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LIFE CYCLE MODELING FRAMEWORK FOR CHINOOK SALMON SPAWNING IN THE SACRAMENTO RIVER

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Life cycle modeling framework for Chinook salmon spawning in the Sacramento River

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Abstract

Understanding how water management decisions in California's Central Valley affect populations of imperiled salmonid species is critical for evaluating the efficacy of management alternatives in meeting salmon recovery objectives. This is especially true for Sacramento River Chinook salmon (*Oncorhynchus tshawytscha*), whose populations have experienced significant decline and are sensitive to water temperature and flow dynamics that are largely influenced by municipal and agricultural water supply operations. Lifecycle models (LCMs) can provide a powerful tool for evaluating how water operations and habitat restoration influence the long-term population dynamics of Chinook salmon under a range of hydroclimate conditions. These LCMs consist of coupled abiotic-biotic models to integrate effects that span multiple life stages, generations, and hydroclimate conditions. Here, we introduce the Sacramento River Chinook salmon life cycle model (SRCLCM), an LCM framework for winter-run (listed as endangered under the federal Endangered Species Act) and fall-run Chinook salmon spawning in the Sacramento River. The SRCLCM is a network of interconnected models, and relies on flow and water temperature data, hydraulic models, habitat capacity models, and an early life-history model that uses relationships linking in-river water temperature and/or streamflow to smolt production and ocean indicators to predict early marine survival rates and adult abundance. In this document, we describe the framework of the SRCLCM, including the model structure, the stage transition equations, and the required data inputs for the SRCLCM.

I. Introduction

Populations of Chinook salmon (*Oncorhynchus tshawytscha*) are declining along the Northwest Pacific coast of North America, and populations in California's Central Valley have experienced some of the greatest rates of decline (Atlas et al. 2023). This decline is the culmination of over two centuries of unique stressors in the Central Valley that have made Chinook salmon populations particularly vulnerable. In the mid-19th century, Chinook salmon returning to the Central Valley began experiencing significant population declines due to a multitude of stressors including over-fishing, habitat loss, and hydraulic mining (Yoshiyama et al. 1998, Munsch et al. 2022). Additional stressors arrived in the mid-20th century, with the development of large water supply projects that transformed the California Central Valley rivers into a highly regulated conveyance system that delivered water throughout the state for a variety of municipal and agricultural uses. The development of water project facilities included the construction of diversions and levees that altered flow dynamics and the construction of dams that blocked access to much of the historical Chinook salmon spawning habitat.

Following ~150 years of accumulated stressors, two of the four distinct "runs" of Central Valley Chinook salmon (winter, spring, fall and late-fall) were listed as federally threatened (spring-run, NMFS 1999) and endangered (winter-run, NMFS 1994) under the Endangered Species Act (ESA). Fall-run Chinook salmon are not listed under the ESA, however their population size has become increasingly variable (Satterthwaite and Carlson 2015), and has experienced years with such low abundance that the California salmon fishery was closed completely during some years (PFMC 2023, Lindley et al. 2009).

Although hatchery supplementation and water temperature management programs have aimed to mitigate for various stressors, these efforts have failed to sustain fisheries or recover Central Valley Chinook salmon. For example, fall-run Chinook salmon hatchery practices have contributed to reductions in life history diversity (Huber and Carlson 2015), genetic diversity (Williamson and May 2005) and population asynchrony (Satterthwaite and Carlson 2015), all of which contribute to buffering populations from an unpredictable environment. Additionally, water temperature management programs below dams have failed to meet temperature targets during multiyear drought periods, resulting in high rates of egg mortality (Martin et al., 2017; SWFSC 2023). Not only have these stressors accumulated over time, but they are anticipated to intensify as temperatures increase and droughts become more extreme with climate change (Ullrich et al. 2018). Because California Central Valley Chinook populations are in such peril, it is critical to understand how the dominant habitat drivers of hydroclimate and water supply operations will affect their long-term population dynamics and potential for recovery.

Chinook salmon are a migratory species with a complex life history that spans freshwater, estuarine, and marine environments (Williams 2006), and therefore understanding how specific stressors affect long-term population dynamics is a continuous challenge. For example, Lindley et al. (2009) used a conceptual model of the Chinook salmon life cycle to identify that poor ocean conditions and very low marine survival contributed to the low fall-run adult returns that prompted the closure of the commercial fishery in 2008. Similarly, other studies have identified the negative effects of reduced streamflow on smolt outmigration survival (Michel et al. 2021), and increased water temperature on egg-to-fry survival (Martin et al. 2017) and smolt outmigration survival (Michel et al. 2020) for Central Valley Chinook salmon. However, without evaluating how these effects on survival propagate throughout multiple life-stages, generations and environmental conditions, it remains unknown what effect they have on long-term population dynamics. Consequently, there is a need to develop a tool that can integrate multiple stressors across multiple habitats on salmonid population dynamics.

Life cycle models (LCMs) allow for a comprehensive evaluation of how changes to the environment affect population dynamics that span multiple life stages, habitats, generations, and environmental conditions. To date, LCMs have been developed for Central Valley fall-run (Friedman et al. 2019), spring-run (Cordoleani et al. 2020), and winter-run (Hendrix et al. 2014) Chinook salmon. Here, we introduce the Sacramento River Chinook salmon life cycle model (SRCLCM) as an improved version of Hendrix et al.'s (2014) winter-run LCM. The SRCLCM includes several advancements from Hendrix et al. (2014), including improved relationships between abiotic drivers and stage-specific vital rates, increased model flexibility from additional covariates, detailed descriptions of model inputs, and a generic framework that can be applied to Chinook salmon that spawn in the mainstem Sacramento River (winter-run and fall-run). In this document, we present the model framework by describing the structure of the SRCLCM, the transition equations that define the movement and survival throughout the life cycle, and the required data inputs.

II. Model Structure

The SRCLCM is a stage-structured, stochastic life cycle model; it is spatially-structured to include several habitats for several life history stages. The SRCLCM uses coarse categories of developmental stages and geographic areas in order to strike a balance between model complexity and tractability. This results in a model that is complex enough to address the motivating questions yet is not overwhelmed with the dimensionality of parameters.

Fall-run and winter-run ecotypes are so named due to the timing of the adult entry into the freshwater environment. Both fall-run and winter-run spawn within a few months of returning to freshwater, and the temporal structuring of developmental stages are unique to each run (Figure 1). We captured these stages within the SRCLCM by using eggs, fry, smolts (physiological and behavioral changes to prepare for seaward migration), smolts in the Gulf of the Farallones, sub-adults in the ocean (ages 2, 3, and 4), and mature adults (spawners) (Figure 1). The SRCLCM begins in the month of March (LCM month = 1), to mark the initiation of spawning for winter-run Chinook salmon. We keep the same month assignments for fall-run Chinook salmon despite their later adult return and spawn timing. This is to set the stage for future model versions of the SRCLCM that can allow investigation of interactions and interdependencies between the population dynamics of winter-run and fall-run Central Valley Chinook salmon using a common timeframe.

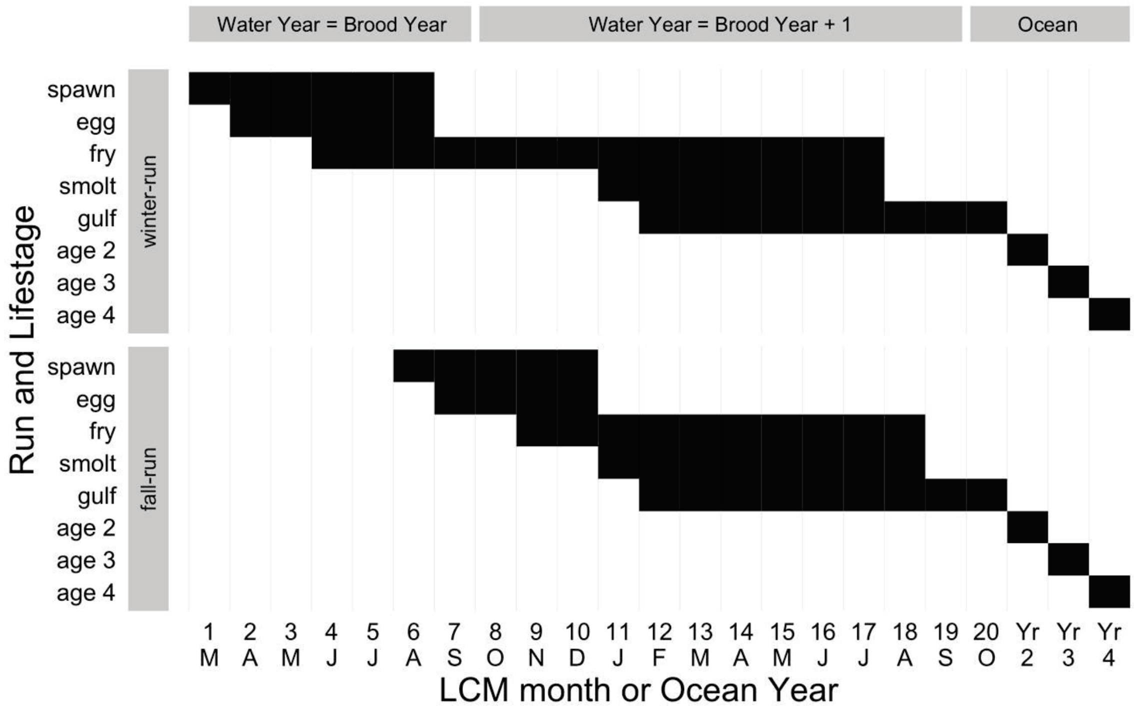

Figure 1. Temporal structure of the different developmental stages of winter-run and fall-run Sacramento River Chinook salmon within the SRCLCM. **For a given broodyear, the SRCLCM begins in March and generates fish abundance by developmental stage, geographic area, and month for the freshwater life history stages (LCM months 1 – 20). Freshwater life history stages span two water years for winter-run and are primarily within one water year for fall-run. The SRCLCM then transitions to an annual timestep once fish enter the ocean to estimate abundance for age 2, 3, and 4 subadults and spawners. Year 2, 3, and 4 begin in March for winter-run and begin in August for fall-run. Timing of developmental stages were informed by Vogel and Marine (1991) and del Rosario et al. (2013).**

Each life history stage within the SRCLCM is specific to a geographic area. For the developmental stages that occur within the Sacramento River watershed and San Francisco Bay (e.g., spawners, eggs, fry, smolts, and smolts entering the Gulf of the Farallones), we further define their life history stage by discrete geographic areas of the Upper River, Lower River, Yolo Bypass, Delta, and Bay (Figure 2). For developmental stages that occur in the ocean (e.g., age 2, 3, and 4 subadults), we use only one geographic area of the Ocean.

Within the Sacramento River system, the largest contiguous area of floodplain habitat is contained in the Yolo Bypass and is therefore recognized as a distinct geographic area in the SRCLCM because of the unique habitat it can provide during high flow events. Within each geographic area, however, the SRCLCM also distinguishes between different categories of habitat quality by quantifying habitat in terms of water depth, velocity, and other habitat features (see *Habitat Capacity*, Section IV). Some of these high-quality habitat categories share qualities of floodplain habitat (e.g., shallow, low-velocity), which increases habitat capacity and influences the downstream density-dependent movement patterns at the fry stage (see *Rearing*, Section III). Throughout this document, any reference to the floodplain refers to the Yolo Bypass, unless otherwise indicated.

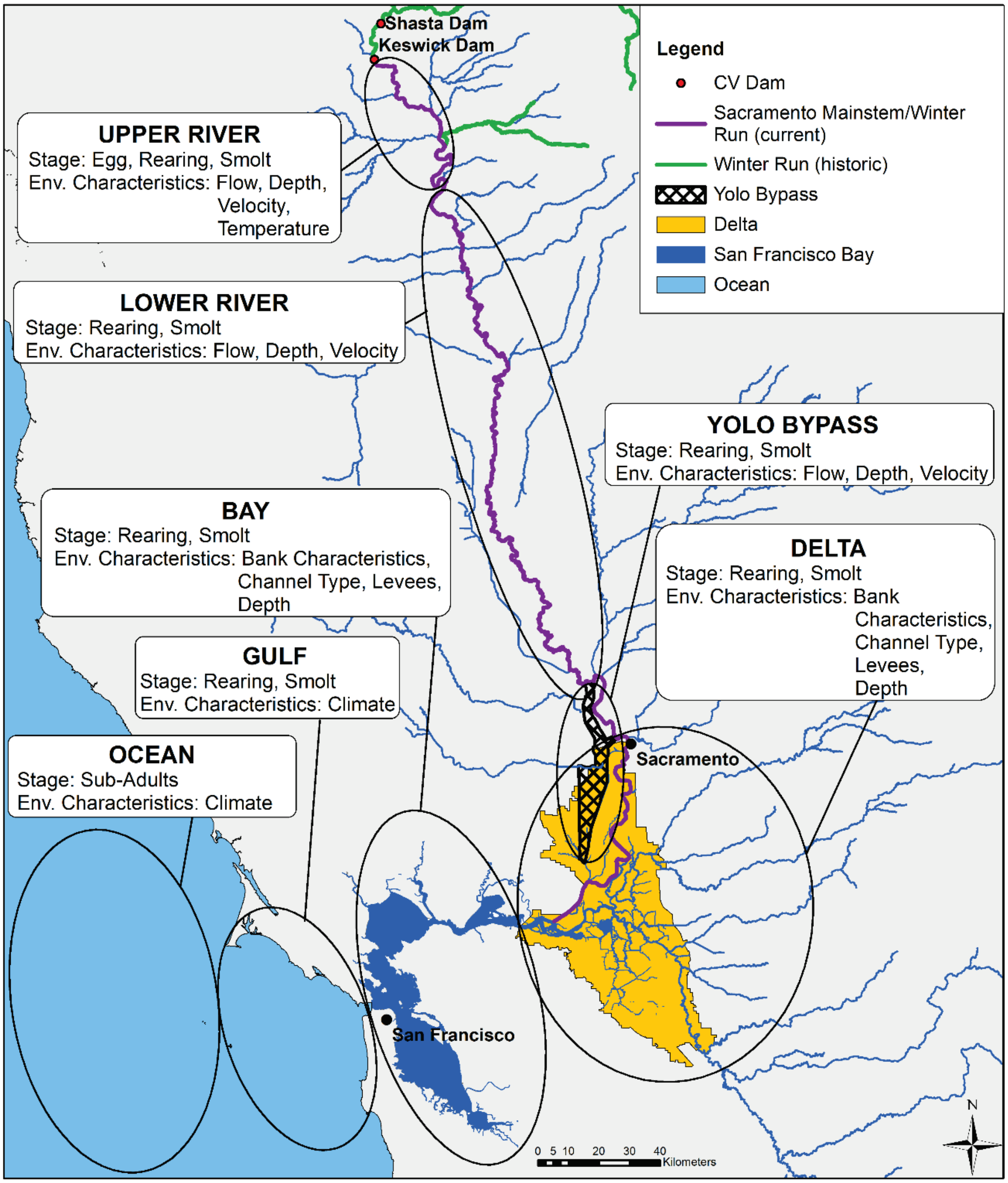

Figure 2. Geographic distribution of Chinook life history stages and examples of environmental characteristics that influence survival.

The SRCLCM links flow and temperature drivers, which are under management control in the Central Valley, to population dynamics (Figure 3). Specifically, the SRCLCM operates as an interconnected network of data inputs and submodels that estimate the quantity and quality of rearing and migratory habitat. The vital rates of reproduction, survival, and movement for many life history stages within the SRCLCM are directly or indirectly functions of velocity, depth, and temperature preferences and tolerances. Management actions are linked to the salmon life cycle through the key drivers of reproduction, survival, and migration of freshwater life stages. This linkage is used to quantify how changes to abiotic conditions affect population dynamics of Chinook salmon.

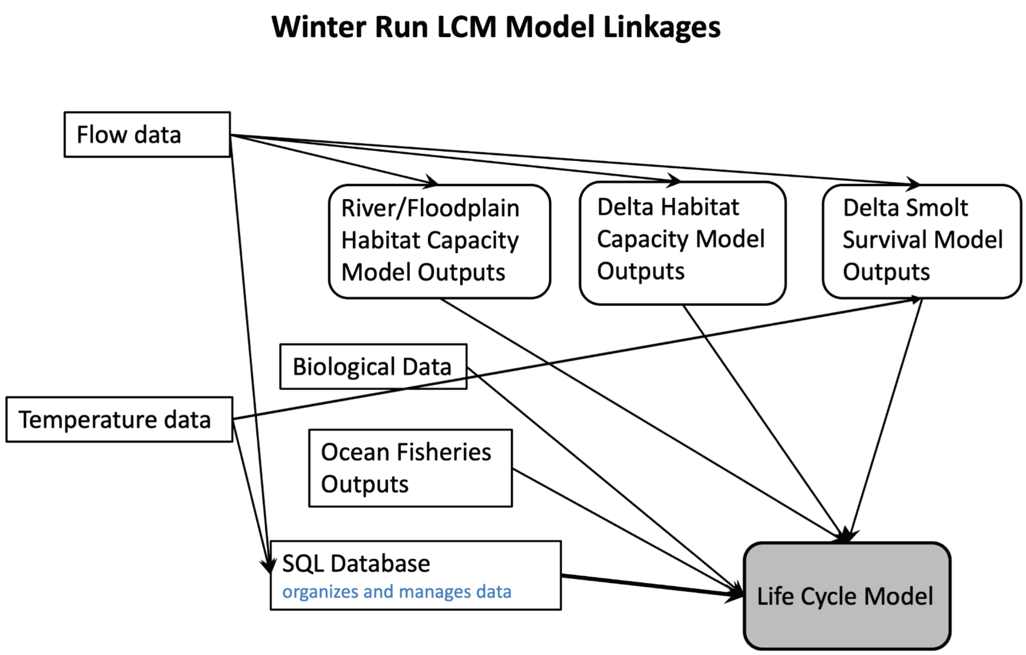

Figure 3. Data and submodels that support and provide physical drivers and parameters that feed into the life cycle model.

III. Model Transition Equations

Below, we explain each of the stage transitions for Sacramento River Chinook salmon spawning in the Sacramento River, where each transition is assigned a unique number (Figure 4). The transitions below are described for an annual cohort and for one run of Chinook salmon; however, in most cases we have not included a subscript for the cohort brood year or for the specific run to simplify the equations. For those transitions in which there are multiple cohorts, such as the production of eggs in transition 23, a subscript to distinguish cohort is included in the equation. A description of the parameters in the SRLCM are included in Table A1.

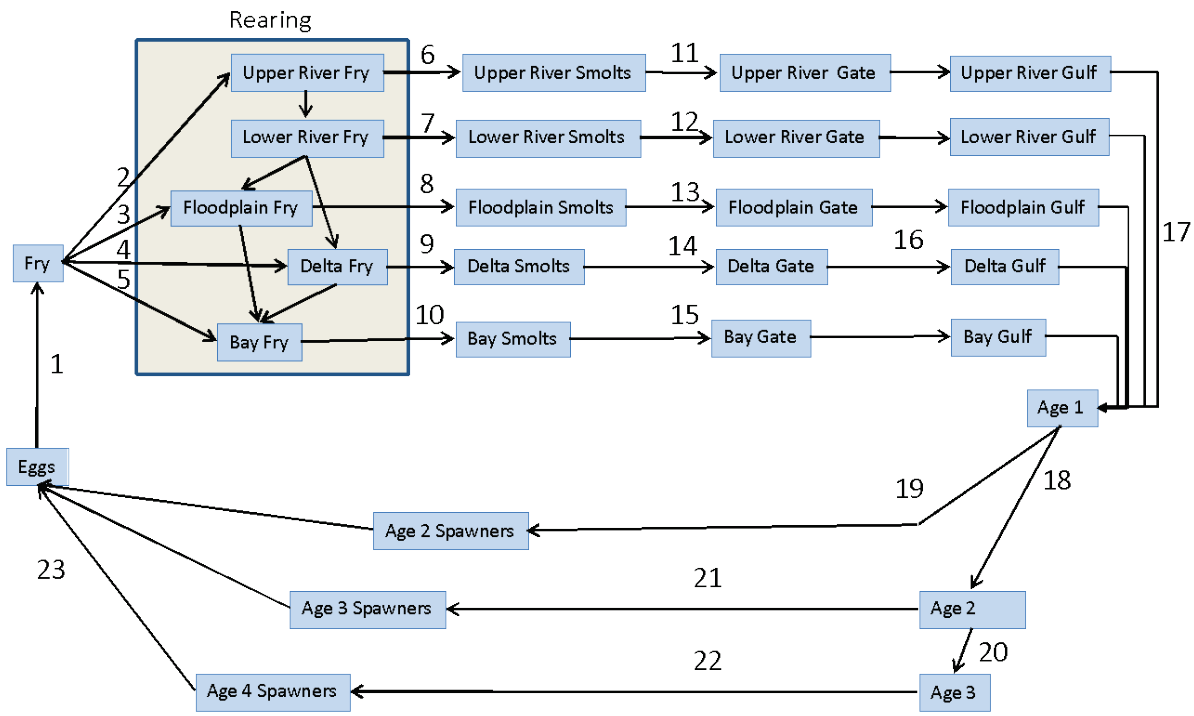

Figure 4. Central Valley Chinook transition stages. Each number represents a transition equation through which we can compute the survival probability of Chinook salmon moving from one life stage in a particular geographic area to another life stage in another geographic area.

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 eggs 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 decline), logit(x) = log(x/[1-x]) is a function that ensures that the survival rate is within the interval [0,1], for months *m* which correspond to the first month through the last month of spawning. Winter-run spawn in months *m* = (2, …, 6) (April to August). Fall-run spawn in months *m* = (7, …, 10) (September to December).

$B0_1 = B0_a + B1_a * X1$

Where $B0_a$ is the intercept and $B1_a$ is the slope of the regression relating the covariate X1 to the background survival rate. The covariate X1 could be used to adjust background survival, such as incorporating annual differences in mortality due to thiamine deficiency (Mantua et al 2021).

The covariate $TEMP_m$ is defined as a weighted average of the month of spawning *m* and the following 2 months. Two additional parameters are used to define the weighting, namely w1 (weight during month of spawning *m*) and w2 (weight during month *m+1*), with w3 = (1 – w1 – w2). The weights can reflect different levels of influence of the monthly temperatures, such as equally weighted (e.g., w1 = w2 = 0.33) or with an emphasis on the first month (w1 = 0.8, w2 = 0.1, w3 = 0.1). The default option is to equally weight temperature across all three months, but unequal weights can be defined in the model code.

Identifying environmental drivers that influence egg survival is an active subject of research (Martin et al. 2017, Martin et al. 2020, Zeug et al. 2012). A recent study by Martin et al. (2020) suggests additional environmental covariates such as intragravel flow may also influence egg survival. Furthermore, intragravel flow may be dependent a variety of factors, including river flow, water depth of the redd, and redd morphology (Bhattarai et al. 2023). The model structure of Transition 1 is flexible and it can be modified to account for additional functional forms (e.g., logistic regression model) or additional covariates that may explain patterns of egg survival as the understanding of factors affecting egg survival continues to evolve.

Transition 2

Definition: Fry emerged in a given month either remain in the Upper River (UR) as rearing fry ($RearFry_{UR,m}$) or disperse downstream as tidal fry ($TidalFry_m$) to the *h* habitats = Yolo Bypass (*YB*), Delta (*DE*), and Bay (*BA*) in months *m*, which corresponds to two months after the month of spawning. Winter-run fry emerge in months *m* = (4, …, 8) (June to October). Fall-run fry emerge in months *m* = (9, …, 12) (November to February).

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

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

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*), Yolo Bypass (*YB*), Delta (*DE*), and Bay (*BA*) arriving in months *m*, which corresponds to the month following emergence. Winter-run tidal fry disperse in months *m* = (5, …, 9) (July to December). Fall-run tidal fry disperse in months *m* = (10, …, 13) (December to March).

Yolo Bypass Tidal Fry (Transition 3)

Whenever there are flows into the Yolo Bypass, a proportion of the juvenile fish (tidal fry in addition to other juvenile life stages) move into the floodplain habitat. There are two options for modeling the entrance to the Yolo bypass. The first option (default) or the second option can be selected via a switch in the model code.

Option 1

The first option models the access to Yolo as a step function in which there is no access below the flow threshold and access to Yolo at a value of $B1_{YB}$ when the Yolo is flooding.

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

where = $S_{TF,YB}$ is the survival of tidal fry in the Yolo Bypass. To reflect the dynamics of access to the Yolo bypass, the following transition equation was used to describe the proportion of tidal fry that enter the Yolo bypass ($P_{YB,m}$)

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

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 (991.1 m^3s^{-1} = 35000 cfs), and $B1_{YB}$ is the proportion of fry that enter the Yolo under flooding conditions.

Option 2

The second option models the access to Yolo bypass as a linear function of the proportion of flow in the Yolo.

$P_{YB,m} = B_{YB} * R_{Yolo,m}$

where $R_{Yolo,m}$ is the ratio of flow entering into the Yolo bypass relative to flow at Verona, $R_{Yolo,m} = Q_{Yolo,,m} / (Q_{Verona,m.} + Q_{Yolo,,m})$

Delta and Bay Tidal Fry (Transition 4 and 5)

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

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

where $S_{TF,DE,m}$ is the survival to the Delta by tidal fry and $S_{TF,DE\text{-}BA}$ is the survival of tidal fry to the Bay from the Delta.

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

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

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

where $B0_5$ and $B1_5$ are model parameters, and $Q_{RioVista,m}$ is the flow anomaly (subtract mean and divide by standard deviation over the historical period).

Rearing

Definition: Fry rear among Upper River, Lower River, Yolo Bypass, Delta, and Bay habitats according to a density dependent movement function in months *m*, which corresponds to all months of rearing following the month of emergence. Winter-run fry rear in months *m* = (5, …, 17) (July to the following July (brood year + 1)). Fall-run fry rear in months *m* = (10, …, 18) (December to August).

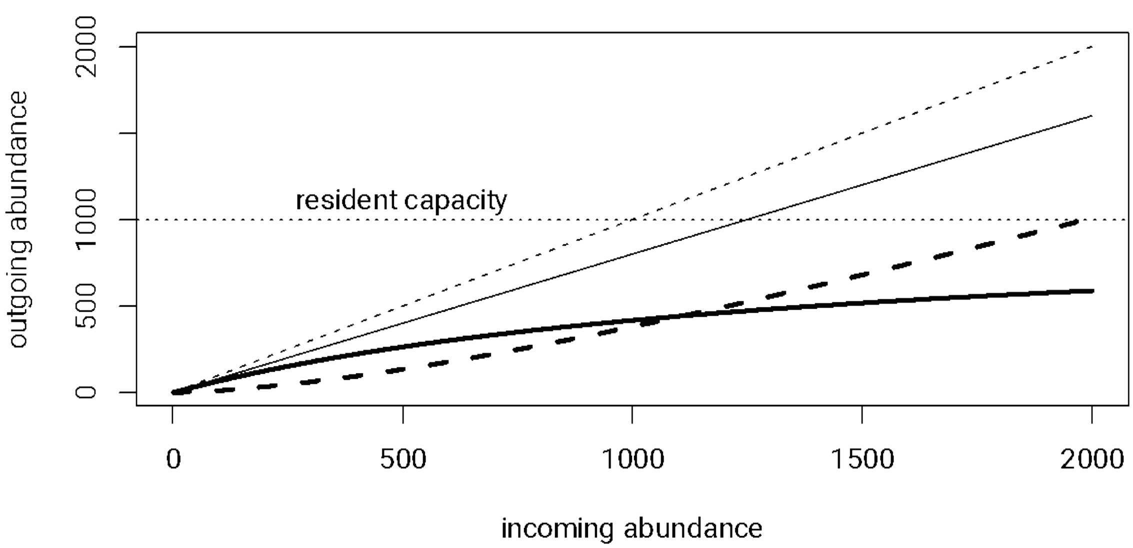

Figure 5. Example of the Beverton-Holt movement function in which the outgoing abundance (thin solid black line) is split between migrants (thick dashed line) and residents (solid dark line), that are affected by the resident capacity (thin dotted line). The 1:1 line (thin dashed line) is also plotted 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 defines the process by which 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 5):

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

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

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 6) 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

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

whereas in other habitats and months the migration rate $mig_{h,m}$ is a value that can vary by the habitat. For example, the upper river to the lower river (mig_{LH}) can be different from the migration rate from the Yolo Bypass to the delta, the delta to the bay. Some of the migration rates in the absence of density dependence can be set to the same values, especially where observations of Sacramento River chinook salmon are scarce. For example, the same migration rate could be used from the Yolo Bypass to the delta, the delta to the bay, and the bay of to the gulf (this is the default option).

<u>Survival of fry</u>

Survival of resident and migrant fry $S_{FRY,h,m}$ are modeled as a function of a covariate $X_{h,m}$ that can vary for each habitat and month. The monthly survival rate of fry in habitat *h* and month *m* is modeled as

$$\text{logit}(S_{FRY,h,m}) = B0_F + B1_{F,h} * X_{h,m}$$

Transitions 6 – 10

Definition: Smolting of *Residents* in the Upper River, Lower River, Yolo Bypass, Delta, and Bay habitats in months *m.* Winter-run smolt in months *m* = (11, … ,17) (January to July in the calendar year after spawning). Fall-run smolt in months *m* = (11, … ,18) (January to August 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:

$\text{logit}(P_{SM,\, m}) = Z_k + B1_{\text{SMOLT}} * T_{H,m}$

where $-\infty < Z_1 < Z_2 \ldots < Z_k < \infty$ are the monthly rates of smoltification based on photoperiod (k = 1, …, 7 encompassing January to July), $T_{H,m}$ is the monthly temperature anomaly for habitat H (mean of 0) and $B1_{\text{SMOLT}}$ is the effect of the temperature anomaly on the smolting schedule (Björnsson et al. 2011). Setting either the $T_{H,m.}$ or the $B1_{\text{SMOLT}}$ to zero will result in the same smolting schedule among all habitats (the default).

Note that during months where smoltification occurs, 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 (Figure 6 shows connectivity among habitats)
3. Survival and movement of the fry calculated in step 2

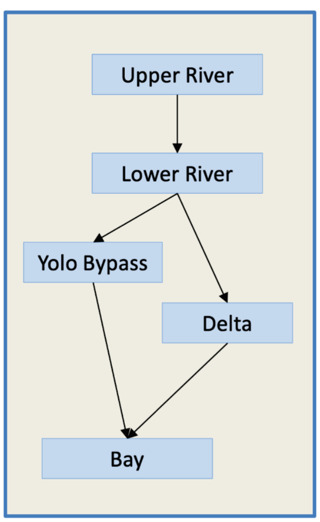

Figure 6. Connectivity among habitats for Sacramento River Chinook fry. Connections between the Lower River and Yolo Bypass occur due to flooding of the Yolo Bypass and are thus ephemeral.

Transitions 11 – 15
These transitions use a Smolt Survival Model (SSM) to calculate the smolt survival through the delta portion of their outmigration. We have described the transition equations generically to be able to use the survival estimates in month *m* and habitat *h* using the acronym $SSM_{h,m}$ in the descriptions below.

Different SSM models may be used to calculate this survival including models developed from the statistical analysis of coded wire tag recoveries (Newman 2003), statistical analysis of acoustically tagged winter-run (Dalton et al., 2022) and late fall-run (Perry et al. 2018) Chinook salmon, and a mechanistically based enhanced particle tracking model (ePTM, Sridharan et al. 2023) that simulates smolt movement at fine temporal (15 min) and spatial (DSM2 8.2 grid structure) resolution.

The SSM must provide the following information for use in the SRCLCM:

- Monthly smolt survival estimates for fry that initiated the smolting process in the Lower River, Yolo, and Delta
- Optional - uncertainty in the monthly smolt survival estimates (probability distribution or samples from the distribution) for fry originating from the Lower River, Yolo, and Delta

The following equations use the output from the ePTM smolt survival model and are tailored to the DSM2 grid structure for input (e.g., Sacramento River nodes) and output locations (e.g., Chipps Island); however, the model structure can accommodate each of the other SSMs described above.

Transitions 11 & 12
Definition: Smolts that reared in the Upper River and Lower River habitats migrate over one month and arrive at the Golden Gate and thus end the freshwater phase of their life cycle in month *m*, which corresponds to the month following their transition as smolts. Both winter-run and fall-run arrive at the Golden Gate in months *m* = (12, … ,20) (February to October).

Upper River smolt outmigration (Transition 11)

$$Gate_{UR,m} = S_{11,UR,m-1} * Smolts_{UR,m-1}$$

Lower River smolt outmigration (Transition 12)

$$Gate_{LR,m} = S_{12,LR,m-1} * Smolts_{LR,m-1}$$

where survival $S_{T,h,m}$ is the smolt survival rate from transition *T* (11, ..., 15) in habitat *h* (*UR, LR, YB, 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.

$S_{11.UR,m} = {}^{A}S_{11,UR,m} * {}^{B}S_{12,LR,m} * {}^{C}S_{11}$
$S_{12,LR,m} = {}^{A}S_{12,LR,m} * {}^{B}S_{12,LR,m} * {}^{C}S_{11}$

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

$\text{logit}({}^{A}S_{11,UR,m}) = B0_{11,UR} + B1_{11} * q.bb_{m}$
$\text{logit}({}^{A}S_{12,LR,m}) = B0_{12,LR} + B1_{11} * q.bb_{m}$

where $B0_{11,UR}$, $B0_{12,LR}$ and $B1_{11}$ are model parameters, and $q.bb_{m}$ is the monthly flow anomaly at Bend Bridge (mean of 0 and standard deviation of 1, standardized relative to period of record used for Bend Bridge flows).

${}^{B}S_{12.LR,m} = SSM_{LR,m}$

where $SSM_{LR,m}$ is a mean monthly survival rate for smolts originating from the Sacramento River through the Delta to Chipps Island as calculated by the Smolt Survival Model. The value ${}^{C}S_{11}$ 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 Yolo Bypass migrate over one month and arrive at the Golden Gate in month m, which corresponds to the month following their transition as smolts. Both winter-run and fall-run arrive at the Golden Gate in months m = (12, … ,20) (February to October).

$Gate_{YB,m} = S_{13,YB,m-1}\, Smolts_{YB,m-1}$

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

$S_{13,YB,m} = {}^{A}S_{13,YB,m} * {}^{B}S_{13,YB,m} * {}^{C}S_{11}$

where ${}^{A}S_{13,YB,m}$ is survival in the Yolo Bypass until the Smolt Survival Model estimate is applied for survival through the Delta.

${}^{B}S_{13.YB,m} = SSM_{YB,m}$

where $SSM_{YB,m}$ is a mean monthly survival rate for smolts originating from the Yolo Bypass through the Delta to Chipps Island as calculated by the Smolt Survival Model.

Transition 14

Definition: Smolts that reared in the Delta migrate over one month and arrive at the Golden Gate in month *m*, which corresponds to the month following their transition as smolts. Both winter-run and fall-run arrive at the Golden Gate in months *m* = (12, … ,20) (February to October).

$Gate_{DE,m} = S_{14,DE,m-1} * Smolts_{DE,m-1}$

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.

$S_{14,DE,m} = {}^{A}S_{14,DE,m} * {}^{C}S_{11}$

where ${}^{A}S_{14,DE,m} = SSM_{DE,m}$

where $SSM_{DE,m}$ is a mean monthly survival rate for smolts originating from the Delta to Chipps Island as calculated by the Smolt Survival Model.

Transition 15

Definition: Smolts that reared in the Bay migrate over one month and arrive at the Golden Gate in month *m*, which corresponds to the month following their transition as smolts. Both winter-run and fall-run arrive at the Golden Gate in months *m* = (12, … ,20) (February to October).

$Gate_{BA,m} = S_{15,BA} * Smolts_{BA,m-1}$

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

Transition 16

Definition: Smolts that reach the Gulf of the Farallones (past the Golden Gate Bridge) enter the ocean and transition to marine waters in months *m*, which corresponds to the same month as the Gate lifestage. Both winter-run and fall-run enter the gulf in months *m* = (12, … , 20) (February to October).

$Gulf_{h,,m} = Gate_{h,m-1} * S_{GULF,\ m-1}$

where the first product is the accumulation of the previous month's Gulf juveniles where $S_{GULF,m-1}$ is the survival rate in the Gulf.

The period of ocean entry can be a critical period of transition for salmonids and lack of available resources can have strong detrimental effects on the year class (Lindley et al. 2009). We therefore model the survival at ocean entry by using an indicator of ocean productivity as

$$\text{logit}(S_{GULF,m}) = B0_{GULF} + B1_{GULF} * OI_{,m}$$

where $B0_{GULF}$ is a parameter describing the average survival rate , $OI_{,m}$ is an ocean index, and $B1_{GULF}$ is the coefficient describing the strength of the ocean index effect on ocean entry survival. The ocean index could reflect ocean productivity due to upwelling strength (Schroeder et al. 2013) or an index of predation intensity (Friedman et al. 2019, Wells et al. 2017).

Transition 17

The total number of Age 1 fish entering the ocean are a combination of two stages: 1) newly arriving juveniles from the Gulf stage, and 2) earlier arriving juveniles that are retained. In this transition we accumulate the smolts in the Gulf as the model is shifting from a monthly time step to an annual one. We use a Transitional stage (*Trans*) to accumulate fish across months *m*, which corresponds to all months with the Gulf lifestage. Both winter-run and fall-run accumulate Age 1 fish entering the ocean in months $m = (12, \ldots, 20)$ (February through October). The Age 1 abundance equals the number of juveniles at the end of the Transitional stage, which for both winter-run and fall-run is model month 20.

$$Trans_m = Trans_{m-1} * S_{TRANS,\, m-1} + \Sigma_{h=1:5}\, Gate_{h,m}$$

$$Age1 = Trans_{m=20}$$

where the monthly survival rate for the transition phase is calculated from the ocean survival rate from model month 20 to Age 2 (S_{17}). For winter-run, the period from model month 20 to Age 2 spans a 4-month period (described below), therefore the monthly survival rate (S_{TRANS}) is the fourth root of the winter-run survival rate from model month 20 to Age 2, $S_{17}^{\ 1/4}$. For fall-run, the period spans a 9-month period (described below), therefore the monthly survival rate (S_{TRANS}) is the 9th root of the fall-run survival rate from model month 20 to Age 2, $S_{17}^{\ 1/9}$.

Transition 18

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

$$Age2 = Age1_{m=20} * (1 - M_{2,S}) * S_{17}$$

Where S_{17} is a model parameter representing the survival rate of fish from model month 20 in the ocean to Age 2 and $M_{2,S}$ is a model parameter representing the sex-specific maturation rate that leads to 2-year old spawners. Maturation rate is sex-specific based on recent cohort reconstruction analyses of winter-run conducted by Chen et al (2023). The model transitions from a monthly time step (used for Transitions 1 through 17) to an annual time step (used for Age 2, Age 3 and Age 4 fish) in this transition. For winter-run, the S_{17} survival represents a 4-month survival rate, from model month 21 (November) through model month 24 (February). For fall-run, the S_{17} represents a 9-month survival rate, from model month 21 (November) through model month 29 (July), when the fall-run cohort has reached 2 years of age.

Transition 19

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

$Sp_{2,F} = Age1_{m=20} * S_{17} * M_{2,S} * Fem_{Age2} * S_{sp2}$
$Sp_{2,M} = Age1_{m=20} * S_{17} * M_{2,S} * (1 - Fem_{Age2}) * S_{sp2}$

where S_{17} and $M_{2,S}$ are model parameters for maturation and survival as described in Transition 18. 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.

$\text{logit}(S_{sp2}) = S0_{sp} + S1_{sp} * X3$

Where $S0_{sp}$ is the intercept and $S1_{sp}$ is the slope of the regression relating the covariate X3 to the background survival rate. The covariate X3 could be used to adjust background survival, such as incorporating annual differences in survival due to environmental conditions, such as water temperature (Bowerman et al 2021).

Transition 20

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

$Age3 = Age2 * (1 - I_3) * S_{19} * (1 - M_{3,S})$

where I_3 is the fishery impact rate for fish that will spawn at Age 3, S_{19} is a model parameter representing natural survival rate for fish between Age 2 and Age 3, and $M_{3,S}$ is a model parameter representing sex-specific maturation rate of Age 3 fish.

Transition 21

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

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

where I_3 is the fishery impact rate for fish that will spawn at Age 3, and $M_{3,S}$ and S_{19} are the Age 3 sex-specific maturation rate and survival rate as described in Transition 20. 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.

$\text{logit}(S_{sp3}) = S0_{sp} + S1_{sp} * \text{X3}$

Where $S0_{sp}$ is the intercept and $S1_{sp}$ is the slope of the regression relating the covariate X3 to the background survival rate. The covariate X3 could be used to adjust background survival, such as incorporating annual differences in survival due to environmental conditions, such as water temperature (Bowerman et al 2021).

Transition 22
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 fishery impact rate for fish that will spawn at Age 4, 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.

$\text{logit}(S_{sp4}) = S0_{sp} + S1_{sp} * \text{X3}$

Where $S0_{sp}$ is the intercept and $S1_{sp}$ is the slope of the regression relating the covariate X3 to the background survival rate. The covariate X3 could be used to adjust background survival, such as incorporating annual differences in survival due to environmental conditions, such as water temperature (Bowerman et al 2021).

Transition 23
Definition: Number of eggs produced by spawners of Ages 2 – 4 in months *m* which correspond to the first month through the last month of spawning. Winter-run spawn in months *m* = (2, …, 6) (April to August). Fall-run spawn in months *m* = (7, …, 10) (September to December).

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

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, and $K_{Sp,m}$ is the capacity of eggs in the spawning grounds per month. $P_{SP,m}$ is the proportion of spawning that occurs in month m and can be a function of water temperature. For winter-run, $P_{SP,m}$ is a function of April average water temperature at Keswick Dam as supported by a recent study that demonstrated a positive correlation between April water temperatures and spawn timing (Dusek Jennings & Hendrix 2020). This approach uses a proportional odds logistic model which includes an intercept and slope term for each month to account for the probability of winter-run spawning in that month as a function of April temperatures. Because the April temperature can vary among years, the winter-run monthly distribution varies as well to reflect observed patterns in spawn timing among years.

$TSp_{2,F} = Sp_{2,F} - hat.f_{AGE2} + Sp_{2,F,Hatchery}$

$TSp_{3,F} = Sp_{3,F} - hat.f_{AGE3} + Sp_{3,F,Hatchery}$

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

where $hat.f$ is the number of spawning females removed for use as hatchery broodstock, and $Sp_{j,F,Hatchery}$ for j = (2,3,4) is the spawners of age j of hatchery origin, which are estimated annually in the Sacramento River (e.g., Killam 2022).

IV. Inputs to the Sacramento River Chinook salmon life-cycle model

Covariates must be supplied for all transition equations described above. We briefly review the covariates that need to be supplied for the SRCLCM.

Water Temperature and Flow

The life cycle model incorporates monthly average temperature in the spawning reaches below Keswick Dam into the calculation 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 Sacramento River Water Quality Model (SRWQM). Measurements of river flow are also used in the SRCLCM. These inputs are described in Table 1.

Table 1. Description of temperature and flow covariates used in the SRCLCM.

Name	Description
$TEMP_m$	Weighted average temperatures of the month of spawning *m* and the following 2 months (*Transition 1: Survival of Egg to Fry*). Temperature data should be representative of spawning locations over the model escapement years.
$Q_{Verona\ m}$	Sacramento River flow (cfs) at Verona (USGS 11425500) (*Transition 3: Yolo Bypass Tidal Fry, and Transition: Rearing*)
$Q_{Yolo,m}$	River flow (cfs) in the Yolo Bypass (USGS 11453000) (*Transition 3: Yolo Bypass Tidal Fry, and Transition: Rearing*)
DCC_m	Proportion of the month that the DCC gate is open (USBR 2022) (*Transition 4 and 5: Delta and Bay Tidal Fry*)
$Q_{RioVista\ m}$	Sacramento River flow (cfs) at Rio Vista (Dayflow QRIO, CDWR 2022) (*Transition 5: Bay Tidal Fry*)
$Q_{Wilkins\ m}$	Sacramento River flow (m^3s^{-1}) at Wilkins Slough (USGS 11390500) (*Transition: Rearing*)
$q.bb_m$	Bend Bridge monthly flow anomaly (subtract mean and divide by standard deviation) (USGS 11377100) (*Transition 11 and 12: Gate*)

Fisheries

Estimates of impact rates on vulnerable age classes of Chinook salmon are also needed to run the SRCLCM. For fall-run, these estimates are computed as part of the Pacific Fisheries Management Council (PFMC) annual postseason estimated catch rates (O'Farrell et al. 2013, PFMC 2022). For winter-run Chinook, analyses of coded wire tag (CWT) groups are used to infer impact rates for age-3 and older (e.g., O'Farrell et al. 2012). To be consistent with the postseason estimates, we assume the impact rate for age 2 is zero.

Habitat Capacity

This section includes details on the habitat capacity models previously developed for the WRLCM (Hendrix et al. 2014) that can also be used for the SRCLCM. Similar summaries of the habitat capacity models described below have been documented elsewhere (Hendrix et al. 2014, Cordoleani et al. 2020), but are included again here for completeness. Note that these habitat capacity models can be updated as new information becomes available, or, alternative habitat capacity models can be used instead.

Juvenile salmonids rear in the mainstem Sacramento River, delta, Yolo Bypass, and bay habitats (Figure 1). The model incorporates the dynamics of rearing 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). Areas with vegetated cover along banks are preferred in other systems by Chinook salmon (Beamer et al. 2005, Semmens 2008), and areas associated with cover in the delta were assumed to be higher quality habitats because they provide protection from predators (Semmens 2008) and offer subsidies of terrestrial insect prey. In the bay, salinity is a factor that predicts suitable habitat. Salinity is a predictor of juvenile Chinook abundance (Toft et al. 2018), and fish monitoring data in both Skagit River and San Francisco Bay have shown high likelihood of fry presence in water with salinity less than 10 ppt (Correigh Greene, personal communication). 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. Note, the current version of the model uses densities from the Skagit River, Washington (Figure 7) and does not include habitat in tributaries, however this information can be updated as information becomes available.

Defining habitat capacity. For each habitat type (mainstem (Upper River, Lower River and Yolo Bypass), 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. Table 2 describes the variables that 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. The exception was mainstem habitats (Upper River, Lower River, and Yolo Bypass), which were subdivided into 4 (2 x 2) bins 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.

Table 2. Habitat variables influencing capacity for each habitat type.

Habitat type	Variable	Habitat quality	Variable range
Mainstem & Yolo Bypass	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

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 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 7).

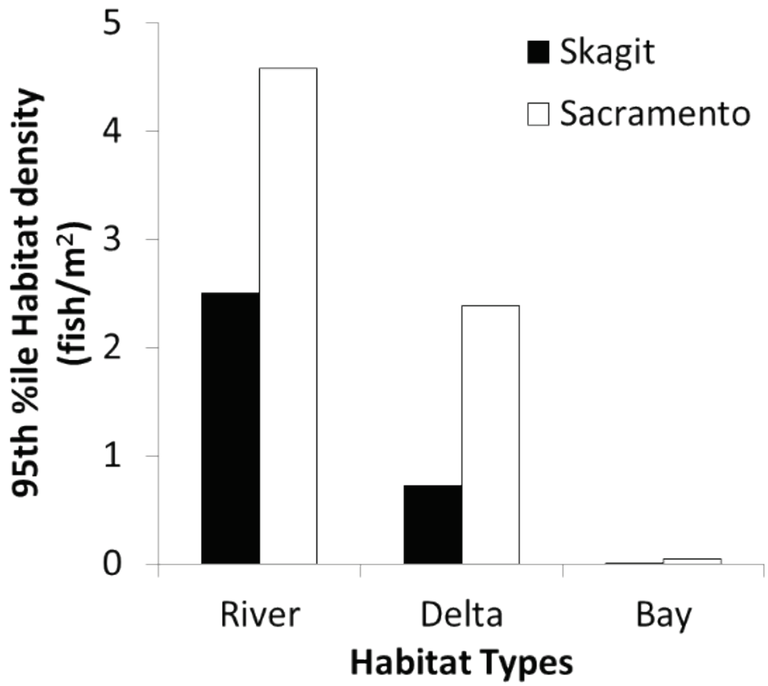

Figure 7. 95th percentile values of densities in river, delta, and bay habitats in the Skagit and Sacramento Rivers. Skagit data are based on electroshocking in mainstems and beach seining in delta and bay habitats (Beamer et al. 2005), while Sacramento data are based on beach seining across all habitat types (USFWS 2007).

Determining habitat areas. Two approaches were used to map the spatial extents of different combinations of habitat variables. To estimate river and Yolo Bypass capacities based on channel velocity and depth, a suite of HEC-RAS models at varying discharge values (2,000-200,000 ft^3/sec) were simulated on the Sacramento River and Yolo Bypass. The HEC-RAS geometry was based on a series of cross-sections that define locations surveyed in the mid-1990s at longitudinal intervals of approximately 500m. From the HEC-RAS output, the cross-sectional width of a given river reach was broken up into 45 lateral sections (i.e., cells), with the main channel composed of 25 cells and the banks composed of 20 cells (10 left and 10 right bank; example shown in Figure 8). Main channel and bank stations are defined in the original HEC-RAS model and denoted in Figure 8 with red cross-section stations. To estimate depth and velocity in each cell, we used the flow distribution methods outlined by HEC, which can be found at https://www.hec.usace.army.mil/confluence/rasdocs/ras1dtechref/latest/overview-of-optional-capabilities/flow-distribution-calculations.

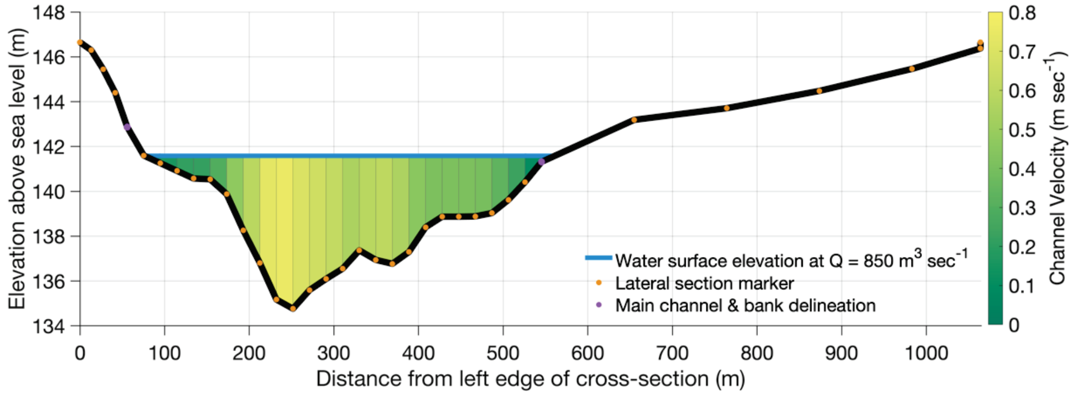

Figure 8. Example of method used to split up a HEC-RAS cross-sectional output into 45 lateral sections. Note that main channel locations are within the purple cross-sections stations and bank locations are outside of the purple cross-sections stations.

At each lateral cell for the mainstem habitat, the HEC-RAS simulated channel depth and velocity were grouped into one of the four habitat quality categories described in Table 2. Each cell in the cross-section has a depth and velocity, and altering the flow changes the depth and velocity of a particular cell. The area of each cell that corresponded to a specific combination of velocity and depth category was tabulated for each mean monthly flow associated with a cross-section. The appropriate density of Chinook salmon for each of the four categories was applied to each lateral cell by taking the product of area for a given preference and the 95th percentile density estimate for that preference. To arrive at a monthly capacity estimate for the Sacramento River and Yolo Bypass habitats, we summed the capacity estimates for each lateral and longitudinal cell in each habitat. Figure 9 shows how habitat capacity changes as a function of flow for the Sacramento River and Yolo Bypass.

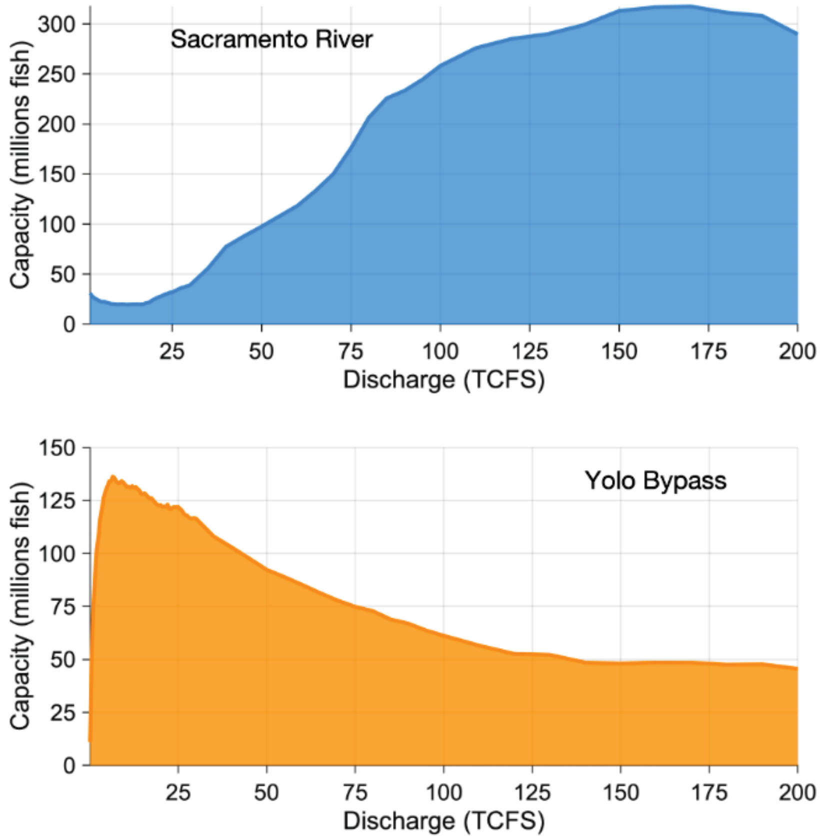

Figure 9. Habitat capacity to flow (thousand cfs) relationship for the Sacramento River and Yolo Bypass under the 95th percentile density estimate.

For the delta and bay, geographic data products were used to map habitat variables, including cover, shoreline type, salinity, and depth. Vector GIS files were converted to raster, and all habitat variables were mapped onto a common $10m^2$ grid. To obtain the spatial extent of channels and wetlands, National Wetland Inventory (NWI) data (USFWS 2006) were used in the delta, and Bay Area Aquatic Resource Inventory (BAARI) v 2.1 data (SFEI ASC 2017) were used in the bay. A geographic buffer was applied where required to ensure that the full extent of the channels were included, and a levee file (DWR 2018) was utilized to ensure that no inaccessible areas were included. For each cell, the habitat variables listed in Table 2 above were determined to be of high or low quality. Cover data were obtained from the Coastal Change Analysis Program (C-CAP) (NOAA OCM 2017). Areas that had vegetation (forested areas, scrub/shrub area, etc.) were considered high quality cover, and cells within 30 meters were marked as high-quality cover. Shoreline data were obtained from BAARI v 2.1 (SFEI ASC 2017) and the Environmental Sensitivity Index (NOAA OR&R 2017). Cells within marshes, tidal flats, and vegetated areas, and cells within 30 meters were marked as high quality, whereas areas near rip-rap, rocky areas, and exposed areas were marked as low quality.

For salinity, monthly X2 values, representing the distance from the Golden Gate Bridge to the 2 ppt isohaline position (Jassby et al. 1995), were obtained from CalSim simulations. X10 values were calculated as 75% of X2 values (Monismith et al. 2002, Jassby et al. 1995). Distance to the Golden Gate was mapped, and cells upstream of the X10 value were marked as high quality.

Water depth was calculated from bathymetric data (Wang et al. 2018) and water level from DSM2 simulations. Each cell was assigned to its corresponding DSM2 channel, and for each DSM2 channel, monthly median water level was calculated. This value was subtracted from the bathymetric measurement in order to obtain monthly water depth for each cell.

Blind tidal channels within wetland areas were not able to be mapped directly with the available data. Therefore, we estimated these areas using allometric relationships between tidal 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:

$$A_{btc} = 0.0024 * {A_w}^{1.56}$$

where A_{btc} is blind tidal channel area in hectares and A_w is wetland area in hectares. We also applied the minimum area requirement (0.94 ha) to form blind tidal channels in a wetland from Hood (2007). To ensure that habitat area was not double counted in wetland areas through the previously described mapping methods and the blind tidal channel calculation, the habitat area of each cell in tidal wetlands was reduced by the proportion of the area of the wetland that is blind tidal channel. Finally, the habitat areas from all cells, along with the habitat area from blind tidal channels, was summed in order to get the total monthly habitat areas for each of the eight habitat quality categories.

Delta smolt survival models

Several different smolt survival models can be used within the SRCLCM to estimate the survival of smolts as they outmigrate through the delta (Transitions 11 – 15). While each model functions as a stand-alone model and operates on its own temporal and spatial resolution, they can also be scaled up to the delta-wide monthly timestep required to serve as inputs into the SRCLCM to estimate outmigration survival through the delta. Each model has its own assumptions and was developed for its own unique combination of observational data, run of Chinook salmon, and environmental conditions. For example, Newman (2003) used a statistical model to estimate delta smolt survival by comparing recapture rates of juvenile hatchery coded-wire-tagged fall-run Chinook salmon released at locations upstream and downstream of the delta between 1979 and 1995. Other survival models used statistical approaches to estimate delta smolt survival using the detection history of acoustically-tagged hatchery smolts during their outmigration through the delta, for late-fall run from 2006 to 2011 (Perry et al. 2018) and for winter-run from 2014 through 2018 (Hance et al. 2022). Using another approach, Sridharan et al. (2023) developed a mechanistic model (the ePTM) that uses fish behavior and finescale hydrodynamic data to simulate smolt survival through the delta. While the ePTM is based on the same acoustically-tagged hatchery late-fall run Chinook salmon data from Perry et al. (2018), its mechanistic approach makes it applicable to other runs of Chinook salmon and across novel hydrodynamic conditions. However, the ePTM relies on finescale hydrodynamic data (i.e., DSM2 HYDRO) which can be more challenging to obtain. Below we summarize the various delta smolt survival models that can serve as inputs into the SRCLCM and the various underlying data necessary for each model (Table 3).

Table 3. Description of the required inputs for various smolt survival models that can be used in the SRCLCM. Covariates and their descriptions were adapted from Newman (2003), Perry et al. (2018), Hance et al. (2022), and Sridharan et al. (2023).

Model/Covariate	Description
Fall-run Coded Wire Tag paired release-recoveries (Newman 2003)	
Size	Average length (mm)
Log flow	Log transformed median river flow during the outmigration period (cfs)
Salinity	Water salinity as measured by resistance (μmho/cm)
Release temperature	River water temperature at time and location of release (°F)
Hatchery temperature	Water temperature in hatchery on day of release (°F)
Tide	A measure of the magnitude of the change in low–low and high–low tides and whether the delta was filling or draining
Exports	Median volume of water diverted during the outmigration period (cfs)
DCC Gate	Indicator for position of the delta cross-channel gate (1 if open, 0 if closed)
Turbidity	Turbidity of water (formazine turbidity units)
Late-fall run acoustic tag survival, travel time, and routing study ("STARS", Perry et al. 2018)	
Flow	River discharge at Freeport (cms)
DCC Gate	Indicator for position of the delta cross channel gate (1 if open, 0 if closed)

Model/Covariate	Description
Size	Fork length of individual (mm)
Winter-run acoustic tag survival, travel time, and routing study ("WR STARS", Hance et al. 2022)	
Freeport Flow	Flow at Freeport (cms, USGS Gage 11447650)
Fremont Weir Stage	Fremont Weir Stage Height (ft)
Yolo Bypass Flow	Flow at Yolo Bypass (cms, USGS 11453000)
Rio Vista Flow	Flow at Rio Vista (cms, USGS 11455420)
Freeport Max Temperature	Maximum daily water temperature at Freeport (°C, USGS Gage 11447650)
Yolo Bypass Max Temperature	Maximum daily water temperature at Yolo Bypass (°C, USGS 11453000)
Export/Inflow	Daily ratio of Delta exports to Delta inflow from Dayflow (CDWR 2022)
enhanced particle tracking model (ePTM, Sridharan et al., 2023)	
Delta Flow and Stage	Flow (cfs) and stage data (ft) at each node in the Delta on a 15 minute timestep from DSM2 HYDRO[1]

[1]DSM2 represents the Delta as a grid (network) of channels with specified geometries (ft) that connect at nodes (Anderson and Mierzwa 2002).

Biological data

Biological data are used to initiate the model, to account for removals for the hatchery program, and to calculate annual sex ratios. For example, total escapement in five years (e.g., 1970 – 1974) is necessary to provide estimates of abundance for the full age structure of returns for two cohorts. The necessary inputs are described in Table 4.

Table 4. Description of biological data used in the SRCLCM.

Biological Data	Description
Spawner abundance estimates	Estimate of spawner abundance (e.g., GrandTab (CDFW 2022)), combined with other data sources to determine sex and age class

Biological Data	Description
Hatchery removals	Annual numbers of male and female spawners by age retained for hatchery broodstock (e.g., Killam 2022)
Annual sex ratios	Annual spawner sex ratio for each age class calculated from adult surveys (e.g., Killam 2022)
Proportion hatchery origin	Proportion of spawners that are hatchery origin (e.g., Killam 2022)
Juvenile abundance estimates	Abundance estimates of juveniles at one or more locations (e.g., Voss and Poytress 2020)

Additional covariates

The following additional covariates can be supplied to run the SRCLCM. If they are not available, they can be "turned off" in the model by setting the values to 0.

$X1_m$ is the egg to fry survival anomaly that describes variation in the annual background survival relative to the mean – standardized to have a mean of 0 and standard deviation of 1 (*Transition 1: Survival from Egg to Fry*).

$X_{h,m}$ is the covariate describing the survival of resident and migrant fry that can vary for each habitat and month - standardized to have a mean of 0 and a standard deviation of 1 (*Transition: Rearing*).

X3 is the covariate describing prespawn mortality - standardized to have a mean of 0 and a standard deviation of 1 (*Transitions 19, 21, 22: Maturation and Migration*).

$OI_{,m}$ is the ocean index - standardized to have a mean of 0 and a standard deviation of 1 (*Transition 16: Gulf*).

V. Conclusion and Next Steps

This document describes the framework for the SRCLCM, a stage-structured, stochastic life cycle model developed for winter-run and fall-run Chinook salmon spawning in the Sacramento River within California's Central Valley. While the overarching goal of the SRCLCM is to simulate the effect of proposed changes to water operations, habitat restoration, and hydroclimate variability on Chinook salmon population dynamics, we first must establish the relationship between empirical observations of the environment with the population response of Chinook salmon. Following are the steps required before applying the model framework described in this document:

1. Review literature and available datasets to identify prior distributions for parameter values.
2. Fit the SRCLCM to historical observations to estimate model parameters.
3. Develop a Decision-Support Tool (DST) version of the SRCLCM that can use water management planning models (e.g., CALSIM) and hydraulic models (e.g., DSM2) to quantify the effect of proposed changes in water operations and habitat restoration on Chinook salmon population dynamics under a range of hydroclimate conditions.

The SRCLCM described in this document is a modeling framework that describes the linkages between abiotic variables, which are under management control, and population vital rates (e.g., survival, movement, and reproduction). To produce a model specific to a population (e.g., winter-run) the model must be calibrated to data from that population. For example, the winter-run Chinook salmon lifecycle model (WRLCM, Hendrix et al. 2014) was specifically developed by the National Marine Fisheries Service to evaluate the effects of proposed water operations and habitat restoration on the population dynamics of federally endangered winter-run Chinook salmon in the Sacramento River. For that effort, we used a model-fitting approach to calibrate the WRLCM to observed historical biological indices (e.g., spawner abundance, juvenile abundance, etc), using observed environmental data (e.g., flow, water temperature) as covariates. This calibrated version of the model is a necessary step to establish the relationships between empirical observations of hydrology, temperature, habitat, and the population response of Chinook salmon. Calibration of life cycle models is beyond the scope of this document; however, a good reference for the steps involved in calibrating life cycle models to observed data is Newman et al. (2014).

Once a calibrated model is completed, a Decision-Support Tool (DST) can be developed where the Chinook salmon population response to proposed changes to water operations or habitat restoration can be simulated. Instead of using observed environmental data, the DST version of the model can use inputs from water planning models (e.g., CALSIM II, CALSIM3), physical models (e.g., HEC-RAS, DSM2) and water temperature models (e.g., USBR river temperature model) to represent conditions during proposed water operations or habitat restoration. For example, DST versions of the WRLCM were used to successfully evaluate the effect of alternative water management actions and large-scale modifications to the Sacramento River system in the Biological Opinion for the California WaterFix Project in Central Valley, California (Hendrix et al. 2017) and to evaluate the effect of alternative management actions without physical modifications in the Biological Opinion on Long-term Operation of the Central Valley Project and the State Water Project (Hendrix et al. 2019). Through these implementations of the model, the WRLCM was used to predict how proposed actions affect long-term population metrics including cohort replacement rate, escapement, and smolt production. Future developments of the SRCLCM including model calibration and the development of DSTs will be documented in future publications.

The shared modeling framework of the SRCLCM can provide valuable insight on how winter-run and fall-run respond to a given suite of management actions and will allow managers to evaluate trade-offs. The shared timestep, geographic area, and lifestages between each run will also set the stage for future efforts to incorporate interactions between each run into the long-term population dynamics, which will result in a more holistic understanding of the effects of management actions on Chinook salmon in the Sacramento River. Although this version of the SRCLCM is focused on the populations of winter-run and fall-run that spawn in the mainstem Sacramento River, future model versions may be expanded to incorporate tributaries. Furthermore, this model framework could be modified for use for other populations of salmonids in other systems.

VI. References

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Appendix A. Description of parameter values

Table A1. Parameter value names and brief description.

Name	Transition	Description
t.crit	1	Critical temperature (ºC) at which egg to fry survival is reduced
B0a	1	Survival below critical temperature value
B1a	1	Role of factor affecting survival below critical temperature
$B1_1$	1	Rate of reduction in egg to fry survival
$P_{TF, m}$	2	Proportion tidal fry
$S_{TF,YB}$	3	Survival tidal fry in Yolo Bypass
B_{YB}	3	Proportion entering Yolo bypass as a function of the ratio of Yolo to Verona flow
$B1_{YB}$	3	Proportion entering Yolo bypass if Verona flow is > 991.1 m^3s^{-1}
$B0_4$	4	Average survival of tidal fry to delta intercept
$B1_4$	4	Effect of DCC gate on tidal fry survival
$B0_5$	5	Average proportion of tidal fry to bay intercept
$B1_5$	5	Proportion tidal fry to bay due to flow anomaly at Rio Vista effect
$S_{TF,DE\text{-}BA}$	5	Survival of tidal fry from delta to bay
$B0_F$	Rearing	Average survival of fry across all habitats
$B1_{F,H}$	Rearing	Survival anomaly in habitat *H* (H = upper river, lower river, delta, Yolo Bypass) relative to average survival
mig_{LH}	Rearing	Proportion of fry in upper river migrating to lower river per month
$B0_M$	Rearing	Wilkins slough movement without trigger
$B1_M$	Rearing	Wilkins slough change in movement with flow trigger of 400 m^3s^{-1}
mig	Rearing	Probability of migration from habitats

Name	Transition	Description
$S_{FRY,BA}$	Rearing	Survival of bay rearing fry pushed to gulf
Z_1	6 to 10	First month smolt probability
Z_2	6 to 10	Second month smolt probability
Z_3	6 to 10	Third month smolt probability
Z_4	6 to 10	Fourth month smolt probability
Z_5	6 to 10	Fifth month smolt probability
Z_6	6 to 10	Sixth month smolt probability
Z_7	6 to 10	Seventh month smolt probability
$B1_{SMOLT}$	6 to 10	Effect of temperature anomaly by month and habitat on smolt probability
$B0_{11,LR}$	12	Smolt survival lower river to delta
$B0_{10,UR}$	11	Survival of upper river fish to lower river
$B1_{10}$	11,12	River smolt survival from flow effect
${}^{B}S_{12,LR,m}$	11, 12	mean monthly survival rate for smolts originating from the Sacramento River through the Delta to Chipps Island as calculated by the Smolt Survival Model (${}^{B}S_{12.LR,m} = SSM_{LR,m}$)
${}^{B}S_{13.YB,m}$	13	mean monthly survival rate for smolts originating from the Yolo Bypass through the Delta to Chipps Island as calculated by the Smolt Survival Model (${}^{B}S_{13.YB,m} = SSM_{YB,m,}$)
${}^{A}S_{14,DE,m}$	14	mean monthly survival rate for smolts originating from the Delta to Chipps Island as calculated by the Smolt Survival Model (${}^{A}S_{14,DE,m} = SSM_{DE,m}$)
${}^{C}S_{11}$	11 - 15	Survival smolt Chipps to Golden Gate
${}^{A}S_{13,YB,m}$	13	Survival from Yolo until Delta
$S_{15,BA}$	15	Survival of smolts Bay to Golden Gate
$B0_{GULF}$	16	Survival in entry to Gulf

Name	Transition	Description
$B1_{GULF}$	16	Effect of ocean productivity on Gulf entry survival
S_{17}	18, 19	Probability of survival from model month 20 to age 2 (a 4 month period for winter-run and a 9-month period for fall-run)
$M_{2,S}$	18,19	Probability of maturation age 2, sex-specific
$S0_{sp}$	19, 21, 22	Survival ocean exit to spawning ground
$S1_{sp}$	19, 21, 22	Role of factor affecting survival ocean exit to spawning ground
S_{19}	20	Probability of survival age 2 to age 3
$M_{3,S}$	20, 21	Conditional probability of maturation at age 3, sex-specific
S_{21}	22	Survival age 3 to age 4
$V_{eggs,2}$	23	Eggs per spawner age 2
$V_{eggs,3}$	23	Eggs per spawner age 3
$V_{eggs,4}$	23	Eggs per spawner age 4
$B0_{SP1}$	23	Intercept for proportion of spawners in first month of spawning, e.g. for winter-run SP1 = April, for fall-run SP1 = September
$B1_{SP1}$	23	Effect of temperature on proportion of spawners in the first month of spawning
$B0_{SP2}$	23	Intercept for proportion of spawners in the second month of spawning
$B1_{SP2}$	23	Effect of temperature on proportion of spawners in the second month of spawning
$B0_{SP3}$	23	Intercept for proportion of spawners in the third month of spawning
$B1_{SP3}$	23	Effect of temperature on proportion of spawners in the third month of spawning
$B0_{SP4}$	23	Intercept for proportion of spawners in the fourth month of spawning
$B1_{SP4}$	23	Effect of temperature on proportion of spawners in the fourth month of spawning

Name	Transition	Description
Fem_{Age2}	19	Proportion of age 2 spawners that are female
Fem_{Age3}	21,22	Proportion of age 3 and 4 that are female
$K_{Sp,m}$	23	Capacity in the spawning reaches by month