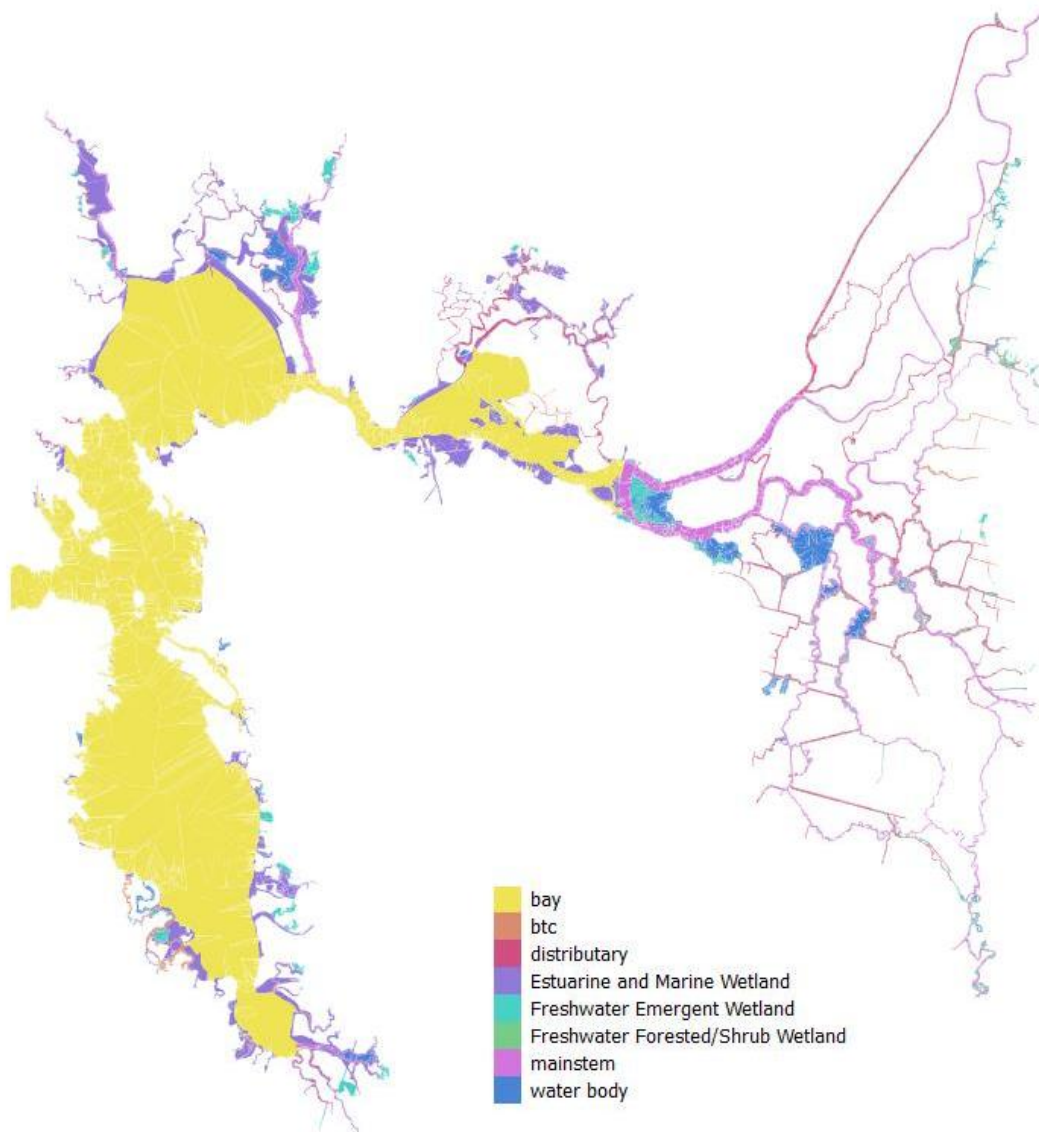
Figure 11. Habitat types delineated for the Sacramento Delta and San Francisco Bay. The abbreviation "btc" stands for blind tidal channel.

Most channel types could be mapped using these datasets except for the blind tidal channels. Instead of directly mapping blind tidal channels, we estimated these areas using allometric relationships between wetland areas and blind tidal channel areas. We tested allometric equations developed in the Skagit River by Beamer et al. (2005) and Hood (2007) to determine which equations were best suited to apply to the Central Valley and chose an allometric equation that returned conservative estimation results:

BTC (ha) = 0.0024*Wetland(ha)^1.56

We also applied the minimum area requirement (0.94 ha) to form blind tidal channels in a wetland from Hood (2007).

Salinity is another factor influencing habitat availability for juvenile Chinook salmon that can vary with water flow. The X2 position describes the distance from Golden Gate Bridge to the 2 ppt isohaline position near the Sacramento Delta (Jassby et al. 1995). This distance predicts amount of suitable habitat for various fish and other organisms. Based on observations of high likelihood of fry presence in water with salinity of up to 10 ppt in both Skagit River and San Francisco Bay fish monitoring data, we defined the low-salinity zone for Chinook as salinity < 10 ppt (i.e., habitats upstream of X10). We calculated X10 values as 75 percent of X2 values (Monismith et al. 2002, Jassby et al. 1995), and mapped these across San Francisco Bay.

Another axis used to evaluate habitat is vegetated cover along river banks. Areas associated with cover were assumed to be higher quality habitats because they provide protection from predators (Semmens 2008) and offer subsidies of terrestrial insect prey. Such habitats are preferred in other systems by Chinook salmon (Beamer et al. 2005, Semmens 2008). The extent of these areas was estimated using Coastal Change Analysis Program (C-CAP) Land Use/Land Cover (LULC) layers. We defined sheltered habitat as forested or shrub covered areas and assumed that other areas, such as urban and bare land, did not provide sheltered habitat.

Restricting habitat areas based on connectivity. Our first analysis of habitat areas assumed all regions of the Delta were equally accessible to Chinook salmon fry. This assumption may be incorrect, however, because much of the fish monitoring has shown that fry do not inhabit certain areas in the Delta. Therefore, a spatial connectivity mask, or exclusion zone, was developed to exclude certain areas from the habitat mapping. This exclusion zone was produced using month- and year-specific fish monitoring data (Figure 12). Poisson regression models were used to predict fish counts based on the relationships between fish counts in beach seine datasets and several covariates including river system (Sacramento or San Joaquin), distance of sampling site to its mainstem (m), physical channel depth (m), physical channel width (m), and DSM2 water stage (m). We selected these parameters based on Akaike's Information Criterion (AIC) analysis of the Poisson regression models with various combinations of the parameters. The resulting Poisson model equation was used to produce a presence-absence map for the entire delta (Figure 12). Restricted capacity estimates were generated by summing habitat areas with predicted fry presence.

Modeling capacity for preferred and no action alternatives. The geospatial tools described above were used to make predictions of capacities of preferred and no action alternatives by routing Calsim2 runs of alternatives through HEC-RAS and DSM2 models. Model changes for these runs included the lowering of the diversion for the Yolo Bypass in HEC-RAS for both alternatives and the diversions and underground tunnels in DSM2 for the preferred alternative.
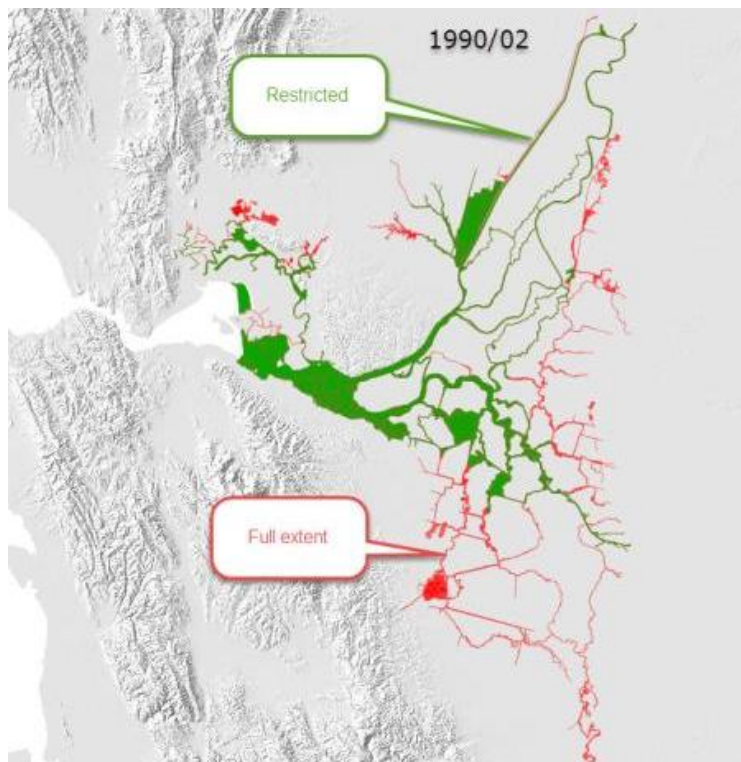
Figure 12. Example results of reduced connectivity applied to the February (02) 1990 map. The presence/absence prediction for connected habitat areas is designated as "Restricted" (green), a smaller area than the full extent of the Sacramento Delta (red).

Newman Equations for Smolt Survival

The survival rate of juvenile Chinook salmon smolts within and migrating through the Delta is modelled using an approach developed by Newman (2003). The Newman survival model is a nonlinear hierarchical model that incorporates biotic covariates, environmental covariates and random effects to estimate survival of juvenile Chinook salmon in the delta. Although more recent models such as the enhanced Particle Tracking Model (ePTM, Sridharan et al. 2015) and the Survival, Travel time, And Routing Simulation (STARS) model (Perry et al. 2018) have been developed to improve the delta survival estimates generated by Newman (2003), the Newman delta survival model remained the preferred model for this version of the WRLCM for two important reasons. First, the ePTM is currently undergoing development and is not ready for incorporation into the WRLCM at this time. Second, the STARS model does not include exports as a covariate, thus could not inform how differences in levels of exports under the COS and PA scenarios affect smolt survival in the delta. Therefore, the Newman survival model was used for this version of the WRLCM because it was the most complete model available that was sensitive to changes in exports.

The Newman model estimates survival through the delta by comparing survival of juvenile hatchery coded-wire-tagged fall-run Chinook salmon released at several locations upstream and downstream of the delta (Newman 2003). Upstream releases were located in the lower Sacramento River (near the cities of Sacramento, Courtland, and Ryde), and thus required juveniles to transit the delta

before reaching the ocean. Lower releases were located just west of Chipps Island (near Port Chicago and Benicia), and thus represented juveniles that did not transit the delta. Survival was estimated from coded-wire tag recoveries in the freshwater by operating a midwater trawl located near Chipps Island following releases (upstream releases only) and in the ocean as released fish reached 2 to 5 years of age and were captured from commercial and recreational fisheries (both upstream and downstream releases). The relative differences in survival between release groups allowed for delta-specific survival estimates.

Several biotic and abiotic variables are included as covariates in the Newman model of delta survival. Covariates in the model include fish length, log transformed median river flow during the outmigration period, water salinity, river water temperature and hatchery water temperature at release, magnitude of the tide, median volume of exports during the outmigration period, indicator for position of the DCC gate located below Courtland (1 = open; 0 = closed), and water turbidity (Newman 2003). Because all of the covariates were standardized in the Newman analysis, we can set the values of the unused covariates to 0 (the mean value during the study) and those terms drop from the equation. Generically, the following equation was employed in the WRLCM to calculate smolt survival (for more details on the model and description of covariates, see Newman (2003)).

$$Newman_{h,m} = B0_{Newman} + B1_{Newman}size_{h,m} + B2_{Newman}temp_{h,m} + B3_{Newman}flow_{h,m} + B4_{Newman}exports_{h,m} + B5_{Newman}DCC_{h,m} + B6_{Newman}SacIndicator_{h,m}$$

where $Newman_{h,m}$ is the Newman model estimate for survival in the delta for fish originating from a given habitat h and month m. The covariate $SacIndicator$ is an indicator value and set to 1 when modeling survival from the Sacramento release locations. For all other release locations, $SacIndicator$ is set to 0. For this version of the WRLCM, we did not include covariates of salinity, release temperature, hatchery temperature, tide, or turbidity because these were not available for evaluation of the operational scenarios. All parameter values included in the Newman model are listed in Appendix B.

The WRLCM adjusted input data into the Newman model to generate specific delta survival estimates for juveniles depending on their habitat of origin. Delta survival for fish originating from the upper or lower river ($Newman_{LR,m}$) used the above equation with the $SacIndicator$ term set to 1. Delta survival from fish originating in the delta ($Newman_{DE,m}$) used the above equation with the $SacIndicator$ term set to 0. Finally, Delta survival from fish in the floodplain ($Newman_{FP,m}$) used the above equation with the $SacIndicator$ term set to 0 and the average length increased by 10mm to account for the higher growth rates in the Yolo Bypass (Takata et al. 2017, Sommer et al. 2001).

Caveats

The Newman survival results are based on a statistical model and environmental covariates that occurred over the time-frame 1979-1995. Furthermore, the Newman model was developed using fall-run juvenile Chinook salmon reared in hatcheries and released in April and May, which is later than the peak outmigration for winter-run Chinook salmon. As a result, the use of the Newman

model for predicting absolute estimates of survival for winter-run Chinook salmon must be considered with caution. The authors expect future versions of the WRLCM to incorporate delta survival from updated models that are developed for winter-run Chinook salmon outmigration timing and are sensitive to exports and other water operations that may influence delta survival. The Newman model does appear capable of reflecting relative changes in survival as a function of important management drivers, however.   Due to the short time frame under which this analysis had to be conducted, the Newman model became the only option, despite its limitations. It is important to note that the WRLCM is being applied to understand the relative differences between scenarios, and relative model outputs may be less sensitive to these caveats.   The Newman model should be considered as an assumption of how smolt survival rates would vary as a function of management drivers with these assumptions being applied equally to the scenarios under evaluation.

IV. Model Calibration

The WRLCM framework is flexible in that it may be used to generate many different trajectories of abundance and spatial patterns of habitat use by varying the parameters of the model. The WRLCM should reflect historical trends and spatial patterns in abundance, however. As a result, we calibrated the WRLCM to multiple winter-run abundance indices by fixing some model parameters and estimating other parameters with a statistical fitting algorithm.

One goal of the WRLCM was to construct a model that was sensitive to alternative hydromanagement actions in the Central Valley; thus the model was structured such that it is sensitive to hydrologic drivers. An unintended consequence of this approach is that the statistical properties of the model are not optimal. In particular, some model parameters are not uniquely identifiable; that is, the same abundance can occur through several different parameter combinations. Because this property of the LCM makes statistical estimation difficult, the values of some parameters must be constrained using biological information, previous studies, or expert opinion, so that other parameters can be estimated.   We provide the parameters that were constrained and provide justification for their values before moving to the statistical estimation of the remaining parameters.

Fixed parameters and their justifications

Spawn timing parameters
Historically, the spawning of winter-run Chinook has not been uniform among the months April to August. Instead, higher proportions of winter-run spawned in June and July relative to April, May, and August. In addition, the proportions of winter-run that spawned in each month were not constant across years, but instead varied annually. We analyzed the historical proportion spawning among each month from 2003 – 2014 using carcass counts (assuming a 2-week period between spawning and senescence), and estimated the proportion of winter-run spawning in each month as a function of April temperatures at Keswick (Appendix A). We compared this model to one that used a static proportion among years, and found that the model based on April temperatures outperformed the static model. The general relationship identified through this multinomial

regression model was that hotter April temperatures caused later initiation of spawning in winter-run Chinook. This may be explained mechanistically if the female spawners were laying their eggs to target an emergence time. Hotter temperatures in April indicated that a shorter incubation window was needed, whereas cooler temperatures indicated a longer incubation window. Please see Appendix A for additional information on this analysis.

These equations provided a method of shifting spawning distribution among months as a function of April temperatures (Appendix A). The April water temperatures were standardized in the analysis and thus need to be standardized for use in the simulation model.

Tidal fry related parameters

Winter-run Chinook generally have not had a high tidal fry proportion (on the order of less than 5%). Furthermore, the location of tidal fry has varied among years, and they have been susceptible to movement downstream in the Sacramento River under high flow conditions (Pat Brandes, USFWS *personal communication*). The WRLCM parameters for the fry stage reflected these assumptions (Table 2).

Table 2. Fixed parameter values related to the tidal fry stage.

Parameter	Value	Description
$P_{TF, m}$	0.047	Proportion tidal fry
$S_{TF,FP}$	0.731	Survival tidal fry in floodplain
$P_{FP,m}$	0.881	Proportion to Floodplain if flooding
$B0_4$	0.5	Average survival tidal fry to delta intercept
$B1_4$	-1.0	Effect of DCC gate (value is in logit space)*
$B0_5$	0.5	Average proportion of tidal fry to bay intercept
$B1_5$	2.0	Effect of Rio Vista flow (value is in logit space)*

*Values in logit space are the untransformed values used in the logit function of the transition equation

Smoltification timing parameters

The timing of smoltification of winter-run Chinook salmon historically begins in January with a majority of winter-run sized smolts outmigrating by March (delRosario et al. 2013). In the WRLCM, all fry are assumed to have smolted by April and migrating in May (Table 5). The timing of smoltification in the WRLCM has been parameterized to coincide with winter-run sized Chinook salmon in Chipps Island trawl data (delRosario et al. 2013) and by using Chipps Island abundance indices as described below in the *Parameter Estimation* section.

Table 3. Smoltification timing parameters for winter-run Chinook.

Parameter	Value	Description
Z_1	0.269	January smolt probability
Z_2	0.5	February smolt probability
Z_3	0.953	March smolt probability
Z_4	1	April smolt probability
Z_5	1	May smolt probability
Z_6	1	June smolt probability
Z_7	1	July smolt probability

Maturation rate probabilities

The age-specific maturation probabilities for winter-run Chinook salmon were fixed to values based on analysis of coded wire tagged hatchery fish (Grover et al. 2004). The probability of maturation of age 2 fish was 0.10 (M_2), the conditional probability of maturation at age 3 was 0.90 (M_3), and the conditional probability of maturation at age 4 was 1.0.

Age-specific sex ratios were applied to obtain age and sex specific escapement values. Males dominate age-2 escapement, thus the female sex ratio for age-2 fish (Fem_{Age2}) was set at 0.01. Estimates of the proportion of age-3 female spawners (Fem_{Age3}) may vary among years, and we accounted for this historical annual variability by using an annual sex spawner ratio value calculated from Keswick trap counts 2001 – 2014 (mean = 0.595, sd = 0.077). These values were also used in the annual calculation of natural origin escapement from carcass surveys over the period 2001 – 2014 (Doug Killam, CDFW Redding, CA, *personal communication*). In the absence of an estimate of the age-3 sex ratio, a value of 0.5 was assumed for 1970 – 2000.

Egg production per age-2 female ($V_{eggs,2}$) was 3200 for age 2 females (Newman and Lindley, 2006) and production per age-3 and age-4 female ($V_{eggs,3}$ and $V_{eggs,4}$) was 5000 (Winship et al. 2014).

Smolt survival

The Newman equation (Newman 2003) calculates month and year-specific delta smolt survival probabilities; however, some survival probabilities were needed to move the smolts from their areas of rearing to the location in which the Newman survival rates were applied. Smolt survival from the Lower River to the Delta ($B0_{11,LR}$) was fixed at 0.8 (estimates of survival ranged from 0.73 - 0.875 Colusa to Sacramento in the 2012-2015 WR acoustic tag data, Arnold Ammann, SWFSC NMFS Santa Cruz *personal communication*). Smolt survival from the Upper River to the Delta ($B0_{10,UR}$) was fixed at 0.4 (estimates of survival averaged 0.456 from release to Sacramento in the 2012-2015 WR acoustic tag data, Arnold Ammann, SWFSC NMFS Santa Cruz *personal communication*). Smolt

survival from the Yolo bypass to the location where the Newman survival rates were applied ($^AS_{13,FP}$) was assumed to be 0.924 per month.

Survival of smolts from Chipps Island to the Golden Gate bridge ($^cS_{11}$) was assumed to be 0.82, and survival of smolts that reared in the Bay to the Golden Gate bridge ($S_{15,BA}$) was assumed to be 0.5.

Ocean survival
Survival of smolts that reared in the Upper River, Lower River, and Yolo habitats, River and Yolo habitats (S_{G1}) which is estimated (see below in the *Parameter Estimation* section).

Survival during the first four months in the ocean (S_{17}) was assumed to have a rate of 0.79, which equates to an annual survival of 0.5, whereas annual survival in the ocean for age-3 and age-4 (S_{19} and S_{21}) was assumed to be 0.8. These annual natural survival rates are consistent with winter-run reconstruction conducted annually as part of the fishery management of Sacramento River salmon (Grover et al. 2004, O'Farrell et al. 2012). Annual impact rates of age-3 (I_3) and age-4 (I_4) were obtained from estimated harvest rates over the 1970- 2014 period (O'Farrell and Satterthwaite 2015). Survival of age-2 (S_{sp2}), age-3 (S_{sp3}), and age-4 (S_{sp4}) through the freshwater prior to spawning is assumed to be 0.9 to incorporate in-river harvest, which historically included levels of approximately 7 percent (Grover et al. 2004) and pre-spawn mortality.

Formulation of the Floodplain habitat access for calibration
To reflect the historical dynamics of access to the Floodplain habitat (Yolo bypass), the following transition equation was used to describe the proportion of Tidal Fry that enter the floodplain habitat ($P_{FP,m}$)

$$P_{FP,m} = B1_{FP}*\text{I}(Q_{Verona,m} > 991.1 \text{ m}^3\text{s}^{-1})$$

where $Q_{Verona,m}$ was the Sacramento River flow at Verona in month m, I( ) is an indicator function that equates to 1 when the condition in the parenthesis is met, and $B1_{FP}$ is the proportion of fry that enter the Yolo under flooding conditions, which was 0.881.

Statistical estimation
One of our objectives is to ensure that the WRLCM is capable of reflecting the historical patterns in winter-run Chinook population dynamics in the Sacramento River. In order to meet this objective, we calibrated the LCM to observed winter-run indices of abundance throughout the life cycle (Table 4). Not all indices of abundance were available for the entire period of model calibration of 1970-2014. This data limitation is not a problem for fitting the WRLCM, however. The WRLCM can be fit to the specific indices of abundance for the period over which they were available by pairing observed indices of abundance with WRLCM predictions over the appropriate period. Then, the sampling distribution provided a likelihood function by which the model predictions were statistically evaluated given the observed data (Hilborn and Mangel 1997).

This type of model, in which multiple data sources are used to inform multiple life-history stages, is called an integrated population model and has notable advantages over piece-wise model composition (Newman et al. 2014). In particular, the model parameter estimates can utilize all of

the available data simultaneously, which can improve the parameter estimates by allowing the model to "fill in the gaps" over portions of the life cycle that are unobserved (Newman et al. 2014).

Table 4. Indices of abundance used to calibrate the winter-run life cycle model.

Data	Date	Coefficient of Variation	Sampling Distribution	Data time step
Natural Escapement	1970-2014	1.0 (1970-1986) 1.5 (1987-2000) 1.0 (2001-2014)	lognormal	Annual
RBDD monthly juvenile counts	1996-1999, 2002-2014		lognormal	Monthly
Knights Landing monthly catches	1999 - 2008	NA	multinomial	Monthly
Chipps Island monthly juvenile abundance	2008 - 2011	1.5	lognormal	Monthly

Maximum Likelihood Estimation

Given the fixed parameter values described above, the remaining parameters were estimated in a statistical fitting framework. An initial evaluation of model complexity (not shown) indicated that 10 parameters could possibly be estimated in the mechanistic portion of the model, depending upon which parameters were chosen. Previous calibrations of the model indicated that there were high correlations among several of those parameters, however. Due to the short time frame under which to calibrate the WRLCM using the Newman equation for smolt survival, we estimated 4 population dynamics parameters (and calculated an empirical estimate for the variance of the random effects) in addition to 45 annual random effects (i.e, the ε_y) in the model calibration.

These parameters were estimated by maximizing the likelihood (the likelihood specified by the sampling distribution) of observing the winter-run abundance indices (Hilborn and Mangel 1997). That is, parameter combinations can be used to make predictions on the escapement in each year, the number of juveniles passing RBDD in each month, the catches at Knights Landing, and monthly abundance estimates at Chipps Island. Some parameter combinations provide predictions that are closer to the observed abundance indices than others. The parameter combination that provides the closest fit to the observed indices is the one that maximizes the likelihood, and is thus called the maximum likelihood estimate (MLE).

Model parameters were estimated using a Monte-Carlo Expectation-Maximization (MCEM) algorithm (Wei and Tanner 1990, Levine and Casella 2001). In our case we used two blocks of parameters: 1) parameters associated with the mechanistic population dynamics and 2) the annual random effects. The specific implementation of the algorithm uses Monte Carlo draws so that parameter estimates that describe the winter-run population dynamics integrate across the annual random effects. The algorithm switches between a) maximizing the likelihood of the parameters given a set of random effects (the maximization step) and b) drawing sets of random effects given a fixed set of parameter values. (the expectation step). The algorithm iterates between these two steps until the parameter estimates become stable.

In practice, the expectation step can be difficult to implement when the model is complex. Approaches to overcome this difficulty have included using Markov Chain Monte Carlo (MCMC) to draw values of the random effects given the current estimates of the model parameters (McCullough 1997). Levine and Casella (2001) extended this approach by drawing many vectors of random effects via MCMC initially, e.g., 4000 vectors of annual random effects, each vector with 45 elements. Each of the random effects vectors is then reweighted at each iteration of the algorithm to reflect the likelihood of that random effects vector given the current values of the model parameters. We employed the Levine and Casella (2001) implementation of the MCEM here to estimate the WRLCM model parameters.

Fits to abundance indices

Fits to the abundance indices generally followed patterns in the observed data. Annual patterns in natural origin escapement were well estimated by the model (Figure 13), as were monthly patterns in juvenile abundance estimates at RBDD (Figure 14).
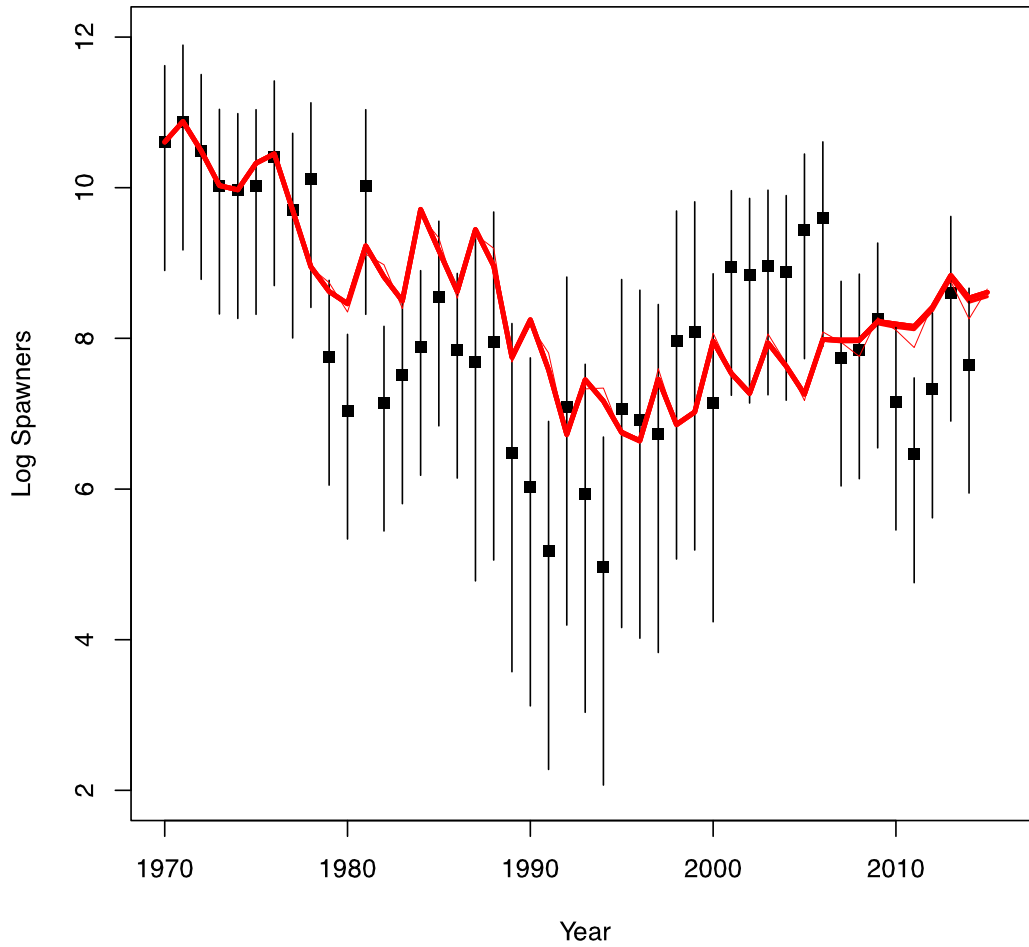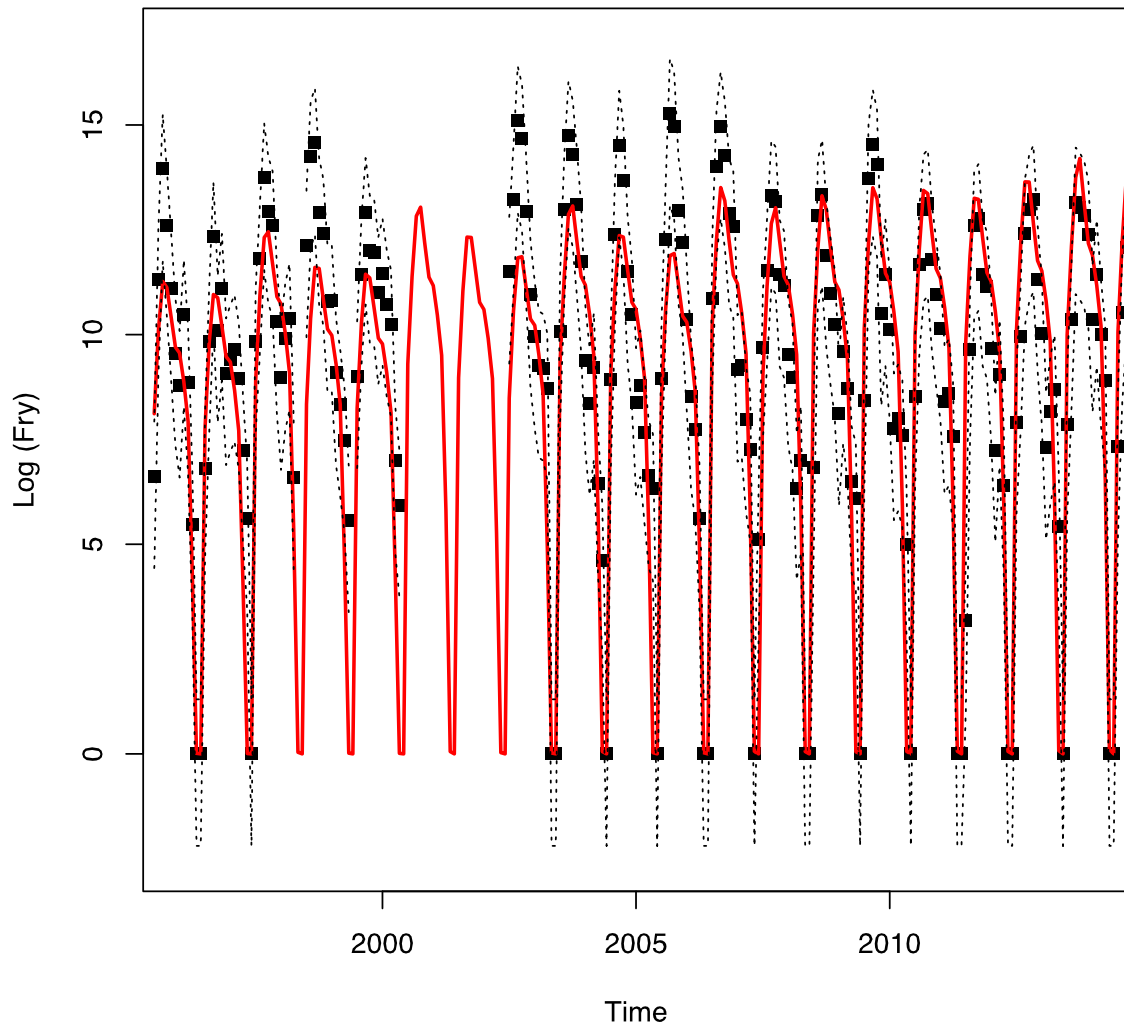
Figure 13. Model fits (red lines under different random effects vectors with the width of the line related to the weight of the random effects vector) to log natural origin escapement data (squares) with 95% interval on measurement error (vertical lines).

Figure 14. Model fit (red line) to monthly juvenile abundance estimates at Red Bluff Diversion Dam from 1996 to 2014 (squares) with 95% interval on measurement error (dashed lines).

Finally, the WRLCM was able to capture the monthly patterns in Chipps Island abundance trends from 2008 – 2011, reflecting the outmigration patterns of winter-run from each of the rearing habitats (Figure 15).
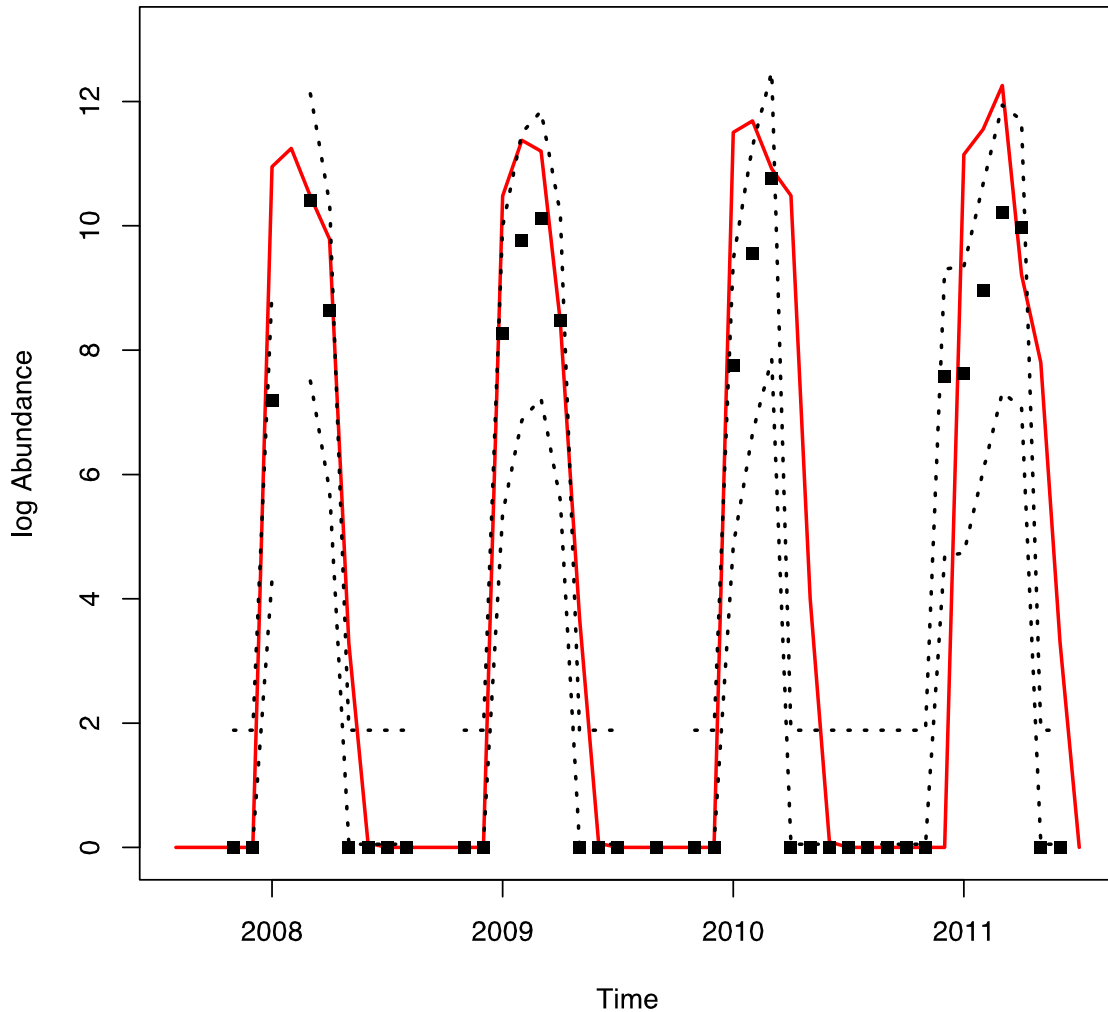
Figure 15. Model fits (red line) to monthly Chipps Island abundance estimates (black squares) from 2008 to 2011 with 95% interval on measurement error (dashed lines).

Comparison of model to Knights Landing Catch

Although catches at Knights Landing were not used to estimate the parameters of the WRLCM, we calculated the proportion of fish predicted by the model to the observed total catches in a given year. The WRLCM used the flow triggers at Wilkins Slough (Rearing transition) of greater than 400 m^3s^{-1} to move fish past Knights Landing, and the model was able to capture the general patterns in movement among years as a function of the flow trigger (Figure 16 and 17).
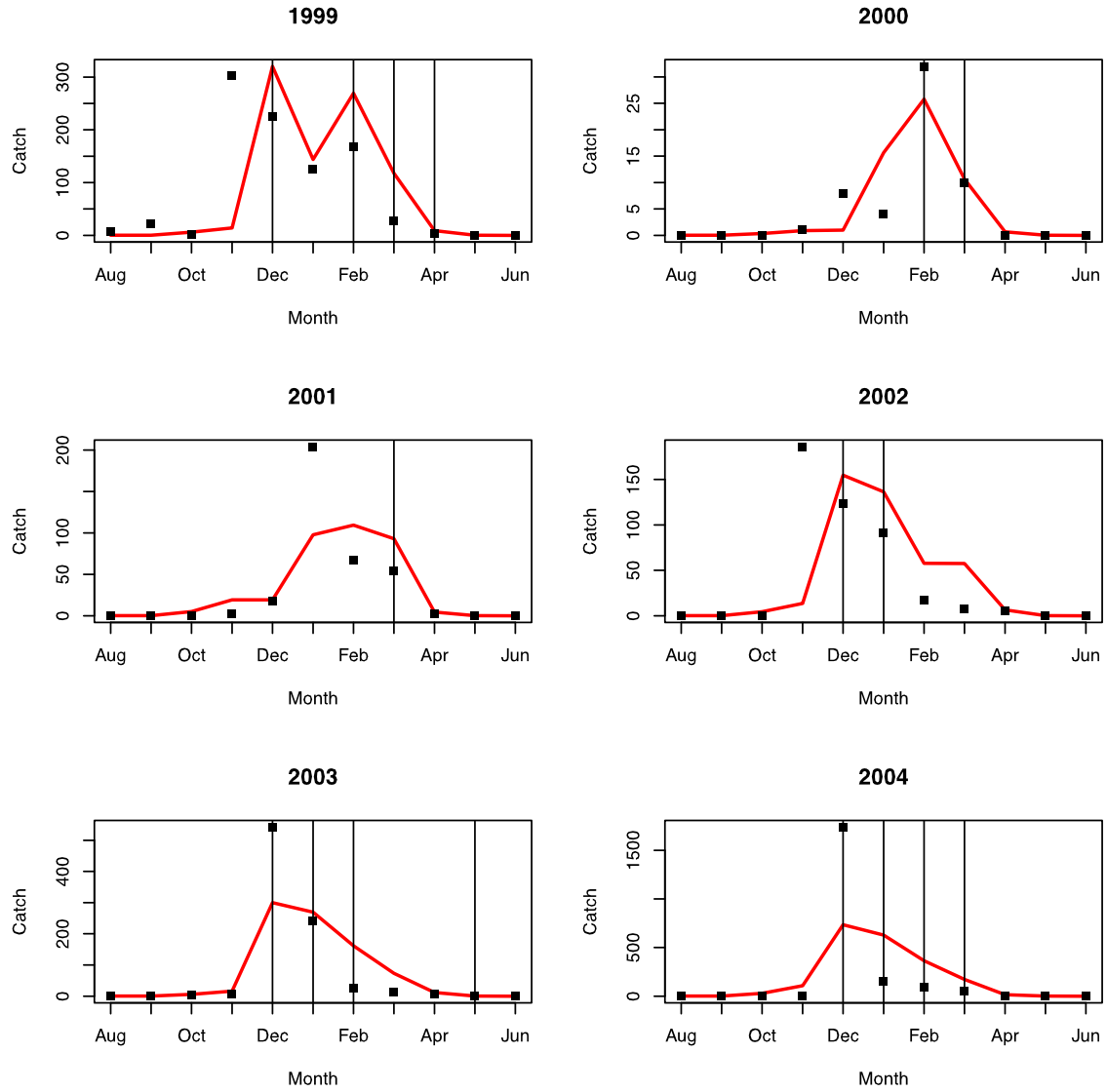
Figure 16. Model predictions (red line) to Knights Landing catch data (black squares) from 1999 to 2004. Vertical lines indicate months in which the average flow at Wilkins Slough was greater than 400 m³s⁻¹.

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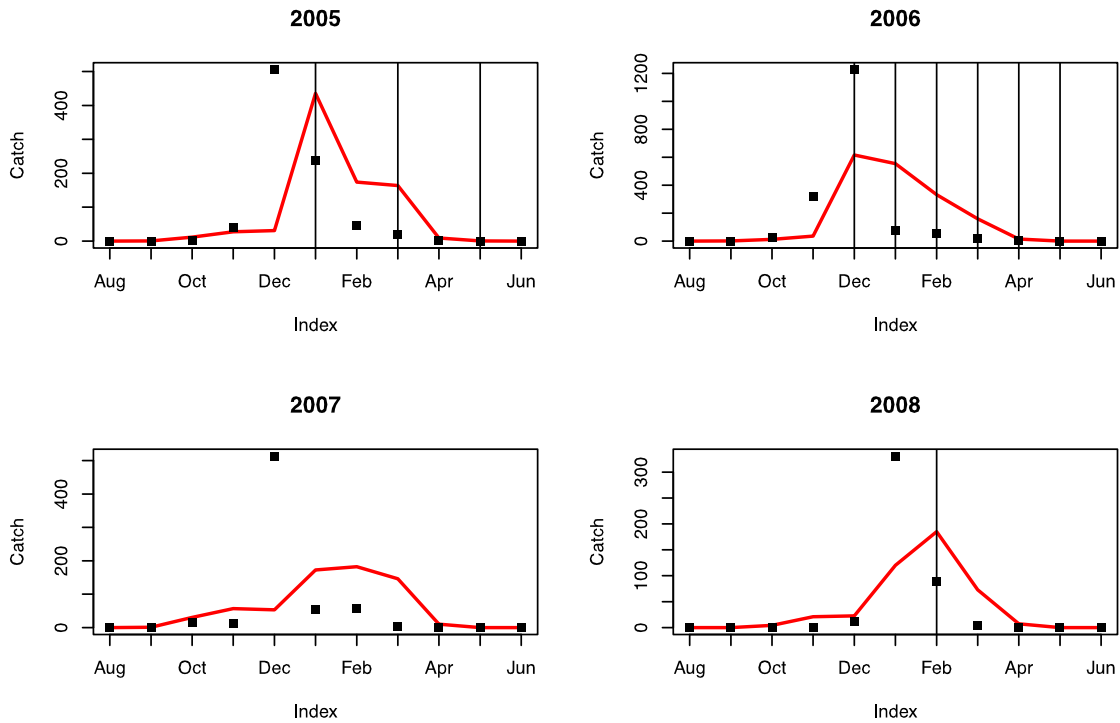
Figure 17. Model predictions (red line) to Knights Landing catch data (black squares) from 2005 to 2008. Vertical lines indicate months in which the average flow at Wilkins Slough was greater than 400 m³s⁻¹.

The estimated parameter values from the MCEM algorithm are provided in Table 5. The table provides the parameter estimate, the standard deviation of the estimate (SD), a transformed value of the parameter estimate, and a note defining the parameter. We attempted to estimate all parameters of the survival of egg to fry as a function of temperature (Transition 1); however, there was strong correlation among the three parameters that caused problems with parameter identifiability. We assumed that the survival rate from egg to fry in the absence of thermal mortality was 0.321, which is consistent with historical estimates of egg to fry survival values (Poytress et al. 2014). The 3-month trailing average (spawn month and trailing 2 months) threshold ($t.crit$) was 13.5 ^{0}C (56.3 ^{0}F). The survival of egg to fry below this critical temperature was 0.321 ($B0_1$) for the 3-month period, whereas above this threshold the survival was reduced by $B1_1$ for each degree of centigrade (within the logistic regression). The monthly fry survival rate (S_{FRY}) was estimated to have a rate of 0.761 per month, and the proportion of fry in the Upper River that were estimated to move to the Lower River per month was 0.327. Finally, flow at Bend Bridge was found to have a positive effect on survival of smolts originating in the Upper River (Table 5).

The MCEM algorithm can be used to make an empirical calculation of the variance of the random effects. We used the 4000 vectors of random effects and their associated weights to calculate the empirical weighted variance of the random effects. The range of the random effects was restricted such that the annual random effect parameters (ε_y) had values of approximately $\pm$ 1. These parameter values corresponded to a range in annual variability in survival of (0.36, 2.7) due to the lognormal structure of the random effects.

Table 5. WRLCM parameter estimates from the model calibration to winter-run indices of abundance (Table 4).

Parameter	Estimate	SD	Transformed Value	Notes
$B0_1$ *	-0.75	0	0.321	Survival below critical temperature value (logit space)
$t.crit$*	13.5	0	13.5	Critical temperature (C) at which egg to fry survival is reduced
S_{FRY}	1.16	0.002	0.761	Winter run fry survival (logit space)
mig_{LH}	-0.721	0.003	0.327	Proportion of fry in upper river migrating to lower river per month (logit space)
$B1_{10}$	0.211	0.005	NA	River smolt survival from flow effect
σ_ε^2**	0.207			Variance of annual random effects in process noise

* parameters fixed in estimation but are relevant for the estimation portion of the model
** empirical estimate from weighted random effects vectors

Using the Hessian matrix (second derivative of parameter estimates with respect to the likelihood surface at the maximum likelihood estimate), we were able to calculate the Fisher information matrix, and obtain estimates of the standard deviation of the model parameters (Table 5) and the correlation among estimated model parameters (Table 6).   Several parameters had high correlations. Correlation among the estimated parameters was less than $\pm$ 0.7 with the highest correlation occurring between fry survival and the rate of decline in egg to fry survival as a function of thermal mortality ($B1_1$). The correlation was negative indicating that similar abundances could be obtained due to a decrease in fry survival or an increase in thermal mortality due to surpassing the critical temperature of 13.5 ^{0}C.

Table 6. Correlation matrix for estimated parameters in the WRLCM calibration.

	$B1_1$	S_{FRY}	mig_{LH}	$B1_{10}$
$B1_1$	1	-0.654	-0.115	0.290
S_{FRY}	-0.654	1	-0.508	-0.462
mig_{LH}	-0.115	-0.508	1	-0.006
$B1_{10}$	0.290	-0.462	-0.006	1

Developing parameter sets for Monte Carlo simulations

To compare alternative hydromanagement actions, Monte Carlo simulations should be run under each of the actions. We have obtained estimates of parameter uncertainty and correlation (Table 6) in the model calibration from the Hessian matrix to incorporate into the Monte Carlo simulation. For those parameters that were estimated, Monte Carlo parameter values were drawn from multivariate normal distribution centered on the maximum likelihood estimates (MLE) and using the covariance matrix estimated from the Hessian obtained at the MLE.   The draws from the multivariate normal distribution incorporated the relative uncertainty in the estimated parameters and preserved the correlation structure among several of the life cycle model parameters that were identified in the correlation matrix of the parameter estimates (Table 5). In addition, we used samples from the posterior distributions for the coefficients of the Newman model (Appendix B). For the random effects, iid normal N(0, σ_ε^2) random variables were drawn to reflect the annual random effects in the process noise. All other parameters were set to their fixed values as described above. Please see Appendix B for a list of all parameter values.

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Appendix A. Analysis of winter-run monthly spawn timing

To estimate the proportion of winter-run spawning among the months of April to August, we conducted an analysis of the numbers of winter-run carcasses detected in each of the months April to August. We were interested in understanding whether the proportions spawning among months were static across all years, or alternatively, whether the proportions varied among years due to the environmental conditions in that year. That is, whether there were some environmental conditions that caused shifts to earlier spawning in some years.

Data

Winter-run carcass observations by date were shifted two weeks earlier to generate "observed" number of fish spawning by date. These spawning numbers by date were coalesced by month to form $N.spawn_{m,t}$ the observed (based on carcass counts) number of winter-run Chinook spawning in month m in year t.

To evaluate annual variability in the proportion spawning in a given month, we calculated a spawning proportion anomaly as the standardized proportion of fish spawning each month ($SP_{m,t}$). For example, the values of the standardized April values were

$$SP_{Apr,t} = \frac{P.spawn_{Apr,t} - mean(P.spawn_{Apr})}{std\ dev(P.spawn_{Apr})}$$

where the proportion spawning in each month for a given year t (subscript suppressed) was calculated as

$$P.spawn_m = \frac{N.spawn_m}{\sum_m N.spawn_m}.$$

To understand how these annual anomalies varied as a function of water temperature, we calculated the Pearson's correlation coefficient between mean monthly temperature below Keswick Dam between January and June and the standardized proportions (Figure A1).
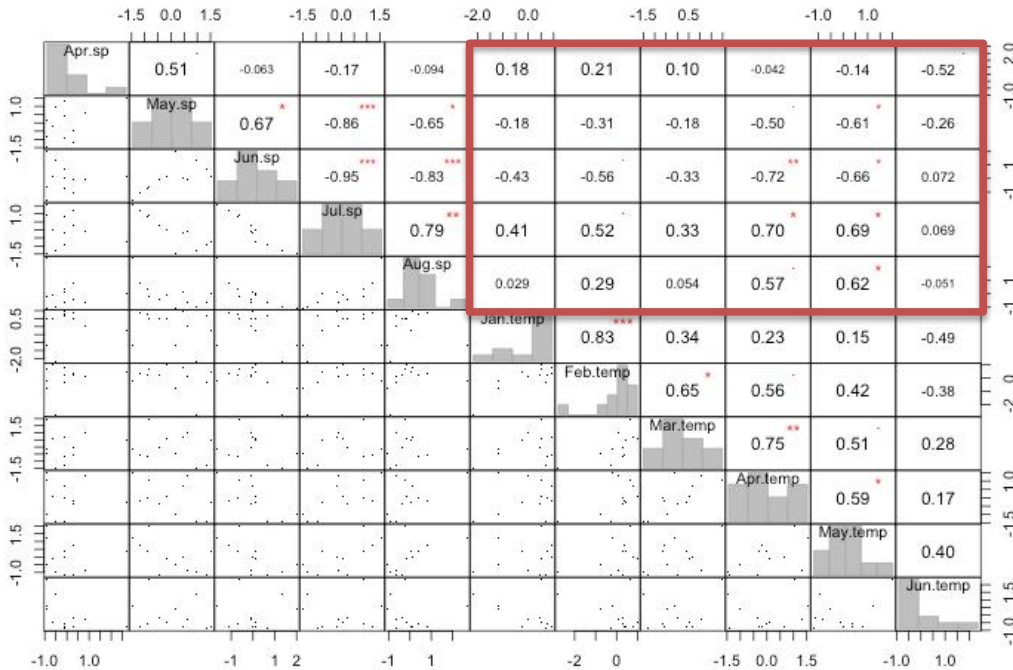
Figure A1. Pearson correlation coefficients (upper triangle), histograms (diagonal) and scatter plots (lower triangle) for all combinations of monthly spawning proportion anomalies and Keswick water temperatures. The red box indicates the month by temperature correlations, and red asterisks indicate significant correlation coefficients.

Statistical analysis

We fit a multinomial logistic regression using the *multinom* function from the *nnet* package in R to the number of winter-run Chinook spawning in each month, $N.spawn_{m,t}$. We evaluated the ability of April Keswick temperatures to explain annual variability in the spawning timing. We focused on April temperatures because April is the first month of spawning, and April would allow this physical variable to be used as a predictor of spawn timing for future years. The monthly average April temperatures at Keswick were standardized (subtracted mean and divided by standard deviation) for use in the multinomial model.

We fit a base model without the April temperature effect and we fit the model with the April effect and used Akaike Information Criterion (AIC) to compare the models. The AIC value for the base multinomial model was 75822, whereas the value for the multinomial model including April temperature as a covariate was 74209. The difference in AIC was 1613, providing strong support for the model with the April temperature covariate.

The model coefficients for the multinomial model with April covariate indicated increasing spawning in July and August (positive coefficient values) when April temperatures increased (Table A1 and Figure A2). The model coefficients (Table A1) can thus be used for making predictions of spawning proportions using standardized April temperatures as displayed in Figure A2.

Table A1. Coefficient estimates of the multinomial model including April covariate. The effect of the April covariate is reflected in the B1 coefficient estimate.

	Estimate		Standard Error	
Month	B0	B1	B0	B1
Apr	-4.145	0.054	0.06	0.062
May	-1.796	-0.203	0.02	0.02
Jul	-0.332	0.385	0.012	0.012
Aug	-3.443	0.792	0.044	0.045
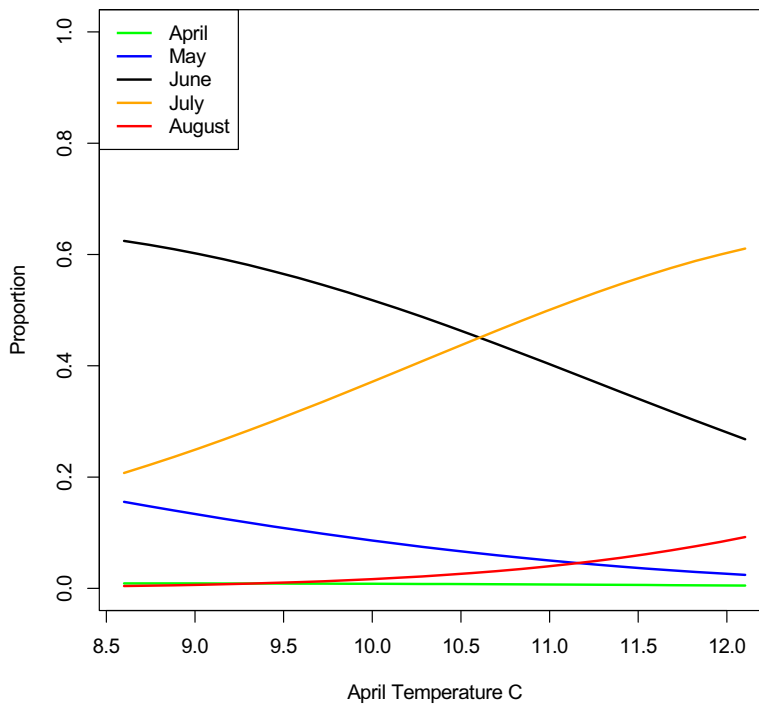
Figure A2. Predictions of the proportion of winter-run Chinook spawning from the multinomial regression model using April temperatures at Keswick Dam as a predictor variable.

Appendix B. Table of parameter values for WRLCM

Table B1. Parameter values, standard deviation (SD), transformed values, transition numbers in which parameters are found and brief description of parameter.

Name	Value	SD	Transformed Value	Transition	Description
$t.crit$	13.5	0	13.5	1	Critical temperature (C) at which egg to fry survival is reduced
$B0_1$	-0.75	0	0.321	1	Survival below critical temperature value (logit space)
$B1_1$*	-0.574	0.002	NA	1	Rate of reduction in egg to fry survival (logit space)
$P_{TF, m}$	-3	0	0.047	2	Proportion tidal fry
$S_{TF,FP}$	1	0	0.731	3	Survival tidal fry in floodplain
$min.p$	0.05	0	0.05	3	Minimum proportion entering Yolo bypass under flow < 100 cfs
$p.rate$	1.1	0	NA	3	Rate of increase in proportion entering Yolo bypass for flows > 6000 cfs
$B0_4$	0	0	0.5	4	Average survival tidal fry to delta intercept
$B1_4$	-1	0	NA	4	Effect of DCC gate (value is in logit space)*
$B0_5$	0	0	0.5	5	Average proportion of tidal fry to bay intercept
$B1_5$	2	0	NA	5	Proportion tidal fry to bay - flow at Rio Vista effect
$S_{TF,DE-BA}$	-1	0	0.269	5	Survival of tidal fry from delta to bay
S_{FRY}*	1.16	0.002	0.761	Rearing	Winter run fry survival
mig_{LH}*	-0.721	0.003	0.327	Rearing	Proportion of fry in upper river migrating to lower river per month
$B0_M$	-6	0	0.003	Rearing	Wilkins slough movement without trigger
$B1_M$	5.5	0	NA	Rearing	Wilkins slough change in movement with flow trigger, movement rate under flow trigger is 0.377
mig	-3	0	0.047	Rearing	Probability of migration from habitats
$S_{FRY,BA}$	-7	0	0.001	Rearing	Survival of bay rearing fry pushed to gulf
Z_1	-1	0	0.269	11 to 15	January smolt probability
Z_2	0	0	0.5	11 to 15	February smolt probability
Z_3	3	0	0.953	11 to 15	March smolt probability

Name	Value	SD	Transformed Value	Transition	Description
Z_4	8	0	1	11 to 15	April smolt probability
Z_5	10	0	1	11 to 15	May smolt probability
Z_6	10	0	1	11 to 15	June smolt probability
Z_7	10	0	1	11 to 15	July smolt probability
$B0_{11,LR}$	1.39	0	0.801	12	Smolt survival lower river to delta
$B0_{10,UR}$	-0.4	0	0.401	11	Survival of upper river fish to lower river
$B1_{10}*$	0.211	0.005	NA	11,12	River smolt survival from flow effect
$^{C}S_{11}$	1.5	0	0.818	11 - 14	Survival smolt Chipps to ocean - assume 0.82
$^{A}S_{13,FP,m}$	2.5	0	0.924	13	survival from Yolo until Delta, assume 0.92 (at least until insertion point into smolt survival via Newman in Delta)
$S_{15,BA}$	0	0	0.5	15	Survival of smolts bay to ocean
S_{G1}	-2.2	0	0.0997	11, 12, 13	Gulf entry survival for upper river, lower river, floodplain (delta and bay when $D_{G2I}=0$)
D_{G2}	0	0	NA	14, 15	Gulf entry survival decrement for delta and bay (value in logit space)
σ_ε^2	0.207	0	NA	11-15	Variance of annual random effects in process noise
S_{17}	1.35	0	0.794	17, 18	Probability of survival age 1 to age 2 over 4 months
M_2	-2.2	0	0.1	17,18	Probability of maturation age 2
S_{sp2}	2.2	0	0.9	18	Survival ocean exit to spawning ground age 2
S_{19}	1.4	0	0.802	19	Probability of survival age 2 to age 3
M_3	2.2	0	0.9	19, 20	Conditional probability of maturation at age 3
S_{sp3}	2.2	0	0.9	20	Survival ocean exit to spawning ground age 3
S_{21}	1.4	0	0.802	21	Survival age 3 to age 4
S_{sp4}	2.2	0	0.9	21	Survival ocean exit to spawning ground age 4
$V_{eggs,2}$	3200	0	3200	22	Eggs per spawner age 2
$V_{eggs,3}$	5000	0	5000	22	Eggs per spawner age 3
$V_{eggs,4}$	5000	0	5000	22	Eggs per spawner age 4

Name	Value	SD	Transformed Value	Transition	Description
$B0_{Apr}$	-4.145	0	NA	22	Intercept for proportion of spawners in April
$B1_{Apr}$	0.0538	0	NA	22	Effect of temperature on proportion of spawners in April
$B0_{May}$	-1.796	0	NA	22	Intercept for proportion of spawners in May
$B1_{May}$	-0.2031	0	NA	22	Effect of temperature on proportion of spawners in May
$B0_{Jul}$	-0.332	0	NA	22	Intercept for proportion of spawners in July
$B1_{Jul}$	0.3852	0	NA	22	Effect of temperature on proportion of spawners in July
$B0_{Aug}$	-3.443	0	NA	22	Intercept for proportion of spawners in August
$B1_{Aug}$	0.7921	0	NA	22	Effect of temperature on proportion of spawners in August
Fem_{Age2}	0.01	0	0.01	18	Proportion of age 2 spawners that are female
Fem_{Age3}	0.5	0	0.5	20	Proportion of age 3 and 4 that are female
$K_{Sp,m}$	40000	0	40000	22	Capacity in the spawning reaches by month
$B0_{Newman}$	-1.02	0.1	0.26	11-14	Baseline survival parameter in Newman (2003)
$B1_{Newman}$	0.1	0.05	NA	11-14	Size parameter in Newman (2003)
$B2_{Newman}$	-0.56	0.07	NA	11-14	Temperature parameter in Newman (2003)
$B3_{Newman}$	0.56	0.09	NA	11-14	Log Freeport flow parameter in Newman (2003)
$B4_{Newman}$	-0.21	0.07	NA	11-14	Exports parameter in Newman (2003)
$B5_{Newman}$	-0.6	0.13	NA	11-14	DCC gate position parameter in Newman (2003)
$B6_{Newman}$	-0.24	0.13	NA	11-14	Sacramento River indicator parameter in Newman (2003)

*Estimated parameter values have associated standard deviations (SD)