

# Modeling the effect of habitat availability and quality on endangered winter-run Chinook salmon (*Oncorhynchus tshawytscha*) production in the Sacramento Valley

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## ABSTRACT

Reconciliation between water uses and sustaining aquatic species populations requires an effort to identify and quantify essential habitat characteristics for ecosystem health and valuation methods to predict ecosystem response to restoration actions. This process is particularly challenging for anadromous fish species such as California's Sacramento River winter-run Chinook salmon, due to their limited geographic range and diverse life history habitat requirements. Tools, such as life-cycle models, are needed to manage population dynamics and quantify the composite effects of processes across space and time. Nevertheless, complex institutions can hinder result interpretation and communication, and limit model use in decision-making. This paper focuses on the federally endangered and endemic Sacramento River winter-run Chinook (*Oncorhynchus tshawytscha*) by developing a Winter-Run Habitat-based Population Model (WRHAP). WRHAP is a conceptual, freshwater rearing stage model that includes alternative rearing habitats reported in the literature (e.g., floodplains, off-channel and tributaries), defines rules of habitat use based on instream conditions, and incorporates a juvenile growth module that combines bioenergetics modeling with empirical growth rates. Model outputs reasonably follow observed out-migration patterns and provide a realistic smolt size distribution arriving at the San Francisco Bay. This effort demonstrates the importance of currently "non-critical" habitats (as defined by the Endangered Species Act) for juvenile development, with floodplain habitat contributing to a quarter of out-migrating biomass (despite < 18% availability and < 10% of total rearing days), and off-channel growth being one of the most sensitive parameters (explaining ~13% of average juvenile weight variance). The model shows the utility of a simple population model to explore relationships between habitat quality/quantity and juvenile development, and to assist water/environmental management and decision-making processes focused on species recovery.

## 1. Introduction

Over the past century, humans developed an extensive water management system in California's Sacramento River basin. This system is managed for multiple and sometimes competing objectives, including irrigated agriculture, flood control, hydropower, water supply, and ecosystems. In the past, priority was given to human water uses, producing sharp declines in anadromous fishes and other native species. This, in turn, led to increased political, legal and resource management efforts to enhance aquatic ecosystems and native fishes. However, despite substantial investments (Yoshiyama et al., 1998), these efforts have been insufficient to sustain Sacramento River winter-run Chinook

salmon (Evolutionary Significant Unit, ESU; Waples 1991). This endemic population has declined dramatically from the 1970s to the present, with fewer than 975 adults returning in 2017 (84.5% from hatchery origin; USFWS, 2019).

Four runs of Chinook salmon, named after the season adults return to spawn, occur in the California Central Valley (CVV) basin, each with unique life histories. Sacramento River winter-run Chinook adults migrate during winter and spawn during late spring and early summer (Moyle 2002) below Keswick Dam on the Sacramento River after reaching maturity typically after two years in the ocean. Juveniles rear in freshwater habitats for 5–10 months before out-migrating to the ocean. They exhibit a diverse rearing history with habitats that include

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the Sacramento River mainstem, Sutter and Yolo bypasses (Jones and Stokes Associates 1993; Sommer et al., 2001), and other off-channel habitats. Recently, winter-run Chinook have also been found to rear in non-natal tributaries such as the Lassen tributaries (i.e., Deer, Mill and Battle Creeks) and the Feather and American Rivers (Phillis et al., 2018). Winter-run declines are strongly driven by the closure of Shasta and Keswick Dams and near elimination of lateral habitat connectivity in the lower watershed from leveeing floodplain habitat and water diversions. Thus, winter-run Chinook have been cut-off from 100% of their historical spawning habitat along the McCloud and Pit Rivers (cold, volcanic spring-fed rivers), and currently only spawn in non-natal habitats (Sacramento River below Keswick Dam) (Yoshiyama et al., 1998; Lusardi and Moyle 2017). The ESU is vulnerable to extinction principally because it is restricted to a single spawning area between Red Bluff and Keswick Dam between late-April and August (NMFS, 2014). As such, the ESU relies on cold water releases from Keswick dam, since winter-run embryos are the most sensitive life stage to higher temperatures and require temperatures less than 12°C in the field, several degrees lower than those reported by laboratory studies, ~15.4°C (USFWS, 1999; Martin et al., 2017). Although temperature-related regulations to govern dam operations were established to protect endangered winter-run salmon eggs during incubation (NMFS, 2009), such regulations have been insufficient for critically high temperatures during extended droughts (Williams et al., 2016; Adams 2018), likely to become more common as the climate warms (Martin et al., 2017).

Despite a long history of awareness of the decline of winter-run Chinook and the mechanisms of decline, few studies combine human water and land uses with explicit ecological objectives (Horne et al., 2016). Reconciling water uses and sustainable ecological goals requires identifying habitat characteristics essential for ecosystem health and developing effective methods to predict ecosystem response to water control decisions (Jager and Smith 2008). This is particularly challenging for migratory and multi-life-stage species exhibiting broader geographic ranges and complex habitat shifts from evolved life histories, affecting survivorship over time and space (Phillis et al., 2018).

Freshwater habitat designated under ESA as critically important for long-term persistence of winter-run is limited to the out-migration corridor (i.e., mainstem Sacramento River below Keswick Dam to the Golden Gate Bridge), and excludes tributaries and seasonally inundated floodplain habitats. However, recent research shows non-natal tributaries are important for winter-run Chinook rearing and development, with 44–65% of returning adults having used these areas for at least three weeks during their juvenile life stage (Phillis et al., 2018). Such habitats likely provide diverse rearing conditions and possibly support growth and survival during out-migration (Maslin et al., 1996; Limm and Marchetti 2009). Similarly, seasonal floodplains, such as the Yolo and Sutter bypasses, provide critical rearing habitat where the growth of juvenile salmonids has outperformed congeners reared in the mainstem Sacramento River during the same period (Sommer et al., 2001, 2020; Jeffres et al., 2008, 2020; Katz et al., 2017). Sacramento River winter-run Chinook salmon appear to rely on a more diverse set of rearing habitats than previously acknowledged, suggesting expanded conservation opportunities for species recovery (Phillis et al., 2018).

Population dynamic models show linkages between salmon survival and ecosystem variables such as temperature and flow, and are often related to infrastructure control decisions in regulated systems. They are insightful mathematical tools for evaluating the complex effects of water project operations and restoration on salmon population dynamics (e.g., Jager and Rose 2003). Such models offer a flexible conceptual structure and are defined and parametrized by expert knowledge, empirical and laboratory studies, and tested against ecological field observations (Dilão 2006). However, complex institutions and methods often hinder result interpretability and communication, hindering decision-making based on their output (Horne et al., 2016). Most existing models do not represent the diverse rearing habitats within large river systems, such as the Sacramento Valley. Recent modeling efforts (e.g., Beer et al.,

2017, Hendrix et al., 2017) also lack representation of juvenile growth in available rearing habitat, despite its relationship to expected survival during out-migration and in the marine environment (Claiborne et al., 2011; Iglesias et al., 2017). Here we present a conceptual population dynamic model integrating existing knowledge of early life stages of winter-run Chinook salmon (e.g., growth, survival rates, egg critical water temperature) from empirical data and previous modeling efforts. The intent is to more systematically examine how off-mainstem habitats may be better represented and managed for salmon conservation. As such, a simple conceptual structure and output interpretability was stipulated as a main goal for this modeling effort to improve communication of results to decision-makers and for scientific synthesis. This model, the Winter-run Habitat-based Population Model (WRHAP), (i) includes in its structure four alternative available habitats: floodplain, tributaries, off-channel and mainstem, expanding the geographic extent represented in previous efforts; and (ii) formulates the value of each available habitat for the number and size of out-migrating salmon populations.

## 2. Methods

### 2.1. Model description and structure

WRHAP is a simplified model to estimate the number and biomass of juveniles out-migrating from California's Sacramento Valley to the Sacramento-San Joaquin Delta (hereafter denoted as Delta) in a given year, as a function of estimated winter-run spawners and physical habitat variables along the Sacramento River (Fig. 1). The model structure consists of four modules arranged sequentially (Fig. 2), each representing a coarse discretization in space and time to account for the different life stages and to follow the rearing movements of juveniles through the system as described in the literature (Grover et al., 2004; del Rosario et al. 2013; see Table 1). Experienced growth and survival are applied on a daily time step within each module. The Delta stage is greatly simplified, and ocean stages are excluded from the model structure to focus on year-to-year variability in freshwater habitat quantity and quality. As such, WRHAP is not a full life-cycle model. This avoids exogenous sources of uncertainty that could hinder the interpretability of results.

### 2.2. Winter-run juvenile habitat selection and out-migration

#### 2.2.1. Spawning area

This first module estimates the number of juveniles leaving spawning grounds below Keswick Dam to rear and move downstream along the Sacramento River system. During each year, the number of spawners ( $N_{spawn}$ ) was obtained from the GrandTab database (Azat 2019), which already accounts for adult pre-spawn mortality. We considered the annual proportion of females ( $r_{fem}$ ) and fecundity ( $f$ ) reported by Poytress (2016) and Voss and Poytress (2020), derived from carcass surveys and annual average of egg counts of winter-run brood stock spawned at the Livingston Stone National Fish Hatchery, respectively. Egg-to-fry survival was computed as a combination of natural ( $\beta_{Fry,N}$ ) (without habitat effects), density-dependent and temperature-induced mortality rates over the incubation period. Density-dependent effects are expected due to the greater concentration of spawners on the uppermost river segment since the completion of the reengineered Anderson-Cottonwood Irrigation District (ACID) fish ladders in 2001 (Poytress et al., 2014). We evaluated the impact on egg-to-fry survival including the Beverton-Holt density-dependent term fitted by Martin et al. (2017). Temperature-induced mortality was simulated using the phenomenological model for winter-run Chinook salmon embryos developed by Martin et al. (2017). This model determines the instantaneous mortality rate ( $h_d; d^{-1}$ ) that an embryo experiences during the  $d$ th day of its development with temperature  $T_{KW,d}$  (downstream Keswick Dam). The model is parametrized with  $T_{crit}$ , the temperature below

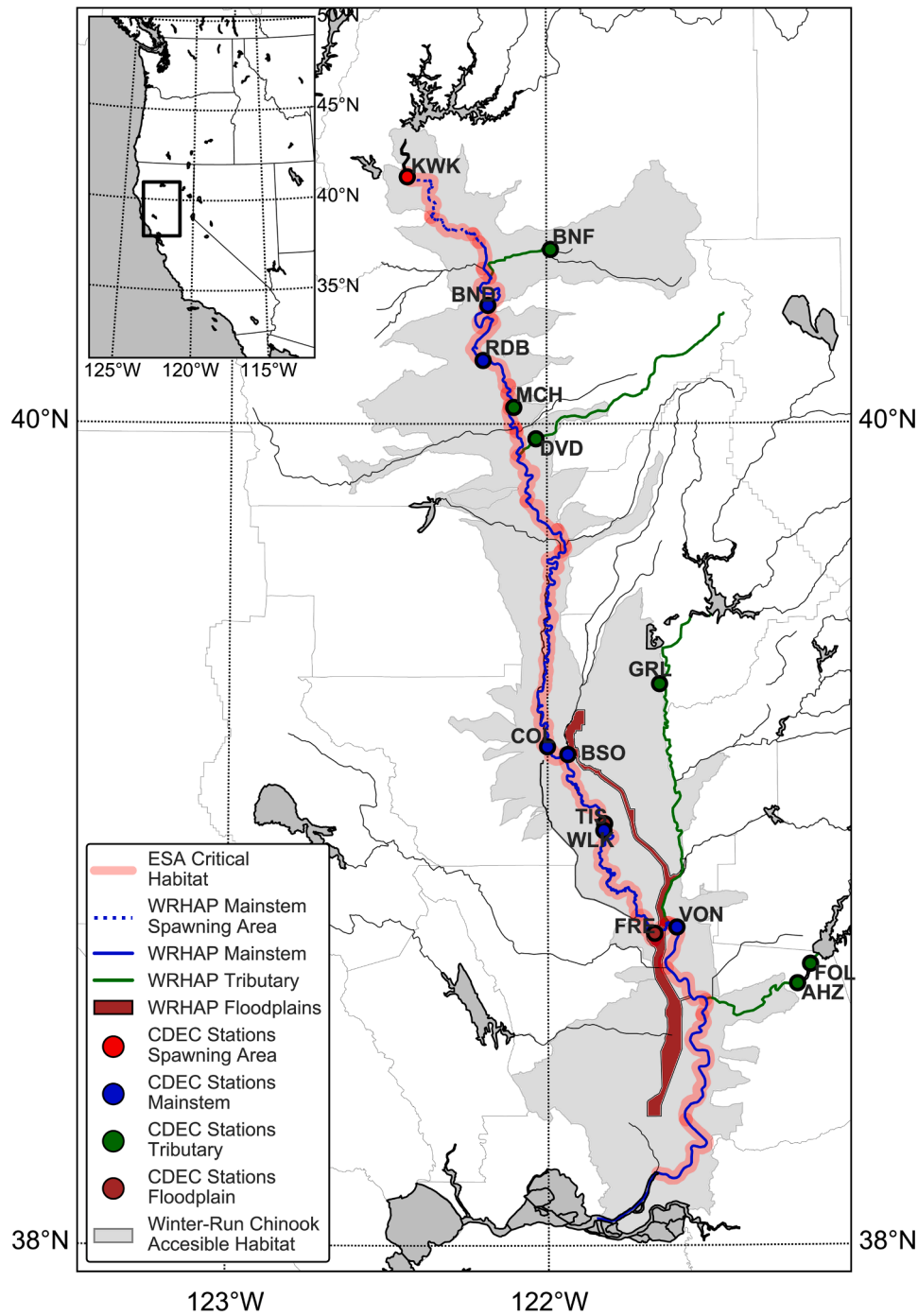


Fig. 1. WRHAP spatial coverage of winter-run Chinook salmon habitat, from spawning grounds below Keswick Dam to the out-migration to the Delta.

which there is no temperature-related mortality and  $b_T$ , the slope at which mortality rate increases with temperature.

$$h_d = b_T \max(T_{KWK,d} - T_{crit}, 0) \tag{1}$$

The length of this development period ( $n$ , days) was modeled using a temperature-dependent maturation function (Zeug et al., 2012). Then, the temperature-dependent survival for each year ( $\beta_T$ ) is computed as the average survival for all redds within every brood year (BY).

$$\beta_T = \frac{1}{N_{redds}} \sum \left[ \prod_{d=1}^n e^{-h_d} \right] \tag{2}$$

The spawning dates and number of redds ( $N_{redds}$ ) were estimated

from aerial redd surveys (CDFW, 2020). Winter-run juvenile production ( $P_{J,0}$ ) is estimated using the following equation:

$$P_{J,0} = \frac{\beta_{Fry,N}}{1 + N_{spawn} r_{jem} / K} N_{spawn} r_{jem} f \beta_T \tag{3}$$

where  $K$  is the capacity parameter of the Beverton-Holt term. Parameter values, description and sources are summarized in Table 2.

### 2.2.2. Upper sacramento river rearing

This module represents the dispersal of juveniles from natal reaches to rearing habitats within the Upper Sacramento River. Phillis et al. (2018), using otolith analysis, found that several Mount Lassen

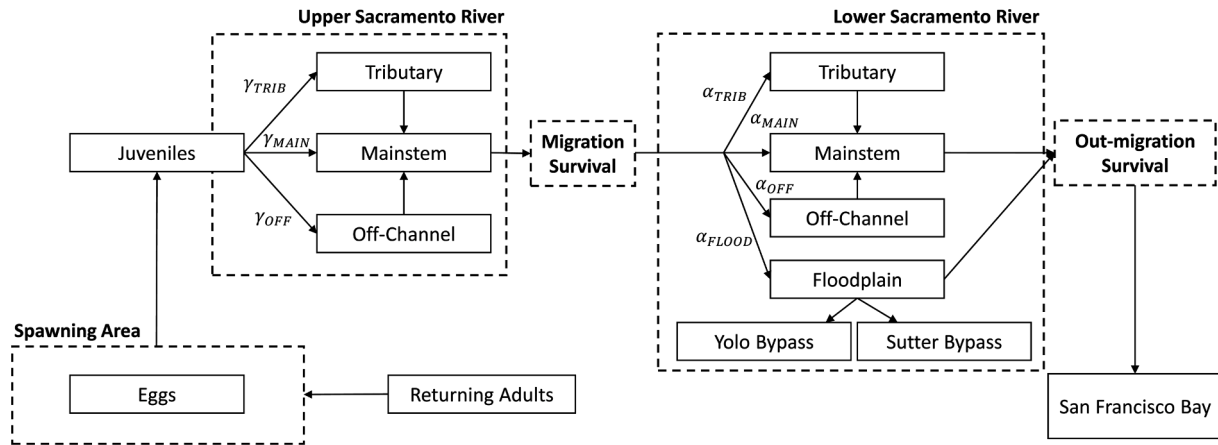


Fig. 2. WRHAP links between the different spatial discretization areas and considered rearing habitats in them. Dashed lines represents each of the model modules (Table 1).

Table 1

WRHAP modules description and data requirements. CDEC stations used in the analysis are represented in Fig. 1. A detailed structure of the module elements and links between them is shown in Fig. 2.

Modules	Spatial Extent	Time Period	Description	Data Requirements
Spawning Area	Keswick Dam to Red Bluff	Mid-April to mid-September	Models the number of produced eggs and the impact of temperature on egg-to-fry survival	Escapement (GrandTab; Azat, 2019), Keswick Dam release temp. (CDEC)
Upper Sac. River	Keswick Dam to Colusa	September to December-February	Estimates juvenile growth and survival based on rearing habitat availability at the mainstem, tributaries and off-channel areas (function of instream flow conditions)	Flow and temperature at each of the rearing habitats (CDEC)
Migration to Lower Sac. River	Through Knights Landing	December-February	Estimates migration survival of juveniles to Lower Sacramento River during a high flow event (> 400 m <sup>3</sup> /s at Wilkins Slough; del Rosario et al. 2013)	Flow at Wilkins Slough (CDEC)
Lower Sac. River	Colusa to Chipps Island	December-February to February/April	Estimates juvenile growth and survival in the lower reaches based on rearing habitat availability at the mainstem, tributaries, off-channel areas and floodplains (function of instream flow conditions)	Flow and temperature at each of the rearing habitats (CDEC)

tributaries (e.g., Battle, Mill and Deer Creeks) are primary non-natal rearing habitats (Phillis et al., 2018). Suitable habitat availability ( $A_{TRIB}$ , m<sup>2</sup>) was estimated for Mill (MC) and Deer Creek (DC) from Weighted Usable Area (WUA) relationships (Bartholow 2004) derived from stage-discharge curves and average cross-sections (Kondolf et al. 2001; CDFW 2017a, 2017b) to define the percentage of preferred rearing areas (i.e., depths between 0.5–2 m) (NMFS, 2014). A constant available habitat area was considered for Battle Creek (BC) representing the Preferred Alternative flows scenario defined in the Battle Creek Restoration Program (Appendix B; ICF International, 2016). Then, the maximum percentage of juveniles accessing tributary habitat is computed following

$$\gamma_{TRIB} = \frac{\rho_{TRIB,US}}{P_{J,0}} [A_{TRIB,MC}(h_{TRIB,MC}) + A_{TRIB,DC}(h_{TRIB,DC}) + A_{TRIB,BC}] \quad (4)$$

where  $\rho_{TRIB,US}$  [#fish/m<sup>2</sup>] is the juvenile density at tributary habitats (Table 2) and  $h_{TRIB,t}$  is the stage at tributary  $t$  (retrieved from CDEC daily data).

Off-channel habitat was defined as pools and areas adjacent to the Sacramento mainstem that become active above specific flow thresholds. Maslin et al. (1996) and Limm and Marchetti (2009) documented the use and importance of off-channel habitat for juvenile rearing. Total inundated area ( $A_{OFF}$ , acres) was estimated for different flow conditions in the Sacramento River ( $Q_{SAC}$ ) (Fig. 3) based on the modified Normalized Difference Water Index (mNDWI), first proposed by McFeeters (1996) to allow for the measurement of surface water extent. This index was derived from multi-spectral remote sensing imagery produced by the LandsAT Multispectral Scanner (2013– 2020 period), since its finer resolution allows to map smaller flood events (Chen et al., 2014). Generally, the values of mNDWI range from –1 to 1, with values over 0 representing surface water. However, a slight calibration in the threshold value was needed to result accuracy (Ji et al., 2009; Chen et al., 2014). Using surveyed off-channel habitats between Bend Bridge and Colusa (Kondolf and Stillwater Sciences, 2007), a value of –0.05 was established as the cut-off point. The mNDWI values under dense vegetation and/or high cloud cover may be misrepresented (McFeeters 1996), leading to potential underestimation of total inundated area. Finally, habitat capacity estimates, to determine the maximum proportion of juveniles rearing in a habitat ( $\gamma_{OFF}$ ), were based on density estimates of ~3 juveniles per unit of suitable habitat ( $\rho_{OFF,US}$ , m<sup>2</sup>) (Bartholow 2004; Hendrix et al., 2017).

$$\gamma_{OFF} = \frac{4046.86 A_{OFF}(Q_{SAC})\rho_{OFF,US}}{P_{J,0}} \quad (5)$$

The model assumes that juveniles rear in one of two alternative

**Table 2**  
WRHAP model parameters, description, and source. AV refers to annual values.

Modules	Param.	Value	Eq.	Description	Source	Reference	
Spawning Area	$T_{crit}$	12 [°C]	1	Temperature below which there is no temperature-related mortality	Fitted parameter	Martin et al., 2017	
	$b_T$	0.024 [°C <sup>-1</sup> d <sup>-1</sup> ]	1	Slope at which mortality rate increases with temperature	Fitted parameter	Martin et al., 2017	
	$T_{KWK,d}$	[°C]	1	Daily temperature downstream Keswick Dam	Recorded value	CDEC at station <i>KWK</i>	
	$N_{redds}$	AV	2	Number of redds observed each brood year	Field data	CDFW, 2020	
	$f$	AV	3	Winter-run Chinook salmon female fecundity [#eggs/ fem]	Field data	Poytress 2016; Voss and Poytress, 2020	
	$r_{fem}$	AV	3	Proportion of returning adults which are females	Field data	Poytress 2016; Voss and Poytress, 2020	
	$\beta_{Fry,N}$	0.366	3	Egg-to-juvenile survival rate without habitat effects	Fitted parameter	Poytress et al., 2014 Martin et al., 2017	
	$K$	9107	3	Capacity parameter in Beverton-Holt term	Fitted parameter	Martin et al., 2017	
Upper and Lower Sac. River	$T_{50,J}$	20 [°C]	6,10	Water temperature that decreases juvenile survival by a 50%	Lab study	Fish and Wildlife Service USFWS, 1999	
	$b_J$	1.8	6,10	Slope of the sigmoid function	Lab study	Reed et al., 2011	
	$\beta_{OFF}$	0.9916	6,10	Daily rearing survival at off-channel areas	Assumption	Considered equal to $\beta_{FLOOD}$	
	$r_{g,MAIN}$	1.8 [%/day]	14, 15	Daily weight increase while rearing in the Sacramento mainstem	Field study	Sommer et al., 2001; Jeffres 2016	
	$r_{g,TRIB}$	2.2 [%/day]	14, 15	Daily weight increase while rearing in the tributaries	Assumption	Considered 20% greater than mainstem (Limm and Marchetti 2009)	
Upper Sac. River	$prey_{ED}$	3760 [J/g]	12	Mean prey energy density used in the Fish Bioenergetics Model 4.0	Field data	Luecke and Brandt 1993; Tiffan et al., 2014; Haskell et al., 2017	
	$\beta_{MAIN}$	0.975	6	Daily rearing survival at the Sacramento mainstem	Calibrated parameter	Adapted from Peterson and Duarte, 2020	
	$\beta_{TRIB}$	0.98356	6	Daily rearing survival at the tributaries	Assumption	Considered 30% better than monthly mainstem rearing	
	$\rho_{OFF,US}$	3 [#fish/m <sup>2</sup> ]	5	Juvenile density at off-channel habitats	Field data	Bartholow 2004; USFWS 2005; Hendrix et al., 2017	
	$\rho_{TRIB,US}$	6 [#fish/m <sup>2</sup> ]	4	Juvenile density at tributary habitats	Field data	Bartholow 2004; USFWS 2005; Hendrix et al., 2017	
	$A_{TRIB,BC}$	20,640 [m <sup>2</sup> ]	4	Available juvenile rearing habitat at Battle Creek	Model output	Appendix B; ICF International, 2016	
	$d_{OFF}^{LS}$	15–23 [days]	6,14	Residence time at off-channel habitats	Field and remote sensing data	CDEC Sac. River stations; LandsAT Multispectral Scanner	
	$d_{TRIB}^{LS}$	28–40 [days]	6,14	Residence time at tributary habitats (>28 days)	Assumption	Based on values reported by Phillis et al. (2018)	
	Lower Sac. River	$\beta_{FLOOD}$	0.9916	10	Daily rearing survival at the floodplains	Field study	Katz, unpublished data Hinkelman et al., 2017
		$\beta_{MAIN}$	0.98916	10	Daily rearing survival at the Sacramento mainstem	Field study	Sommer et al., 2001; Takata et al., 2017
$\beta_{TRIB}$		0.9916	10	Daily rearing survival at the tributaries	Assumption	Considered equal to floodplain rearing	
$\rho_{OFF,LS}$		2 [#fish/m <sup>2</sup> ]	–	Juvenile density at off-channel habitats	Field data	Bartholow 2004; USFWS 2005; Hendrix et al., 2017	
$\rho_{TRIB,LS}$		5 [#fish/m <sup>2</sup> ]	–	Juvenile density at tributary habitats	Field data	Bartholow 2004; USFWS 2005; Hendrix et al., 2017	
$\beta_{S,Delta}$		81 [%]	11, 16	Migration survival through the Sacramento-San Joaquin Delta	Field study	Michel et al., 2015; Iglesias et al., 2017	
$\beta_{S,Yolo}$		91 [%]	11,16	Migration survival to Chipps Island through Yolo Bypass	Field study	Takata et al., 2017; Hendrix et al., 2017	
$d_{OFF}^{LS}$		15 [days]	10,15	Residence time at off-channel habitats	Remote sensing data	LandsAT-8 Multispectral Scanner	
$d_{TRIB}^{LS}$		28–40 [days]	10,15	Residence time at tributary habitats (>28 days)	Assumption	Based on values reported by Phillis et al. (2018)	

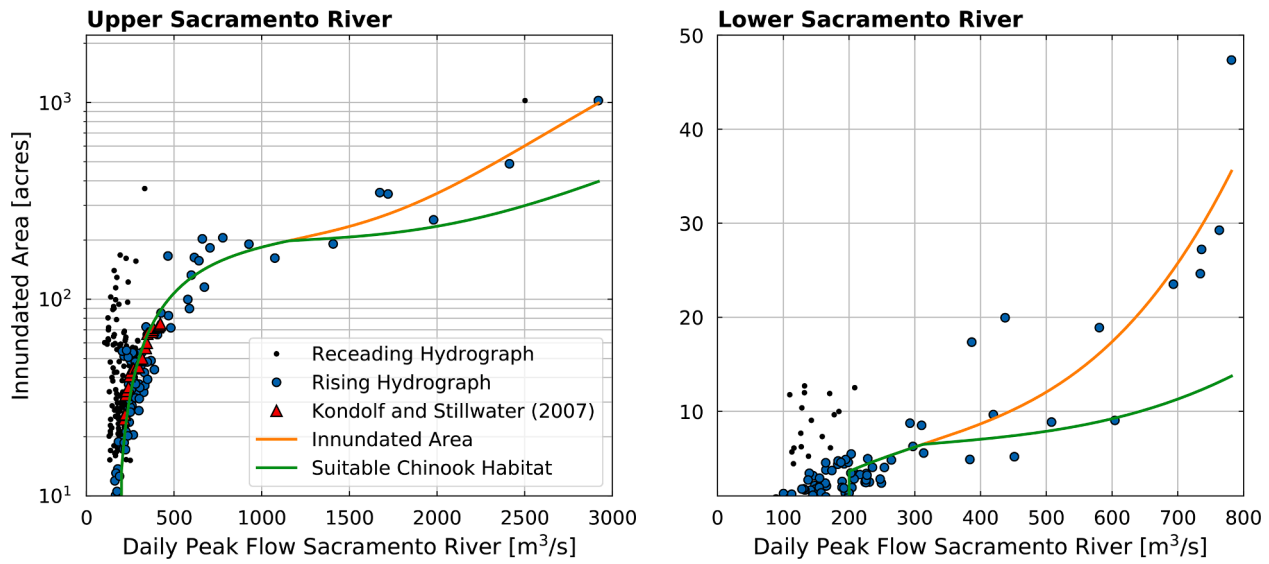


Fig. 3. Available off-channel habitat computed from remote sensing imagery as a function of daily peak flows. Red triangles represent field surveys by Kondolf and Stillwater (2007).

habitats or that fish do not rear in either habitat (i.e., a single individual does not move between tributaries and off-channel areas). The number of juveniles ( $P_{J,k}$ ) that leave the upper Sacramento River after rearing in habitat  $k$ , (OFF: off-channel, TRIB: tributary and MAIN: mainstem exclusively) for  $d_k^{US}$  days is given by:

$$\log(\beta_{M,k}) = 3.9031 Q_{out}/1000 + 1.8680 K_k - 6.1049 \quad (7)$$

The number of juveniles reared in habitat  $k$  that reaches the Lower Sacramento River ( $P_{J,k}^s$ ) is then computed as:

$$P_{J,k} = \gamma_k P_{J,0} (\beta_{MAIN}^{US})^{d_k^{US} - d_k^{US}} (\beta_k)^{d_k^{US}} \left[ 1 - \frac{1}{1 + e^{-b_J(T_k - T_{50J})}} \right]^{\frac{d_k^{US}}{7}} \left[ 1 - \frac{1}{1 + e^{-b_J(T_{MAIN} - T_{50J})}} \right]^{\frac{d_k^{US} - d_k^{US}}{7}} \quad (6)$$

where  $d_k^{US}$  is the residence time [days] at the upper Sacramento,  $\gamma_k$  is the proportion that reared in habitat  $k$ , and  $\beta_k$  is the daily rearing survival rate at habitat  $k$ . Temperature-related survival was fitted to weekly estimates, therefore,  $T_k$  is the average weekly temperature at habitat  $k$  and a factor of 7 is required. Additional parameters are defined in Table 2.

### 2.2.3. Juvenile migration to the lower sacramento river

After rearing in the upper Sacramento River area, all surviving juveniles move downstream, where rearing continues until smoltification. Peak migration through Knights Landing to the Lower Sacramento River occurs during high flow events (i.e., at least  $400 \text{ m}^3 \text{ s}^{-1}$  at Wilkins Slough, rkm 190) (del Rosario et al. 2013), with success rate strongly increasing with event flow rates (Michel et al., 2015). Furthermore, Iglesias et al. (2017) showed a significant correlation between out-migration mortality and poor fish condition (i.e., a proxy of overall health of individual fish). This is characterized using Fulton's  $K$  factor, which describes the ratio of fish weight [g] to fish length [mm]. Therefore, migration survival ( $\beta_{M,k}$ ) is modeled using a generalized linear model (Eq. (6)), fitted with a Gaussian distribution and a logarithmic link to 2007–2012 tagged-fish survival estimates (Iglesias et al., 2017), with peak flows ( $Q_{out}$ ) and juvenile condition from each rearing history ( $K_k$ ) as covariates. Both predictors are related to smolt passage time, which determines exposure to mortality risks.

$$P_{J,k}^s = \beta_{M,k} [Q_{out}, K_k] P_{J,k} \quad (8)$$

### 2.2.4. Lower sacramento river rearing

This module distributes the remaining age-0 population into available rearing habitats and estimates the number ready to out-migrate to the ocean. Juveniles spend, on average, nearly three months rearing in the Lower Sacramento before their departure at Chipps Island (del Rosario et al. 2013). Residence time at this river segment ( $d^{LS}$ ) was estimated from the 50% passage date at Chipps Island (IEP, 2020). As in the previous module, juveniles may rear in a maximum of one alternative rearing area. Off-channel habitat in the lower Sacramento is greatly restricted by intense channelization downstream of Colusa, CA. Flow-habitat relationships were computed following the same procedure described for the upper Sacramento River. Tributaries used by juveniles for rearing and development include the Feather and American Rivers (Phillis et al., 2018). Suitable habitat availability was determined based on stage-discharge and WUA relationships, using the same procedure as the previous module. Estimates were compared with usage percentages for the 2004–2006 brood years from Phillis et al. (2018).

The primary floodplains considered in the model are Sutter and Yolo bypasses, which become active when high flows overtop Tisdale and Fremont weirs, respectively. Nevertheless, fish move into the floodplains exclusively when overtopping occurs concurrently or shortly after (~1–2 weeks) fish migration across Knights Landing. The proportion of

the population entering the bypasses ( $\alpha_{flood}$ ) was modeled following the formulation of [Acierto et al. \(2014\)](#), which assumes juveniles are evenly distributed in the water column and enter the bypasses proportionally to flow.

$$\alpha_{flood} = \rho_{Sutter} + (1 - \rho_{Sutter})\rho_{Yolo}$$

$$\rho_{Sutter} = \frac{Q_{TIS}}{Q_{TIS} + Q_{WLK}} \quad \rho_{Yolo} = \frac{Q_{FRE}}{Q_{FRE} + Q_{VON}} \quad (9)$$

where  $Q_{st}$  is the flow at CDEC station  $st$ . The proportion entering Sutter Bypass is subtracted before considering Yolo Bypass due to its upstream location. Residence time in floodplain habitat was defined as a function of the overtopping event length (number of days) and an average bypass draining period of three weeks ([Takata et al., 2017](#)).

The number of juveniles ( $P_{J,ki}$ ) that reared in habitat  $k$  in the upper Sacramento and now leave the lower Sacramento River after rearing in habitat  $i$  for  $d_i^{LS}$  days is given by:

$$P_{J,ki} = \alpha_i P_{J,k}^s (\beta_{MAIN}^{LS})^{d_i^{LS}-d_k^{LS}} (\beta_i)^{d_i^{LS}} \left[ 1 - \frac{1}{1 + e^{-b_j(T_i - T_{50J})}} \right]^{\frac{d_i^{LS}}{T_i}} \left[ 1 - \frac{1}{1 + e^{-b_j(T_{MAIN} - T_{50J})}} \right]^{\frac{d_k^{LS}-d_i^{LS}}{T_i}} \quad (10)$$

where  $d^{LS}$  is the residence time [days] in the lower Sacramento,  $\alpha_i$  is the proportion that reared in habitat  $i$ ,  $\beta_i$  is the daily rearing survival rate at habitat  $i$ , and  $T_i$  is the average weekly temperature at habitat  $i$ . Additional parameters are defined in [Table 1](#).

Before reaching Chipps Island, smolts out-migrate either along Yolo Bypass or through the Delta complex channel system, experiencing an additional source of mortality. These values are considered constant across years to avoid additional sources of uncertainty introduced by smolt route selection, a function of water management in the Delta ([Perry et al., 2010](#)). Furthermore, [Michel et al. \(2015\)](#) found that the best model to represent out-migration survival for the complete

**Table 3**  
Fish bioenergetics model parameter values and sources (defined in [Deslauriers et al., 2017](#), for Chinook Salmon).

Param.	Value	Source	Param.	Value	Source
C <sub>A</sub>	0.303	<a href="#">Deslauriers et al., 2017</a>	RTL	25	<a href="#">Deslauriers et al., 2017</a>
C <sub>V</sub>	-0.275	<a href="#">Deslauriers et al., 2017</a>	RK1	1	<a href="#">Deslauriers et al., 2017</a>
C <sub>Q</sub>	4.97	<a href="#">Deslauriers et al., 2017</a>	RK4	0.13	<a href="#">Deslauriers et al., 2017</a>
CTO	15	Stewart and Ibarra, 1991	RK5	0	<a href="#">Deslauriers et al., 2017</a>
CTM	20.93	Plumb and Moffit, 2015	ACT	9.7	<a href="#">Deslauriers et al., 2017</a>
CTL	24.05	Plumb and Moffit, 2015	BACT	0.0405	<a href="#">Deslauriers et al., 2017</a>
CK1	0.36	Stewart and Ibarra, 1991	SDA	0.172	<a href="#">Deslauriers et al., 2017</a>
CK4	0.53	Plumb and Moffit, 2015	U <sub>A</sub>	0.0314	<a href="#">Deslauriers et al., 2017</a>
R <sub>A</sub>	0.00264	<a href="#">Deslauriers et al., 2017</a>	U <sub>B</sub>	0.58	<a href="#">Deslauriers et al., 2017</a>
R <sub>B</sub>	-0.217	<a href="#">Deslauriers et al., 2017</a>	U <sub>G</sub>	-0.299	<a href="#">Deslauriers et al., 2017</a>
R <sub>Q</sub>	0.06818	<a href="#">Deslauriers et al., 2017</a>	F <sub>A</sub>	0.212	<a href="#">Deslauriers et al., 2017</a>
RTO	0.0234	<a href="#">Deslauriers et al., 2017</a>	F <sub>B</sub>	-0.222	<a href="#">Deslauriers et al., 2017</a>
RTM	0	<a href="#">Deslauriers et al., 2017</a>	F <sub>G</sub>	0.631	<a href="#">Deslauriers et al., 2017</a>

Sacramento River system held Delta and San Francisco Bay survival constant through time. Therefore, the number of smolts reaching Chipps Island is given by (parameters defined in [Table 2](#)),

$$P_{J,out} = \beta_{S,Yolo} \sum_k P_{J,kFLOOD} + \beta_{S,Delta} \sum_{i \neq FLOOD} \sum_k P_{J,ki} \quad (11)$$

### 2.3. Winter-run juvenile development

#### 2.3.1. Spawning area

Initial juvenile biomass was based on the average weight of fry during emergence from gravel. [Kent \(1999\)](#) and [Titus et al. \(2004\)](#) estimate a value of 0.410 g ( $W_0$ ), equivalent to a 36 mm fish. This is also supported by data from [Vogel and Marine \(1991\)](#) showing millimeter deviation from this value.

#### 2.3.2. Upper and lower Sacramento river

Growth of juveniles in mainstem and tributary habitats was modeled

as a constant percent increase in weight per day, due to the lack of field studies documenting prey composition and prey density data. Growth rates were obtained using an average of reported values by scarce existing field studies ([Sommer et al., 2001](#); [Jeffres 2016](#)). These studies were based on fall-run Chinook juveniles from end-of-January to mid-March when coexisting winter-run juveniles are greater in length. Since daily length increase rates are a function of juvenile length with decreasing marginal increments, the expected rates for winter-run should be less than those reported in the literature. Nevertheless, the weight increase rate is expected to be similar under the same conditions and could be extrapolated to winter-run juveniles ([Jeffres, 2019](#)).

The main drawback of using constant growth rates is the lack of representation of changing conditions in the Sacramento River system between years. However, since growth in floodplains has been more extensively reported ([Katz et al., 2013](#); [Katz et al., 2014](#)), a bioenergetics model was implemented using the Fish Bioenergetics Model 4.0 ([Deslauriers et al., 2017](#)) for this and off-channel rearing habitats, as the latter is considered similar in characteristics (intermittent wetted areas). Simulated daily growth ( $\Delta G$ ) depend on habitat conditions (e.g., temperature and prey availability),

$$\Delta G = C - (R + A + SDA + F + U) \quad (12)$$

where C is the energy input (consumption), R is the metabolism, A is the activity, SDA is the energy required to digest food, F represents egestion and U excretion. Within the model, consumption was modeled as a satiation percentage ( $p$ ),

$$C = pC_{max} \quad (13)$$

where the maximum consumption ( $C_{max}$ ) is a function of temperature and juvenile weight. [Table 3](#) summarizes the bioenergetics parameters and their sources.

The model was tested against four years of recorded growth data (2014–2017) for fall-run Chinook salmon at Knaggs Ranch (Yolo Bypass; [Katz unpublished data](#)). A detailed review of empirical experiments at Knaggs Ranch was compiled by [Sommer et al. \(2020\)](#). The model used satiation percentages within 0.4–1.0, as daily values were not reported, to estimate growth rate ranges along the experiment duration. Daily temperature was available from field measurements and the energy density of the prey was defined based on diet composition from stomach

content data. On average, the diet included Cladocerans (~95%), Chironomidae (~2%) and Copepods (~3%) with energy densities of 3960 J/g, 3248 J/g and 4500 J/g, respectively (Luecke and Brandt 1993; Tiffan et al., 2014; Haskell et al., 2017). The computed daily growth bands were then compared with the experienced growth of juveniles leaving the testing site at successive days. Due to sparse temperature data availability at Yolo and Sutter bypasses after historical overtopping events, we also analyzed the differences in end-of-period simulated daily growth rates using daily versus averaged temperatures during the field experiment, to assess if the latter provide a reasonable approximation.

The weight of a surviving juvenile after rearing in the upper Sacramento for  $d_k^{US}$  days in habitat  $k$  and growth rate ( $r_{g,k}$ ) was computed as:

$$W_k^{US} = W_0 (r_{g,MAIN})^{d_k^{US} - d_k^{LS}} (r_{g,k})^{d_k^{US}} \quad (14)$$

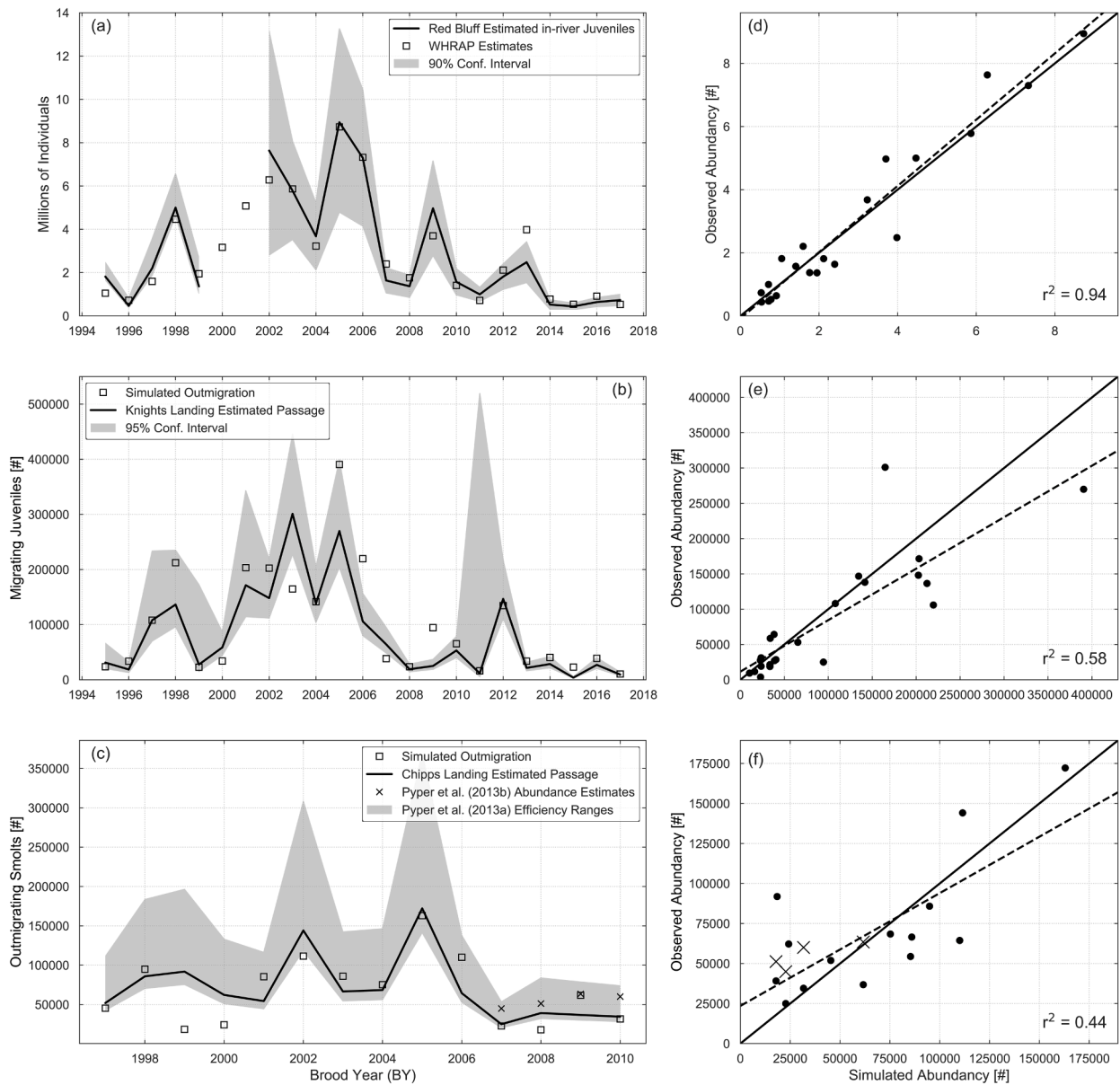
while the weight of a juvenile that reared in habitat  $k$  in the upper Sacramento and in habitat  $i$  in the lower Sacramento for  $d_i^{LS}$  days and growth rate ( $r_{g,i}$ ) is:

$$W_{k,i}^{LS} = W_k^{US} (r_{g,MAIN})^{d_k^{US} - d_i^{LS}} (r_{g,i})^{d_i^{LS}} \quad (15)$$

### 2.3.3. Smolt out-migration to the san francisco bay

The out-migrating biomass ( $B_{out}$ ) was calculated based on out-migration success ( $\beta_{S,Yolo}$ ,  $\beta_{S,Delta}$ ) and the final juvenile weight after the lower Sacramento module ( $W_{ki}^{LS}$ ).

$$B_{out} = \beta_{S,Yolo} \sum_k P_{J,k,FLOOD} W_{k,FLOOD}^{LS} + \beta_{S,Delta} \sum_{i \neq FLOOD} \sum_k P_{J,ki} W_{ki}^{LS} \quad (16)$$



**Fig. 4.** (a) Time series comparison of WRHAP estimates of in-river juvenile production with Red Bluff Rotary Trap records and its 90% confidence interval (gray area); (b) Time series of simulated juvenile migration numbers compared to observed counts at Knights Landing Rotary Trap and its 95% confidence interval (gray area); (c) Time series of out-migrating smolts to the San Francisco Bay compared to observed abundances at Chipps Island and its uncertainty range using the three available efficiency estimates (Pyper et al., 2013a); (d) Simulated vs observed estimate of in-river juvenile production at Red Bluff Rotary Trap; (e) Simulated vs observed estimate of juvenile abundance at Knights Landing Rotary Trap; (f) Simulated vs observed estimate (using Pittsburg efficiency value; Pyper et al., 2013a) of smolt abundance at Chipps Island Midwater Trawl.



## 2.4. Sensitivity analysis

Sobol' indices were selected to analyze the sensitivity of model outputs to every input parameter. These indices are used for a mathematical and more precise estimation of the influence of individual variables or groups of variables on model output. Here, we focused on the first- and total-order indices ( $S_1$ ,  $S_T$ ), which indicates the proportion of total variance explained by the specific parameter by itself and the proportion not explained by all terms (individual parameters and their n-order interactions with other input parameters) excluding those from the parameter analyzed, respectively. This method is superior when relationships between model outputs and input parameters are nonlinear or nonmonotonic (Iooss and Lemaitre 2015).

For the analysis, a sample size ( $n$ ) of 35,000 was selected following Saltelli et al. (2010), within predefined ranges for all 21 model parameters based on observed ranges in field studies, expert knowledge, and feasible values (e.g., 0–1 for habitat use). Parameters defined from observed data, such as ratio of females ( $r_{fem}$ ) or fecundity ( $f$ ), were not considered because they are regarded as observed inputs analogous to temperature or flow. Likewise, the parameters of the bioenergetics model were not included in the analysis, but the bioenergetics output, growth at the floodplains ( $r_{g,FLOOD}$ ) and off-channel areas ( $r_{g,OFF}$ ), was considered in order to analyze their relative importance on juvenile development when compared to remaining rearing habitats. The number and biomass of out-migrants were computed for each of 1,540,000 ( $= 2n \cdot (p+1)$ ) model evaluations to calculate the first and total-order sensitivity index and their 95% confidence interval, using the SALib library in Python (Herman and Usher 2017). This sample size ( $n$ ) was needed to assure convergence in the sensitivity indices computation. Input parameters were ranked based on total-order index value and considered non-sensitive if their confidence intervals included zero. This information helps identify habitat conditions (availability and/or quality) which increase variance in successful juvenile development and can suggest habitat targets for potential management and recovery actions to improve juvenile production in the Sacramento Valley.

## 3. Results

### 3.1. Field data comparison

Computed outputs were compared to recorded winter-run indices of abundance throughout the life cycle. Red Bluff juvenile counts (brood

years 1995–1999 and 2002–2017; Martin et al., 2001; Poytress et al., 2014; Voss and Poytress 2019) allowed comparison of in-river juvenile production that reared in the upper Sacramento River. WRHAP estimates closely follow the observed patterns ( $r^2=0.94$ ; Fig. 4d), generally lying within their 90% confidence interval (Fig. 4a), as expected from using Martin et al. (2017) fitted biophysical model. During previous model iterations, outputs from brood years 1997–1998 differed in more than three times the standard deviation of the data distribution. The discrepancy was from differences in spawner values provided by GrandTab and CDFG carcass surveys (Killam 2006), with values of 836 and 2053 for 1998, respectively. The latter values were adopted as more realistic estimates of fry production compared with Red Bluff records. Drought years with warm releases from Shasta (e.g., 2014–2016) were especially well represented, as shown by the narrower uncertainty in the observed passage, suggesting that egg-to-fry temperature mortality was adequately captured. Knights Landing catches (Snider and Titus 1998; 2000abc; Vincik et al., 2006; Roberts 2007; Roberts et al., 2013, unpublished data; Julienne 2016; McKibbin, 2016; Columbia Basin Research, 2018) provided the observed record to verify the estimated number of migrants to the Lower Sacramento River. A poorer fit was obtained ( $r^2=0.58$ ; Fig. 4e), expected from the more complex interactions occurring along the Upper Sacramento River, with model estimates generally overestimating catch-based abundances. Nevertheless, annual migration patterns were reasonably reproduced (e.g., BY2012–2013), with output values largely within 95% confidence intervals of catch-based estimates (Fig. 4b). Finally, model output was compared with abundance estimates at Chipps Island (Pyper et al., 2013b; IEP 2020) for the 1995–2010 period. Three alternative midwater trawl efficiency values (Pittsburg, Jersey Point and paired-release) were considered to estimate uncertainty bounds because a single best estimate has not been selected (Pyper et al., 2013a). These values were also considered constant through time as recommended by Pyper et al. (2013a). The Pittsburgh efficiency value was used to analyze model fitness since the remaining efficiencies led to unrealistic catch-based estimates, greater than abundance numbers at Knights Landing (e.g., BY1999–2000). Simulated abundances are a reasonable approximation of the historical pattern despite a low coefficient of determination ( $r^2=0.44$ ; Fig. 4f), as simulated values generally lie within the uncertainty bounds (Fig. 4c), deeming acceptable the simplification of Delta out-migration survival as a constant through time. These comparisons showed inconsistencies between catch-based estimates at Knights Landing rotary trap and Chipps Island mid-water trawl, requiring

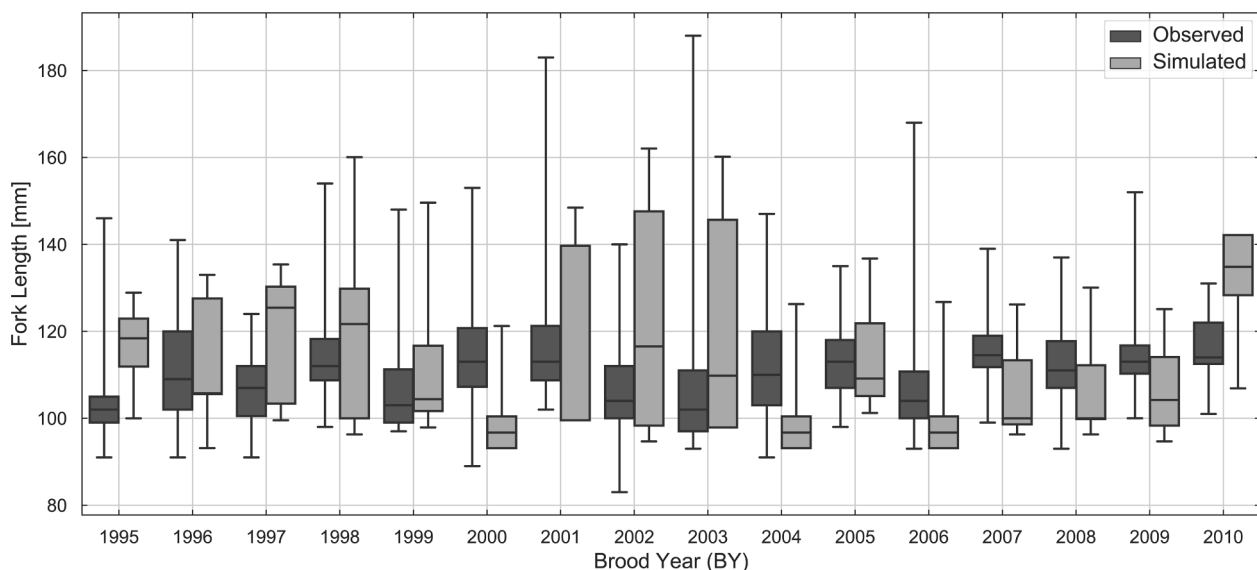


Fig. 5. Observed and simulated fork length distributions at Chipps Island for out-migrating smolts to the San Francisco Bay.

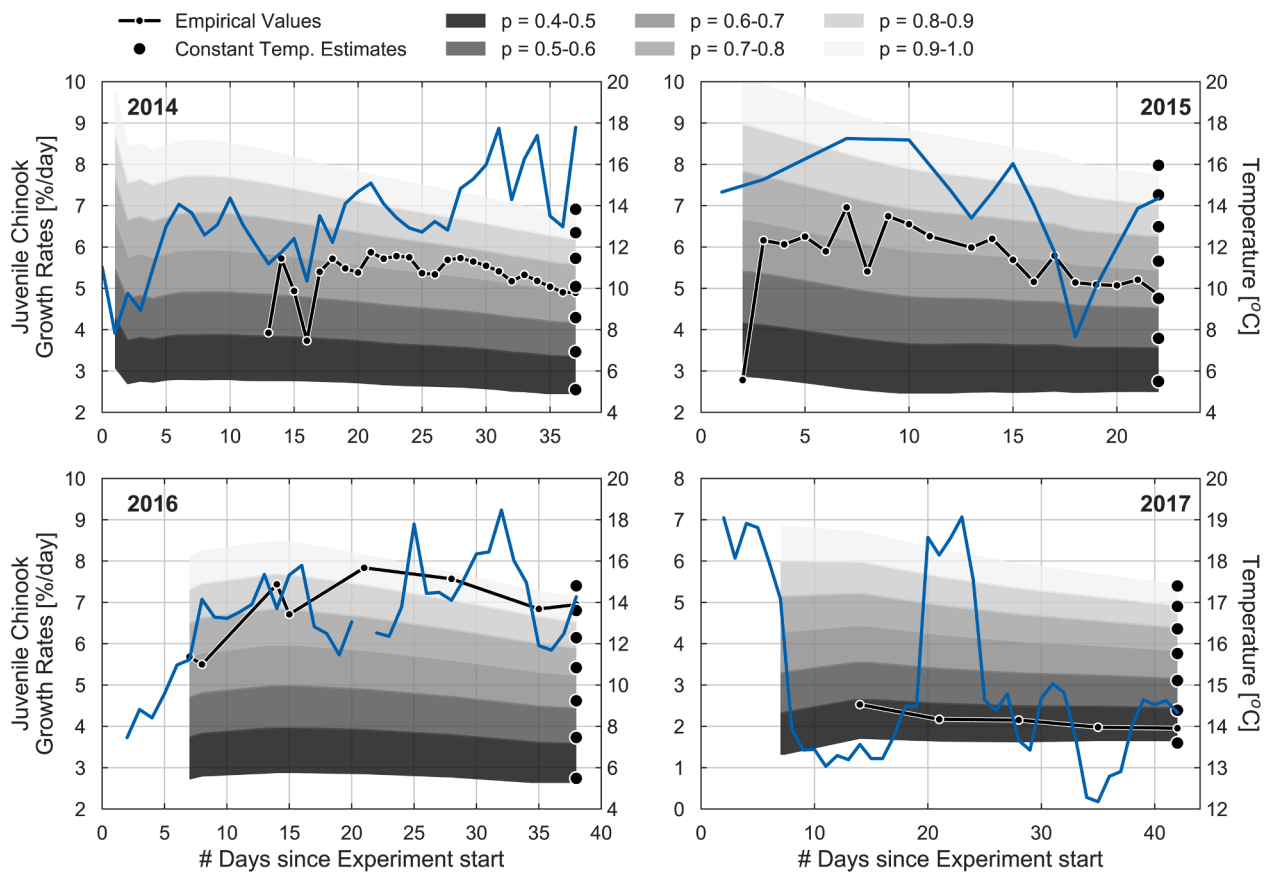


Fig. 6. Observed growth of fall-run Chinook at Knaggs Ranch for years 2014–2017 (Katz, unpublished data). The blue line represents recorded water temperature.

unrealistic survival values ( $\geq 1$ ) to explain the change in population numbers between these two locations. WRHAP estimates lie within the uncertainty bounds at one of the locations when such discrepancies exist (e.g., BYs1999, 2008; Fig. 4bc), suggesting a better representation than

the coefficient of determination values indicate.

To evaluate juvenile growth and migration timing, we compared migrants fork lengths with reported ranges at Knights Landing (Snider and Titus 1998; 2000abc; Vincik et al., 2006; Roberts 2007; McKibbin,

Table 4

First order ( $S_{Ii}$ ) and Total sensitivity index ( $S_{Ti}$ ) with their standard deviation (in parenthesis) for the most influential parameters. They appear from most to least sensitive.

Param	Range	Total Outmigrants $S_{Ii}$	$S_{Ti}$	Param	Range	Avg. Smolt Biomass $S_{Ii}$	$S_{Ti}$
$\beta_{MAIN}$ [%/day]	97.3–98.7	0.5050 (0.0010)	0.5840 (0.0004)	$r_{g,FLOOD}$ [%/day]	2.0–8.5	0.1200 (0.0040)	0.6680 (0.0670)
Rearing survival at mainstem				Growth rate at floodplains			
$r_{g,MAIN}$ [%/day]	0.5–3	0.1030 (0.0008)	0.1350 (0.0001)	$d_{FLOOD}$ [days]	21–90	0.0955 (0.0030)	0.5620 (0.0080)
Growth rate at mainstem				Residence time at floodplains			
$\beta_{FYN}$ [%]	19–38	0.0930 (0.0008)	0.1260 (0.0001)	$r_{g,MAIN}$ [%/day]	0.5–3	0.0700 (0.0054)	0.2840 (0.0068)
Egg-to-fry survival with no temperature effects				Growth rate at mainstem			
$r_{g,TRIB}$ [%/day]	1–5.5	0.0230 (0.0024)	0.0410 (0.0013)	$\alpha_{FLOOD}$ [%]	0–100	0.0084 (0.0012)	0.1720 (0.0104)
Growth rate at tributaries				Prop. of juveniles rearing at floodplains			
$r_{g,OFF}$ [%/day]	2–8.5	0.0190 (0.0037)	0.0400 (0.0020)	$r_{g,OFF}$ [%/day]	2–8.5	0.0190 (0.0026)	0.1300 (0.0090)
Growth rate at off-channel habitat				Growth rate at off-channel habitat			
$\gamma_{OFF}$ [%]	0–100	0.0150 (0.0051)	0.0390 (0.0024)	$d_{OFF}^{US}$ [days]	10–40	0.0074 (0.0000)	0.0780 (0.0000)
Prop. of juveniles rearing at upper Sac. off-channel areas				Residence time at off-channel habitat along upper Sac.			
$d_{OFF}^{US}$ [days]	10–40	0.0190 (0.0120)	0.0360 (0.0110)	$r_{g,TRIB}$ [%/day]	1–5.5	0.0045 (0.0011)	0.0650 (0.0016)
Residence time at off-channel habitat along upper Sac.				Growth rate at tributaries			
$\beta_{S,Delta}$ [%]	60–100	0.0210 (0.0133)	0.0310 (0.0004)	$\gamma_{OFF}$ [%]	0–100	0.0028 (0.0011)	0.0360 (0.0020)
Outmigration survival through the Delta				Prop. of juveniles rearing at lower Sac. tributaries			
$\gamma_{TRIB}$ [%]	0–100	0.0120 (0.0015)	0.0290 (0.0003)	$\alpha_{TRIB}$ [%]	0–100	–0.0001 (0.0006)	0.0220 (0.0002)
Prop. of juveniles rearing at upper Sac. tributaries				Prop. of juveniles rearing at upper Sac. off-channel areas			
$\beta_{TRIB}$ [days]	10–50	0.0150 (0.0013)	0.0250 (0.0003)	$\alpha_{OFF}$ [%]	0–100	–0.0010 (0.0004)	0.0200 (0.0001)
Residence time at tributaries along upper Sac.				Prop. of juveniles rearing at lower Sac. off-channel areas			

2016) and Chipps Island (IEP 2020). Since WRHAP computes individual weight, an empirical relationship ( $L$  [mm] =  $48W^{0.3}$  [g]; Hinkelman et al., 2017) was used to transform the estimates for their comparison. Simulated fork lengths of migrating juveniles to the Lower Sacramento River matched reasonably well for the reported brood years (BY 1995–1999, 2001 and 2011–2012) with a simulated range of 64–109 mm against the recorded 45–119 mm. In most years, the smallest simulated juveniles (~ 65 mm) were larger than the range of shortest captured winter-run (i.e., 45–56 mm), since these values correspond to later fry emergence times than those considered in the model structure. Average fork lengths were well captured, with simulated fork lengths of 89 and 68 mm for BY 2011–2012 against observed 88 and 60 mm, for instance. Model output reasonably approximates recorded fork lengths at Chipps Island, especially maximum fork lengths during brood years with floodplain habitat available (e.g., BY 1998–1999, 2005, 2007–2009; Fig. 5). Similar to Knights Landing data, smallest fork lengths were usually longer than reported sizes due to captured individuals with later emergence times than those considered in the model structure. The greatest differences between modelled and observed length distributions were during low flow years with short residence periods at Lower Sacramento River (e.g., BY 2000, 2004).

### 3.2. Fish bioenergetics model

Observed growth rates throughout all experiments show diminishing growth rates for longer residence times, expected from decreasing percentage increases in weight for increasingly larger juveniles. This temporal pattern was captured by the bioenergetics model bands (Fig. 6), indicating a correct representation of the temperature effects on juvenile development. Modeling results accurately reproduced observed juvenile development with observed growth rates within a single satiation percentage range, especially from 5–6 days before the experiment completion when greater numbers of juveniles (>80%) left the rearing area. Juveniles out-migrating during the experiment's first half (<10% of total) showed poorer growth rates, as expected, since experiencing suboptimal rearing conditions could trigger early movement. Observed growth rates were the lowest during the 2017 experiment, when extensive overtopping at Fremont weir occurred and optimal conditions at floodplain habitats were not present (i.e., shallow and warm waters for zooplankton production; Corline et al., 2017; Jeffres et al. 2020). As such, a satiation percentage under 50% was required to simulate the observed growth rates (Fig. 6), which agree with existing conditions (i.e., lower prey density). In contrast, Knaggs Ranch was disconnected from the Sacramento River during the 2014–2016 experiments, when controlled inundation was implemented, providing optimal or near-optimal zooplankton production and rearing conditions. Hence, simulated satiation percentages were consistently over 60–70%, with almost full satiation during 2016 (>90%). Differences in  $p$  values also could be related to annual changes in *Daphnia* energy density, as it conforms the greatest dietary component (>90%) and their specific caloric value was not recorded during the field study. Therefore,

**Table 5**

Proportion of simulated juveniles that used each available rearing habitat at any life stage and proportion of the total biomass generated within them. Parenthetic value is percentage of simulated juveniles rearing only in the mainstem.

	Total	Mainstem	Tributaries	Off-Channel	Floodplain
<b>Out-migrants</b>	1132,364	100% (21.9%)	45.1%	33.9%	17.5%
<b>Biomass [kg]</b>	19,303	41.3%	19.9%	9.9%	28.9%
<b>Avg. Rearing Time [days]</b>	167	78.1%	11.2%	3.3%	7.4%

bioenergetics model outputs presented a correct coherence with prey densities, rearing conditions, and recorded growth rates.

End-of-experiment growth rates estimated using a constant averaged temperature differed in less than 3.5%, on average, from the fluctuating temperature results (Fig. 6). As such, average temperatures in Yolo and Sutter bypasses after flooding events were used to simulate growth to adjust for sparse temperature data availability in those areas, since they provide a reasonable approximation.

### 3.3. Sensitivity analysis

Sobol' sensitivity indices showed rearing survival at the mainstem ( $\beta_{MAIN}$ ) as the most sensitive parameter for total number of smolts reaching San Francisco Bay, explaining a 50.5% of total variance (first-order index,  $S_1$ ) and 58% when its parameter interactions are considered (total-order index,  $S_T$ ; Table 4). As such, the influence on model output variance is at least three times greater than any other model parameter, and mainly caused by the first-order effect (Nossent et al., 2011). This was an expected outcome, as the complete cohort rears within the mainstem for prolonged periods (~77% of total rearing time, on average; Table 5), when off-mainstem habitats are both available and unavailable. For instance, juveniles that reared in off-channel habitats for two weeks, spent their remaining rearing stage within the mainstem river (Fig. 2). Such rearing behavior coupled with the positive relationship between fish condition (Fulton's  $k$ ) and migration success ( $\beta_M$ ; Eq. (7)) explains (i) the influence of upper Sacramento River growth-related parameters; and (ii) mainstem growth ( $r_{g,MAIN}$ ) total effect being three-fold greater than growth rates at alternative habitats ( $r_{g,TRIB}$  and  $r_{g,OFF}$ ), despite their improved rearing conditions (Maslin 1996; Limm and Marchetti 2009). Nevertheless, the latter and off-channel habitat use ( $y_{FLOOD}$ ) being the fourth-sixth ranked parameters suggest that juveniles taking advantage of these areas have greater chances of successfully out-migrating, lifting their relative importance in the upper Sacramento River. Total out-migrants show high sensitivity to egg-to-fry survival without temperature effects ( $\beta_{Fry,N}$ ), as its interaction with fecundity ( $f$ ) and proportion of females ( $r_{fem}$ ) determines the initial number of juveniles. Out-migration survival through the Delta and Yolo Bypass do not significantly influence the variability of smolt abundance (<3.1% of total variance), indicating that mainstem conditions and available rearing habitats arose as the most limiting factor on Chinook salmon production (Bartholow 2001; Beer et al., 2017). Nevertheless, rearing survival in the alternative habitats show low sensitivity ( $S_{Ti} < 0.015$ ), reflecting similar rearing mortalities independent of the choice of rearing path, as indicated in the literature (Katz et al., 2017). Model outputs were not sensitive to parameters with negative indices values within confidence intervals (Nossent et al., 2011).

As expected, smolt biomass was most influenced by growth-related parameters (growth rates and residence times) and proportion of juveniles rearing at supplemental habitats. The analysis shows floodplains as the most influential rearing habitat in the Valley with its growth rate ( $r_{g,FLOOD}$ ), residence time ( $d_{FLOOD}^S$ ) and proportion of juveniles ( $\alpha_{FLOOD}$ ) as the first, second and fourth most sensitive parameters for out-migrating smolt biomass, respectively. The difference between their first- and total-order indices indicate their influence is mainly from interactions among these parameters. For instance, the interaction between  $r_{g,FLOOD}$  and  $d_{FLOOD}^S$  explains a 17% of the total variance, greater than either of them individually (12% and 9.5%, respectively). The total-effect of floodplain growth rates is around three and six times greater than those associated with mainstem and remaining supplemental habitats, respectively. This agrees with field studies on the importance of floodplain habitat on smolt body condition and, hence, on initial ocean survival (i.e., smolt-to-age-2 survival; Claiborne et al., 2011) by providing enhanced rearing conditions (Sommer et al., 2001; Katz et al., 2017; Jeffres et al. 2020). As could be expected, the second ranked habitat is the Sacramento mainstem ( $r_{g,MAIN}$ ), since juveniles spend prolonged

periods rearing in this habitat, even juveniles using off-mainstem habitats along the upper and lower Sacramento River (Table 5). However, some of its influence on individual biomass (total biomass over out-migrant numbers) is not related to growth conditions, but, rather, its effect on migration survival ( $\beta_M$ ; Eq. (7)), and smolt numbers (second highest rank for total out-migrants in Table 4). The third ranked habitat is off-channel areas, explaining 13% of total variance. Its growth rate total-order effect is just half that of mainstem habitat, despite averaging 31% of mainstem residence times. This shows that this supplemental habitat provides superior rearing conditions, and so becomes an important driver on individual success during the marine stage, agreeing with published literature (Maslin 1996; Limm and Marchetti 2009). Finally, the lowest ranked habitat by influence on average individual biomass is tributaries, explaining 6.1% of total variance. This was somewhat expected since tributary residence time is shorter than that of mainstem habitats, and growth rates were inferior when compared with off-channel habitats (Table 4). As such, its total-effect is nearly two-, four- and ten-fold less than off-channel, mainstem and floodplain areas, respectively.

#### 4. Discussion

WRHAP outputs result from mechanistic understanding of fish survival and growth and agree reasonably well with observed records of winter-run abundances (Fig. 4). Nevertheless, the model greatly simplifies fish ecology and population dynamics. The coarse temporal and spatial discretization neglect some important fish habitat criteria such as peak and minimum water temperatures (NRC 2004). Furthermore, not all instream habitat parameters, except flow and temperature, were directly represented due to data unavailability. Instead, they were

aggregated in the rearing survival estimate, although other water quality parameters (e.g., turbidity) and predation dynamics greatly influence survival and rearing success (National Research Council NRC, 2004). The greatest uncertainty is related to several parameters (e.g., tributary growth rates), and estimates of rearing habitat usage, survival, and residence time due to the lack of available empirical and behavioral studies. Despite the importance of these estimates in understanding juvenile life stage limitations, as illustrated by associated high total sensitivity indices ( $S_{T_i}$ ; Table 4), a significant data gap exists because there is a lack of explicit monitoring for the winter-run (Johnson et al., 2017). As such, only two studies provided mainstem growth rates, and both were limited to three years of data (1998, 1999 and 2016; Sommer et al., 2001; Jeffres 2016). Further, only one study provided a comparison of tributary growth rates to mainstem conditions (Limm and Marchetti 2009) and only three brood years (2004–2006) of otolith growth data were available for estimating tributary rearing (Phillis et al. 2017). Otolith growth data also are based on returning adults, which potentially misrepresent actual habitat use by either underestimating actual numbers from the loss of individuals occurring between juvenile out-migration and adult return or by overstating tributary use due to improved survival, relative to the mainstem (Phillis et al. 2017). These studies also cover only a small proportion of the extensive range of potential conditions experienced by juveniles during rearing and out-migration. A more intensive monitoring program is needed to better understand habitat availability and juvenile development tradeoffs and more accurately simulate the different life stages of winter-run Chinook salmon.

Despite challenges from a lack of observational data, model development was motivated by the neglect or misrepresentation of supplemental rearing habitats in existing modeling efforts, partly due to their

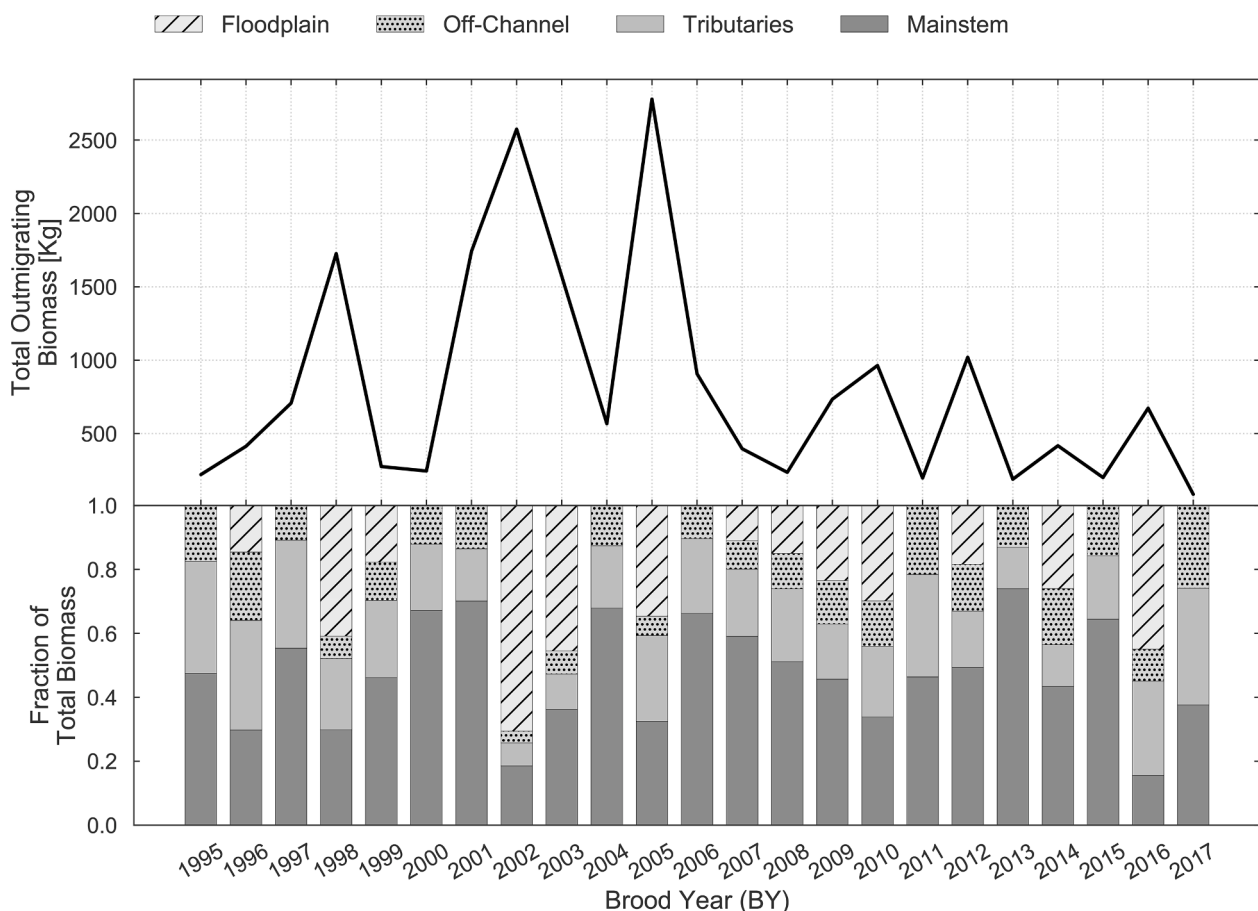


Fig. 7. Simulated out-migrating biomass and fraction generated in each available rearing habitat.

previous conception of a single habitat below a dam (e.g., Jager et al., 1997; Bartholow 2004). Only Hendrix et al. (2017) included more disaggregation of rearing habitats for winter-run Chinook life stages, but omitted tributaries and off-channel areas, shown to be important for Chinook salmon juvenile growth and survival (Maslin et al., 1996; Limm and Marchetti 2009). Other modeling efforts for winter-run Chinook in the Sacramento River only considered ESA designated critical habitat (e.g., Zeug et al., 2012; Beer et al., 2017). For such models, fish survival depended exclusively on temperature during early life-stages, varying with distance and time of travel, function of flows, and smolt swimming speed (e.g., 'X-T model'; Anderson et al., 2005). Although smolt swimming speed also is subject to its body condition, no simulation of growth during the rearing stage of in-river produced winter-run Chinook was included in any model structure.

The expanded conceptual structure of WRHAP allows analysis of the effects of rearing history and alternative habitat constraints/availability on juvenile growth and out-migration success. For instance, model output from brood years with existing floodplain habitat show a consistent high proportion of biomass generated in this rearing area (Fig. 7). As summarized in Table 5, floodplains contribute the second most to total simulated out-migration biomass, approximately 29% (~30% less than mainstem; Fig. 7), despite only 15–20% of total out-migrants being able to access Yolo and Sutter bypasses and a rearing duration averaging only 7–8% of the total rearing period. For instance, several brood years present greater out-migrating biomass despite having fewer individuals reaching San Francisco Bay (e.g., 2002 and 2003, 2006 and 2009; Fig. 7). Thus, WRHAP successfully represents floodplains as providing enhanced rearing conditions compared to adjacent river channels (Sommer et al., 2001; Katz et al., 2017; Jeffres et al. 2020), when adequate flows occur. The importance of this habitat is also stated by the sensitivity analysis, recognizing floodplain-related parameters (growth rate, residence time and proportion of juveniles) as the most sensitive for out-migrating biomass (Table 4). Similarly, average winter-run Chinook fork lengths for during rearing under mainstem Sacramento River conditions were 94 mm, compared to 130 mm for juveniles that reared within floodplain habitat. During periods with frequent high flows overtopping Fremont weir, floodplain habitat quality was more similar to mainstem habitat due to a decline in optimal environmental conditions (shallow and warmer water) for zooplankton production (Corline et al., 2017; Jeffres et al. 2020). Thus, poorer growth rates were expected, as shown by Katz (*unpublished data*; Fig. 6). The model captured this tradeoff, with daily growth rates of 1.5–2.5%/day (e.g., BY 2005, 2016) compared to 5–7%/day under optimal floodplain conditions (e.g., BY 2009, 2010). The timing of downstream migration and weir overtopping events were crucial for juvenile development since floodplain habitat was only available when both occurred concurrently. For instance, during brood year 2001, mainstem migration was triggered by high flows exceeding 400 m<sup>3</sup>/s at Wilkins Slough between late November through mid-December (del Rosario et al. 2013), but Fremont weir overtopping commenced in mid-January. As such, the bulk of the winter-run population migrated downstream of Fremont weir prior to floodplain activation, precluding juveniles from taking advantage of enhanced rearing conditions.

Tributaries and off-channel habitats account for 19.9% and 9.9%, respectively, of total generated biomass (Fig. 7). At first glance, off-channel habitats may appear as the least productive rearing habitat due to its low contribution, despite approximately a third of total out-migrants used these intermittent habitats (Table 5). However, off-channel habitats are active for shorter durations (~ one to three weeks as shown by remote sensing imagery) compared with tributaries (e.g., >28 days) (Phillis et al., 2018) and mainstem habitats. As such, off-channel rearing, when compared to tributaries, showed a residence time over three-fold less and a juvenile occupancy of 75%, but showed just a 50% decline in generated biomass (Table 5). Furthermore, average simulated fork lengths were 106 and 116 mm for tributary and off-channel rearing, respectively, suggesting enhanced rearing

conditions in off-channel habitats (e.g., Maslin, 1996). This tradeoff is also shown by their Sobol' total-order indices, ranking off-channel growth and residence time over tributaries (Table 4). More frequent activation of these habitats (e.g., improving mainstem and side channel connectivity or small pulse flows from reservoir releases) would enhance juvenile salmon residence time and likely improve out-migration biomass and success, as indicated by its total-order sensitivity index (Table 4). Nevertheless, this is not indicative of tributary rearing having a marginal value. Similarly to the remaining off-mainstem habitats, tributary habitats also provided superior rearing conditions when compared to mainstem habitat, generating half of the biomass (19.9% vs 41.3%) with just 11% of rearing time, on average. This suggests that the relative importance of tributary habitat is greater than the inferred from the sensitivity analysis (Table 4).

Survival success during migration to the lower Sacramento River depends, in part, on the existence and use of supplemental rearing habitats, coupled with the timing of high flows. Individual survival success improves with juvenile condition (i.e., weight to length ratio), function of the rearing path in the upper Sacramento River. Juveniles that reared in off-channel habitats or tributaries, when available, regularly exhibited larger sizes and lower migration mortality. This effect is more important for early migration dates, when the contribution of mainstem rearing habitats to fish condition is greatly reduced compared to alternative habitats (e.g., tributaries and off-channel areas). For instance, simulated juveniles that reared in off-channel areas during brood year 2006 (early migration date) exhibited superior condition (~ +7%) when compared with juveniles that used mainstem habitats. In turn, this enhanced migration survival by three-fold. However, juveniles from brood year 2013 (late migration date) exhibited a 3.9% improvement in condition, leading to a 98% increase in migration survival. As such, the marginal value of improved growth conditions decreases with an extended residence period, since juveniles can reach suitable sizes to assure improved migration survival under exclusive mainstem rearing conditions. Regardless, juveniles that reared only in the Sacramento River mainstem exhibited the poorest condition and lowest annual survival. These simulation outputs align with the discussion of Sobol' indices (Section 3.3; Table 4), giving mainstem habitats a high influence on out-migrant numbers due to prolonged rearing periods, and not for superior rearing conditions. As such, off-channel and tributary habitats hold a much greater relative importance than the suggested by the total-order indices. The annual variation in migration survival also reflects the existing tradeoff between migration date and juvenile abundances and condition. Later migration dates exhibited increased rearing mortalities due to extended exposure periods (Anderson et al., 2005), but those individuals that succeeded were in better condition, increasing their chances of survival during migration. Similarly, the growth-survival tradeoff also is expected to be crucial for out-migrants at Chippis Island, with longer residence times at the lower Sacramento River producing fewer smolts in better condition and increasing and individual's probability of returning as an adult.

Modeling, as presented here, suggests that off-mainstem habitats are crucial to out-migration and ocean stage survival and critical to long-term recovery efforts for winter-run Chinook salmon populations. This pattern was consistent throughout historical simulations with the greatest egg-to-smolt mortalities associated with low flow conditions and sparse or limited availability of supplemental habitats (e.g., brood years 2001, 2006 and 2014; Fig. 4). If these conditions were persistent across several years, warm water releases from Shasta Reservoir (associated with cold pool depletion) significantly increase egg-to-fry mortality (Johnson and Lindley, 2016). Low flow conditions also constrain the availability of two main alternative habitats (e.g., off-channel and floodplains), limiting enhanced juvenile growth and out-migration success (as shown by the sensitivity analysis, Table 4). This also suggests that current infrastructure projects to improve floodplain management (i.e., notching Fremont Weir; DWR, 2017) are promising because they offer the ability to provide floodplain access (i) during low

flow years, and (ii) when migration and overtopping events do not overlap. Lastly, dry conditions are generally associated with small pulse flow cues for juvenile migration, increasing their experienced mortality, since the primary driver of smolt migration survival is the magnitude of the high flow event (Iglesias et al., 2017).

WRHAP was not calibrated directly against observed fish population data (e.g., Bartholow 2004), although several parameters were defined from calibrated model outputs (e.g. temperature-related egg-to-fry survival, Martin et al., 2017; Table 1). Parameter estimates were also defined from existing reported values in the literature, empirical and laboratory studies, and expert knowledge (see Table 2). Model calibration faces two major challenges. First, the main model input, number of returning adults to spawning areas (Killam 2006; Azat 2019), is an estimate. Second, the main migration data (catches at Chipps Island, Knights Landing and Red Bluff rotatory traps) have high uncertainty from their efficiency factor estimates (Roberts 2007; Pypers et al., 2013a; Poytress et al., 2014). Therefore, parameter value estimation by calibration to out-migrant estimates probably cannot capture all effects of different physical and biological conditions on juveniles. Regardless, the model's behavior was extensively reviewed to avoid errors and unrealistic hypotheses.

WRHAP represents an initial step to develop a method to understand the relative value and contribution of existing habitats to sustain winter-run Chinook salmon. As such, the model reflects the findings of previous studies on the ecological importance of each individual alternative rearing habitat in the Sacramento Valley (Sommer et al., 2001; Limm and Marchetti 2009), and combines them to more completely represent winter-run spawning, rearing and out-migration. Despite our analysis being driven by historical conditions, it illustrates the potential of WRHAP to assist in important decision-making processes for an endemic and federally endangered fish. From a water resource management standpoint, linkages between water system operations and Sacramento Valley environmental conditions (i.e., flow and temperature regimes that define habitat availability and quality) can be used to define environmental flow requirements that target specific salmonid life stages or to estimate impacts of re-operation policies on federally listed populations. Likewise, WRHAP can assist habitat restoration efforts by estimating effects of proposed recovery actions or programs of actions for winter-run Chinook and, thus, help develop optimized portfolios of habitat restoration actions. Future research will explore the effect of climate change on winter-run juvenile dynamics under proposed and defined restoration portfolios, by forcing WRHAP with available temperature and flow projections in the Sacramento Valley (Brekke et al., 2014).

## 5. Conclusions

This study developed and tested a simplified freshwater rearing phase simulation model for winter-run Chinook salmon in California's Sacramento Valley based on previously published studies, empirical field data, laboratory studies, and expert knowledge. WRHAP developed links connecting rearing habitat availability and quality with existing hydrologic conditions (i.e., flow and temperature regimes), and explained the impact of each individual habitat on juvenile development and out-migration success.

A strength of the model is its capacity to identify important knowledge gaps in observed data, with a flexible structure to allow integration of new data and functional relationships as they become available. Sensitivity analysis showed that estimates of mainstem rearing survival and growth rates, together with observations on use and residence times within high-flow habitats (i.e., floodplains and off-channel areas) greatly influence juvenile productivity and body condition. As such, further studies are required to better understand the variability and temporal dynamics of these parameters, allowing to build confidence on their related assumptions. Despite its simplicity, WRHAP provides realistic estimates of winter-run production in the Sacramento River

Valley, represents several tradeoffs reasonably between in-stream conditions and juvenile development and highlights the importance of off-mainstem habitats for the long-term persistence of winter-run Chinook salmon. This aligns with the conclusions of Lester et al. (2011) in that more complex approaches to representing environmental outcomes do not necessarily improve predictions. Finally, the modeling discussed here can aid resource managers by directly linking water management and habitat restoration actions in an effort to more clearly identify tradeoffs and effects on an endangered species.

## CRedit author statement

**Francisco J. Bellido-Leiva:** Conceptualization, Methodology, Software, Validation, Formal analysis, Data Curation, Model development, Visualization, Writing-Original Draft; **Robert A. Lusardi:** Supervision, Conceptualization, Writing-Review & Editing, Project administration, Resources; **Jay R. Lund:** Supervision, Conceptualization, Writing-Review & Editing, Funding acquisition, Project administrator, Resources.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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