

**Is there hope for winter-run Chinook? An integrated habitat-flow approach for  
species recovery**

By

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*To my family,  
for encouraging me to follow my passion  
And to my future niece,  
I cannot wait to meet you  
Os quiero mucho*

*To my granpa, Manuel Leiva,  
for always personalizing the strive for knowledge*

*To Emily,  
who has always been supportive  
and motivating throughout this journey  
I could not have made it without you*

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## Abstract

Considerable resources have been invested in freshwater restoration worldwide to improve degraded ecosystems, achieving variable degrees of success. To maximize potential ecological benefits with restoration, a prioritization process to select promising conservation plans should occur before investments. Optimization frameworks facilitate this process, allowing the structured coordination of complex watershed-scale efforts. Such frameworks require valuation methods to identify and quantify essential habitat characteristics for ecosystem health and tools to predict ecosystem response to proposed restoration efforts. This is especially important and challenging for species with complex life cycles and a broad geographic range over heterogeneous habitat, such as Pacific Chinook salmon. This research builds an optimization framework to maximize returning adult abundance for the federally endangered and endemic Sacramento River winter-run Chinook (*Oncorhynchus tshawytscha*) in California. We first developed a conceptual freshwater rearing stage model, denoted as Winter-run Habitat-based Population Model (WRHAP), based on published studies, empirical field data, laboratory studies and expert knowledge. It includes off-mainstem rearing habitats, defines rules of habitat use, and incorporates a juvenile growth module. The model was then expanded (e.g., hatchery operations, ocean-stage mortality; WRHAP-SEA), and embedded into the optimization framework to evaluate the population-level response to a set of potential restoration/recovery actions. Optimized portfolios of actions were further analyzed to estimate their effect on winter-run Chinook viability. A case study characterizing spatiotemporal off-channel dynamics, one of the most promising restoration actions identified, shows the potential of remote sensing imagery to inform environmental managers on areas and habitat features (e.g., residence time, inundation flows) for proposed restoration efforts. The results of this research show the crucial importance of 'non-critical' habitats (as defined by the Endangered Species Act) on winter-run Chinook salmon persistence, and the promising recoveries in abundance, spatial structure, diversity, and growth rate from defined optimal portfolios, which could place winter-run Chinook salmon at a low-risk of extinction. As such, this dissertation introduced a method to build robust valuation and decision-making tools to assist environmental management processes focused on species recovery.

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## CHAPTER 1

# Introduction

Historically, Pacific salmon of the genus *Oncorhynchus* were distributed along North America's west coast, from Alaska to California. The great mosaic of local habitats and environmental conditions generated a diverse portfolio of adaptations, which led to the development of unique life history traits such as spawning timing, smoltification and outmigration cues, and age and size structure. This distinctive spatiotemporal behavior branched into different salmon 'runs' (Waples 1998), with four occurring in the California Central Valley (CVV) basin, named after the season adults return to spawn (fall, late-fall, winter, and spring). The rivers draining the CVV and adjacent Cascade Range and Sierra Nevada were once renowned for their production of large number of salmon, and the presence of at least one life history form during most seasons (Yoshiyama et al. 1998). As such, a wide range of inland ecosystems were supported via the distribution of marine derived nutrients. The importance of this annual cycle was reflected in ceremonies of Central Valley Native-American communities to celebrate the prominent place of Chinook salmon in their subsistence, trade purposes and culture (e.g, Patwin, Winnemen Wintu, Nomlaki; Yoshiyama 1999, Houck 2019).

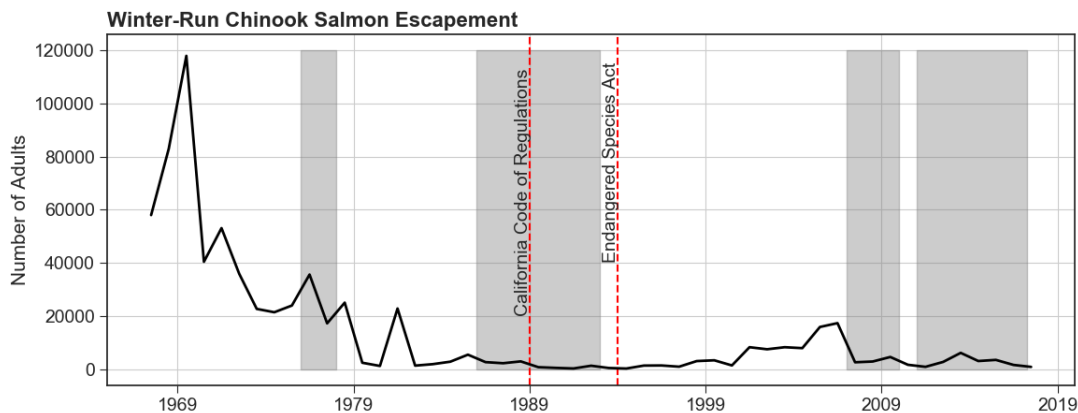


FIGURE 1.1. Winter-run Chinook salmon returning adult numbers. Grey areas represent drought periods.

The development of the CVV's extensive water management system, and its initial operation prioritizing human water uses (e.g., agricultural, urban, hydropower), produced sharp declines in Chinook salmon stocks (Yoshiyama et al. 1998, Moyle et al. 2017). These changes affected each run differently, with dramatic declines in spring- and winter-run Chinook populations (Fig. 1.1), resulting in their state and federal listings as threatened and endangered under the Endangered Species Act (ESA; California Code of Regulations 1989, Federal Register 1994, Moyle et al. 2017).



Winter-run Chinook declines have three main drivers: blockage, habitat degradation and alteration of the natural hydrograph. The construction of Shasta, Keswick and Wildcat Diversion Dams blocked the population from their historical spawning grounds, normally cold, spring-fed rivers (such as McCloud River and North Fork Battle Creek), that provided optimal temperatures for spawning and incubation during summer (Fig. 1.2). This has forced adults to spawn in unique lower-elevation, non-natal habitat between Red Bluff and Keswick Dam (NMFS 2014), responsible for its extinction vulnerability as winter-run embryos depend on cold water releases from Keswick Dam. Despite temperature related regulations established to supply suitable release temperatures (NMFS 2009), they have been insufficient to mitigate critically high temperatures during droughts, with dramatic declines in abundance after droughts (Fig. 1.1; Adams 2018, NOAA 2021). Additionally the near elimination of lateral habitat connectivity in the mid and lower watershed from leveeing floodplain habitat and water diversions have almost extirpated the population from these highly productive habitats where they evolved and to which they are adapted (Katz et al. 2017). In summary, infrastructure has blocked an estimated 1,057 miles of habitat, 48% of the original total (Yoshiyama et al. 2001).

Despite a long history of awareness of the decline and its mechanisms, recovery efforts have been insufficient to sustain ecosystems and populations, and few recovery benchmarks have been achieved (Peterson & Duarte 2020, NOAA 2021). This might be due to (i) lack of studies combining human water and land uses with explicit ecological objectives (Horne et al. 2016); (ii) the complexity of methods applied that reduce their effectiveness in environmental management (Schuwirth et al. 2019); (iii) multiple, poorly coordinated or disconnected restoration actions that lack a comprehensive framework to structure basin-scale recovery efforts (NMFS 2014); and (iv) the misrepresentation of alternative habitats (also off-mainstem habitats) on developed valuation tools (e.g., Bartholow 2004, Zeug et al. 2012, Beer et al. 2017, Hendrix et al. 2017). Extensive literature has showed the importance of off-mainstem habitats on juvenile growth and individual's probability of returning from the ocean (Katz et al. 2017), including non-natal tributaries (Phillis et al. 2018), floodplains (Sommer et al. 2001, Jeffres et al. 2008, Katz et al. 2017, Jeffres et al. 2020, Holmes et al. 2021), and off-channel areas (Maslin et al. 1996, Limm & Marchetti 2009). As such, there is a need to develop a new, comprehensive and science-based approach to restoration (Peterson & Duarte 2020) that overcomes the shortcomings of previous efforts and focus on an improved representation of alternative habitats, and communication and usefulness to environmental management and decision-making processes.

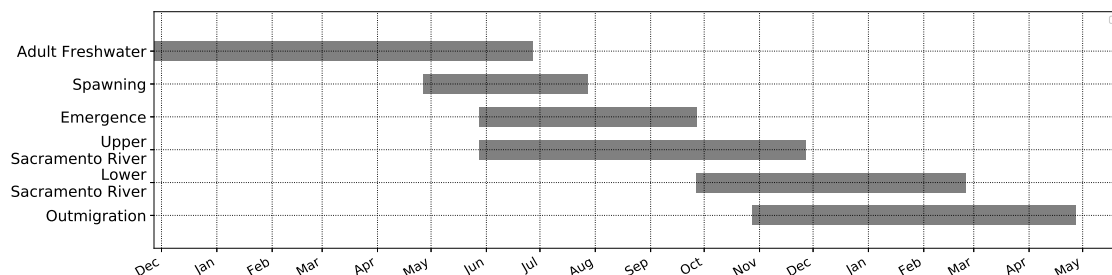


FIGURE 1.2. Winter-run Chinook salmon spatiotemporal behavior during its freshwater stage.

This research develops valuation and management tools to inform and aid decision-making regarding the recovery of the endangered and endemic winter-run Chinook Salmon. A conceptual freshwater rearing model is built in Chapter 2 to explore the importance of reported off-mainstem habitats (e.g., floodplains, tributaries and off-channel; Maslin et al. 1996, Sommer et al. 2001, Phillis et al. 2018) on juvenile development and out-migration success. The model is then expanded in Chapter 3 to a complete life-cycle model, and embedded into an optimization framework (Fig. 1.3), which structures a watershed-scale restoration effort aimed to maximize returning adults abundance. The model is used to evaluate the population-level response to a set of recovery/restoration actions, providing a metric to select optimal restoration portfolios. Chapter 4 contains a detailed analysis of off-channel habitats, a promising restoration action identified in Chapter 3, and one of the least documented rearing habitats along the Sacramento River. This analysis uses remote sensing imagery and characterizes the spatiotemporal features of off-channel habitats, providing a database to inform environmental managers on areas with greater potential for proposed restorations. Chapter 5 presents conclusions of his research and recommendations for further work. Research questions of this dissertation include:

- (*Chapter 2*) What is the effect of off-mainstem habitat availability on juvenile winter-run Chinook development? Which environmental variables (e.g., temperature, flow) are the main drivers of these effects? What is the importance of the rearing history on survival and out-migration success?
- (*Chapter 3*) How can developed linkages between habitat and out-migration success be incorporated into robust decision-making processes? Is it possible to define a set of restoration/recovery actions that reduces winter-run Chinook extinction risk?
- (*Chapter 4*) What are the spatiotemporal characteristics of off-channel habitat along the Sacramento River? Which areas can be most benefited from potential restoration efforts?

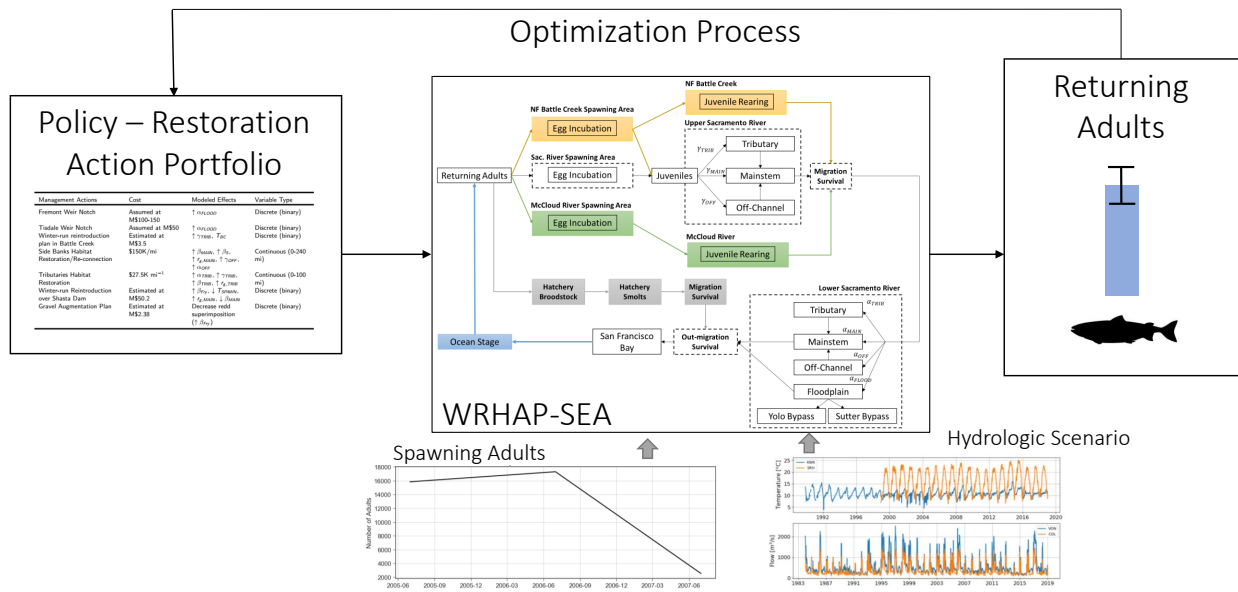


FIGURE 1.3. Sketch of the developed optimization framework for winter-run Chinook salmon recovery in Chapter 3.

The findings of this research provide a method to develop simple, yet effective, ecological and management tools to support environmental management efforts for species recovery. A special attention is given to output interpretability and the effective communication of the data used for parametrization, modeling limitations, and underlying assumptions. This, in turn, creates flexible tools that allow easy modifications in structure and assumptions, from stakeholder inputs, to reduce any possible distrust in the produced results.

## CHAPTER 2

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

### 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.

**KEYWORDS:** Sacramento River, Chinook salmon, juvenile rearing modeling, bioenergetics modeling, ecological valuation, endangered species

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### 2.1. 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

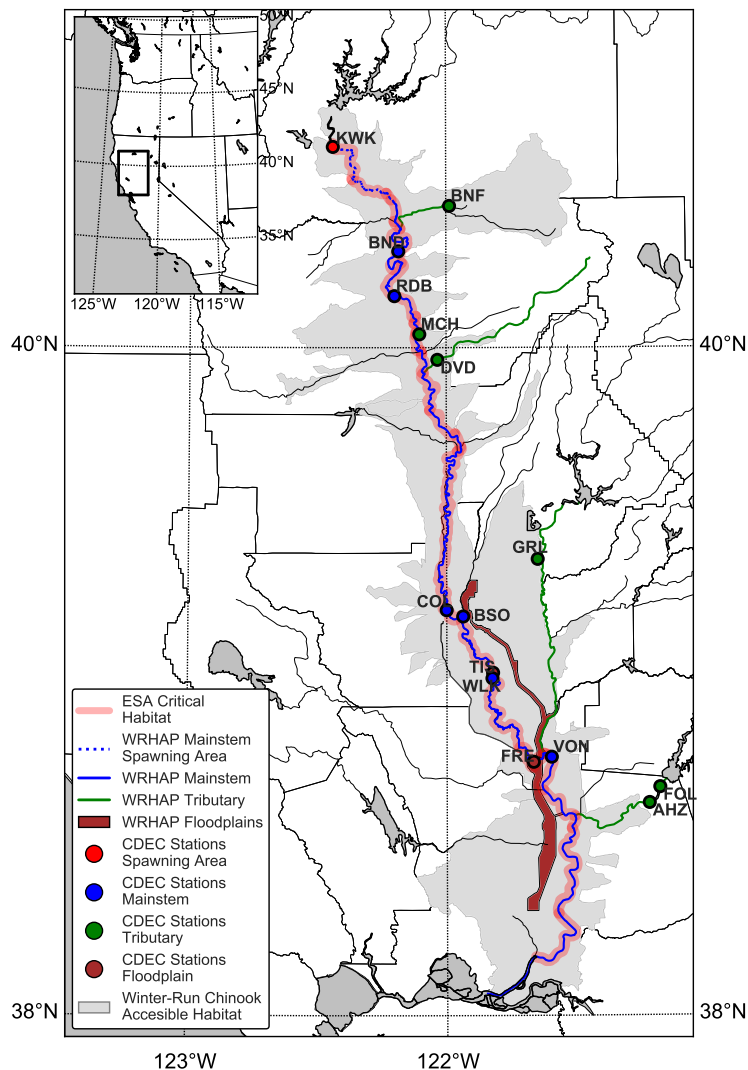


FIGURE 2.1. WRHAP spatial coverage of winter-run Chinook salmon habitat, from spawning grounds below Keswick Dam to the out-migration to the Delta.

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 the Sacramento River mainstem, Sutter and Yolo bypasses (Jones & 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 & 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 et al. 2017), 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 & 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 & 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 & 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.

## 2.2. Methods

### 2.2.1. 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. 2.1). The model structure consists of four modules arranged sequentially (Fig. 2.2), 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 2.1). Experienced

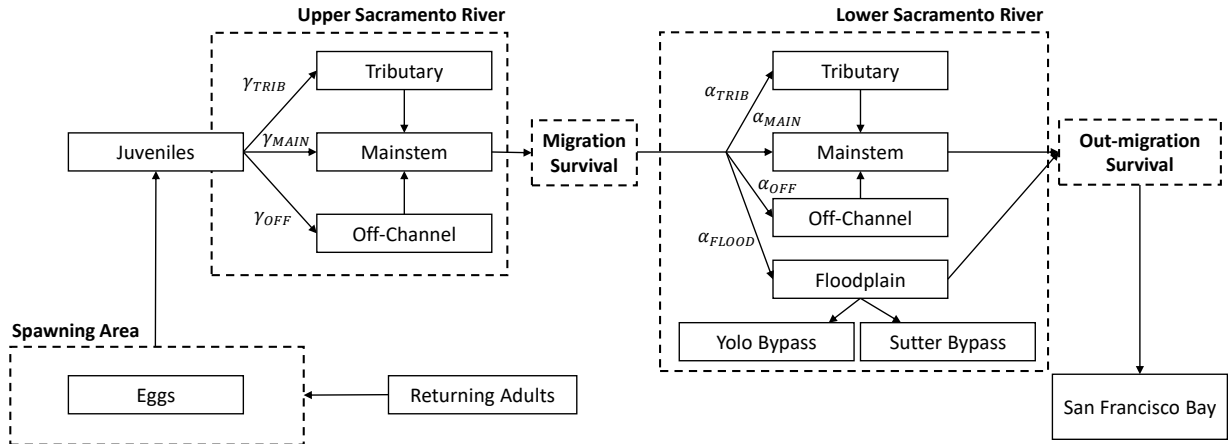


FIGURE 2.2. WRHAP links between the different spatial discretization areas and considered rearing habitats in them. Dashed lines represents each of the model modules (Table 1)

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.

## 2.2.2. Winter-run Juvenile Habitat Selection and Out-migration

### 2.2.2.1. 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 & Carrillo (2016) and Voss & 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

TABLE 2.1. WRHAP modules description and data requirements. CDEC stations used in the analysis are represented in Figure 2.1. A detailed structure of the module elements and links between them is shown in Figure 2.2.

Modules	Spatial Extent	Time Period	Description	Data Requirements
Spawning Area	Keswick Dam to Red Bluff	Mid-Apr to mid-Sep	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. R.	Keswick Dam to Knights Landing	Sep to Dec-Feb	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. R.	Through Knights Landing	Dec-Feb	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. R.	Knights Landing to Chipps Island	Dec-Feb to Feb/Apr	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)



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  $T_{KWK,d}$  (downstream Keswick Dam). The model is parametrized with  $T_{crit}$ , the temperature below which there is no temperature-related mortality and  $b_T$ , the slope at which mortality rate increases with temperature.

$$(2.1) \quad h_d = b_T \max(T_{KWK,d} - T_{crit}, 0)$$

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.

$$(2.2) \quad \beta_T = \sum \left[ \prod_{d=1}^n e^{-h_d} \right] / N_{redds}$$

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:

$$(2.3) \quad P_{J,0} = \frac{\beta_{Fry,N}}{1 + N_{spawn} r_{fem} / K} N_{spawn} r_{fem} f \beta_T$$

where  $K$  is the capacity parameter of the Beverton-Holt term. Parameter values, description and sources are summarized in Table 2.2.

#### 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 tributaries (e.g., Battle, Mill and Deer Creeks) are primary non-natal rearing habitats (Phillis et al. 2018). Suitable habitat availability ( $A_{TRIB}$ ,  $m^2$ ) 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 2017 *a,b*) 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

$$(2.4) \quad \gamma_{TRIB} = \frac{[A_{TRIB,MC} h_{TRIB,MC} + A_{TRIB,DC} h_{TRIB,DC} + A_{TRIB,BC}] \rho_{TRIB,US}}{P_{J,0}}$$

where  $\rho_{TRIB,US}$  [# fish/ $m^2$ ] is the juvenile density at tributary habitats (Table 2.2) 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 & 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 ( $Q_{SAC}$ ; Figure 2.3) 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 & 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  $\sim 3$  juveniles per unit of suitable habitat ( $\rho_{OFF,US}$ ,  $m^2$ ) (Bartholow 2004, Hendrix et al. 2017).

$$(2.5) \quad \gamma_{OFF} = \frac{4046.86 A_{OFF}(Q_{SAC}) \rho_{OFF,US}}{P_{J,0}}$$

The model assumes that juveniles rear in one of two alternative 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:

$$(2.6) \quad P_{J,k} = \gamma_k P_{J,0} (\beta_{MAIN}^{US})^{d^{US} - d_k^{US}} (\beta_k)^{d_k^{US}} \left[ 1 - \frac{1}{1 + e^{-b_J(T_k - T_{50,J})}} \right]^{d_k^{US}/7} \left[ 1 - \frac{1}{1 + e^{-b_J(T_{MAIN} - T_{50,J})}} \right]^{(d^{US} - d_k^{US})/7}$$

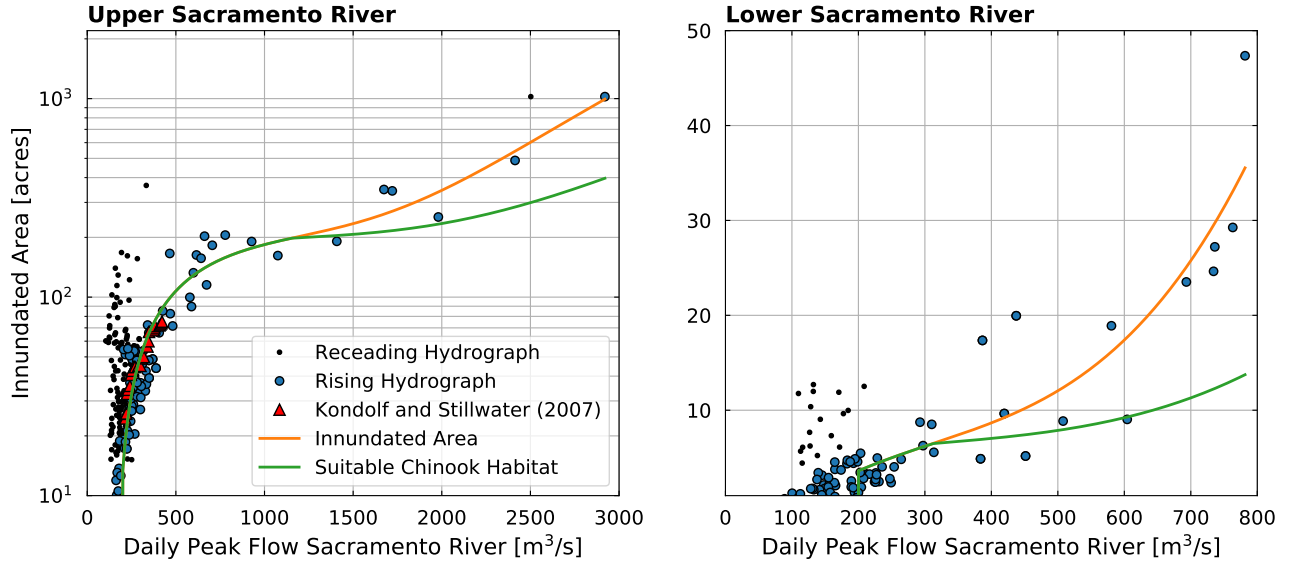


FIGURE 2.3. Available off-channel habitat computed from remote sensing imagery as a function of daily peak flows. Red triangles represent field surveys by Kondolf & Stillwater Sciences (2007).

where  $d^{US}$  is the residence time [days] at the upper Sacramento,  $\gamma_k$  is the proportion that reared in habitat  $k$ ,  $\beta_k$  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.

### 2.2.2.3. 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 m<sup>3</sup>/s 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 Fultons 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. 2.7), 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.

$$(2.7) \quad \log(\beta_{M,k}) = 3.9031Q_{out}/1000 + 1.8680K_k - 6.1049$$

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

$$(2.8) \quad P_{J,k}^s = \beta_{M,k}[Q_{out}, K_k]P_{J,k}$$

### 2.2.2.4. Lower Sacramento 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 et al. 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 ( $\sim$  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.

$$(2.9) \quad \alpha_{flood} = \rho_{Sutter} + (1 - \rho_{Sutter})\rho_{Yolo}$$

where

$$(2.10) \quad \rho_{Sutter} = \frac{Q_{TIS}}{Q_{TIS} + Q_{WLK}} \quad \rho_{Yolo} = \frac{Q_{FRE}}{Q_{FRE} + Q_{VON}}$$

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 3 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:

$$(2.11) \quad P_{J,ki} = \alpha_i P_{J,k}^s (\beta_{MAIN}^{LS})^{d^{LS} - d_i^{LS}} (\beta_i)^{d_i^{LS}} \left[ 1 - \frac{1}{1 + e^{-b_J(T_i - T_{50,J})}} \right]^{d_i^{LS}/7} \left[ 1 - \frac{1}{1 + e^{-b_J(T_{MAIN} - T_{50,J})}} \right]^{(d^{LS} - d_i^{LS})/7}$$

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 2.2.

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 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 2.2),

$$(2.12) \quad P_{J,out} = \beta_{S,Yolo} \sum_k P_{J,kFLOOD} + \beta_{S,Delta} \sum_{i \neq FLOOD} \sum_k P_{J,ki}$$

## 2.2.3. Winter-run Juvenile Development

### 2.2.3.1. 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 & Marine (1991) showing millimeter deviation from this value.

### 2.2.3.2. 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, personal communication).

TABLE 2.2. 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)	
	$T_{KW,K,d}$	[°C]	1	Daily temperature downstream Keswick Dam	Recorded value	CDEC at station KWK	
	$N_{redds}$	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 & Carrillo (2016); Voss & Poytress (2020)	
	$r_{fem}$	AV	3	Proportion of returning adults which are females	Field data	Poytress & Carrillo (2016); Voss & Poytress (2020)	
	$\beta_{FR,N}$	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.	$T_{50,J}$	20 [°C]	6,10	Water temperature that decreases juvenile survival by a 50%	Lab Study	USFWS (1999)
	River	$b_J$	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 (Limn & Marchetti 2009)	
$PREYED$		3760 [J/g]	12	Mean prey energy density used in the Fish Bioenergetics Model 4.0	Field data	Luecke & Brandt (1993); Tiffan et al. (2014); Haskell et al. (2017)	
Upper Sac.		$\beta_{MAIN}$	0.975	6	Daily rearing survival at the Sacramento mainstem	Calibrated parameter	Adapted from Peterson & Duarte (2020)
River		$\beta_{TRIB}$	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)
		$A_{P,TRIB,BC}$	20,640 [m <sup>2</sup> ]	4	Available juvenile rearing habitat at Battle Creek	Model output	Appendix B; ICF International (2016)
		$d_{OFF}^{US}$	7-12 [days]	6,14	Residence time at off-channel habitats	Field and remote sensing data	CDEC Sac. River stations; LandsAT Multispectral Scanner
		Lower Sac.	$d_{TRIB}^{US}$	28-40 [days]	6,14	Residence time at tributary habitats (>28 days)	Assumption
	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)
River	$\beta_{TRIB}$	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); Iglecias et al. (2017)	
	$\beta_{S,Y,olo}$	91 [%]	11, 16	Migration survival to Chipps Island through Yolo Bypass	Field study	Takata et al. (2017); Hendrix et al. (2017)	
	Lower Sac.	$d_{OFF}^{LS}$	15 [days]	10,15	Residence time at off-channel habitats	Remote sensing data	LandsAT Multispectral Scanner
	River	$d_{TRIB}^{LS}$	28-40 [days]	10,15	Residence time at tributary habitats (>28 days)	Assumption	Based on values reported by Phillis et al. (2018)

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, 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),

$$(2.13) \quad \Delta G = C - (R + A + SDA + F + U)$$

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),

$$(2.14) \quad C = pC_{max}$$

where the maximum consumption ( $C_{max}$ ) is a function of temperature and juvenile weight. Table 2.3 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%), Chiromidae (~2%) and Copepods (~3%) with energy densities of 3960 J/g, 3248 J/g and 4500 J/g, respectively (Luecke & 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:

$$(2.15) \quad W_k^{US} = W_0(r_{g,MAIN})^{d^{US}-d_k^{US}}(r_{g,k})^{d_k^{US}}$$

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:

$$(2.16) \quad W_{k,i}^{LS} = W_k^{US}(r_{g,MAIN})^{d^{LS}-d_i^{LS}}(r_{g,i})^{d_i^{LS}}$$

### 2.2.3.3. 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 ( $W_{ki}^{LS}$ ).

$$(2.17) \quad B_{out} = \beta_{S,Yolo} \sum_k P_{J,k,FLOOD} W_{kFLOOD}^{LS} + \beta_{S,Delta} \sum_{i \neq FLOOD} \sum_k P_{J,ki} W_{ki}^{LS}$$

TABLE 2.3. Fish bioenergetics model parameter values and sources (defined in Deslauriers et al. (2017), for Chinook Salmon)

Param.	Value	Source	Param.	Value	Source
CA	0.303	Deslauriers et al., 2017	RTL	25	Deslauriers et al. (2017)
CV	-0.275	Deslauriers et al. (2017)	RK1	1	Deslauriers et al. (2017)
CQ	4.97	Deslauriers et al. (2017)	RK4	0.13	Deslauriers et al. (2017)
CTO	15	Stewart & Ibarra (1991)	RK5	0	Deslauriers et al. (2017)
CTM	20.93	Plumb & Moffitt (2015)	ACT	9.7	Deslauriers et al. (2017)
CTL	24.05	Plumb & Moffitt (2015)	BACT	0.0405	Deslauriers et al. (2017)
CK1	0.36	Stewart & Ibarra (1991)	SDA	0.172	Deslauriers et al. (2017)
CK4	0.53	Plumb & Moffitt (2015)	UA	0.0314	Deslauriers et al. (2017)
RA	0.00264	Deslauriers et al. (2017)	UB	0.58	Deslauriers et al. (2017)
RB	-0.217	Deslauriers et al. (2017)	UG	-0.299	Deslauriers et al. (2017)
RQ	0.06818	Deslauriers et al. (2017)	FA	0.212	Deslauriers et al. (2017)
RTO	0.0234	Deslauriers et al. (2017)	FB	-0.222	Deslauriers et al. (2017)
RTM	0	Deslauriers et al. (2017)	FG	0.631	Deslauriers et al. (2017)

#### 2.2.4. 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 & Lemaître 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 ( $= 2n(p+1)$ ) model evaluations to calculate the first and total-order sensitivity index and their 95% confidence interval, using the SALib library in Python (Herman & 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.

## 2.3. Results

### 2.3.1. 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 & 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. 2.4d), generally lying within their 90% confidence interval (Fig. 2.4a), 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 & Titus 1998, 2000*a,b,c*, Vincik et al. 2006, Roberts 2007, Roberts et al. 2013, 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. 2.4e), 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. 2.4b). Finally, model output was compared with abundance estimates at Chipps Island (Pyper, Garrison, Cramer, Brandes, Jacobson & Banks 2013, IEP et al. 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, Garrison & Cramer 2013). These values were also considered constant through time as recommended by Pyper, Garrison & Cramer (2013). 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. 2.4f), as simulated values generally lie within the uncertainty bounds (Fig. 2.4c), 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 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. 2.4bc), 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 & Titus 1998, 2000*a,b,c*, Vincik et al. 2006, Roberts 2007, Roberts et al. 2013, Julienne 2016, McKibbin 2016, Columbia Basin Research 2018) and Chipps Island (IEP et al. 2020). Since WRHAP computes individual weight, an empirical relationship ( $L \text{ (mm)} = 48W^{0.3} \text{ (g)}$ ; 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 ( $\sim 65$  mm) were larger than the range of shortest captured



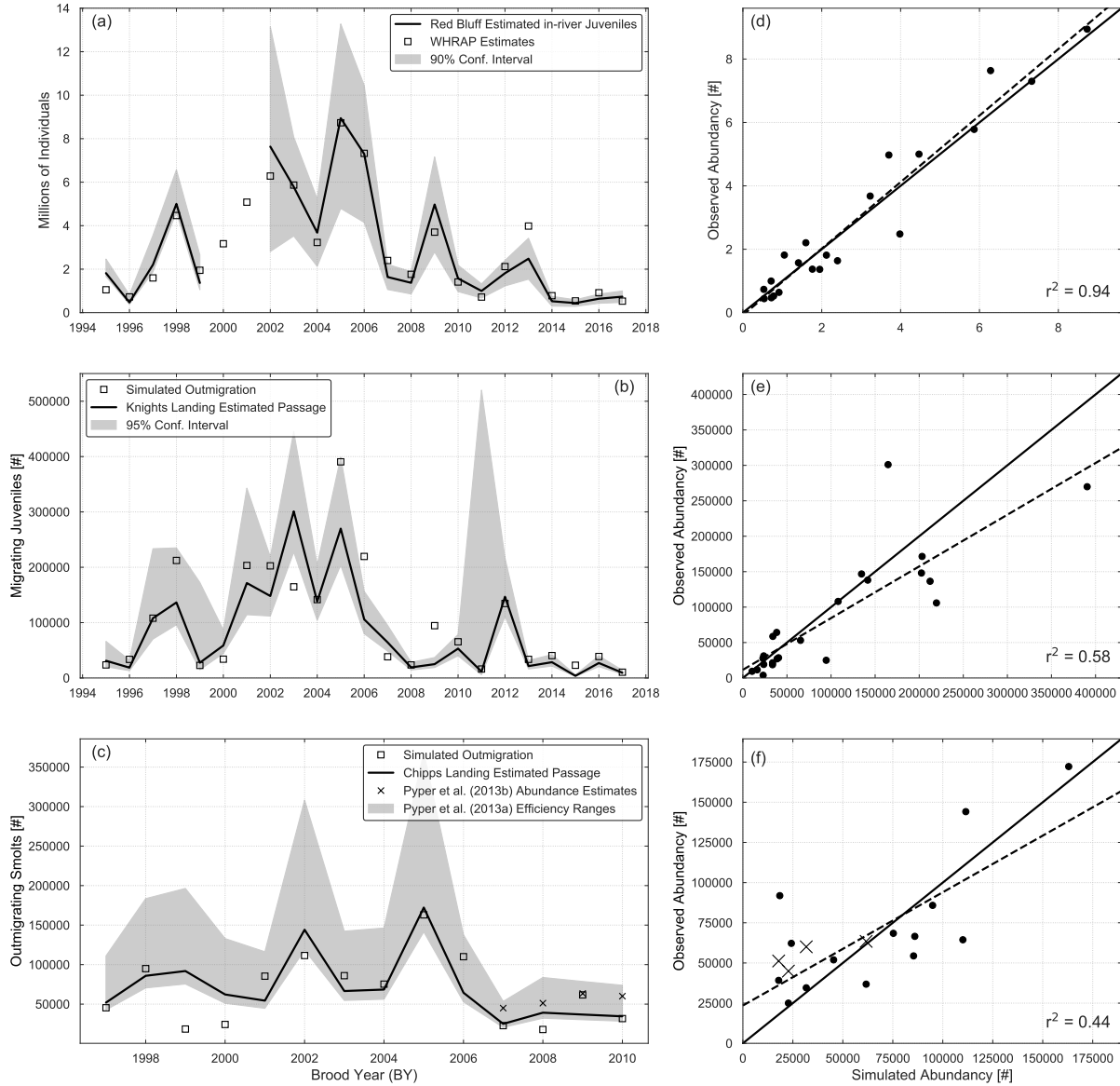


FIGURE 2.4. (a) Time series comparison of WRHAP estimates of in-river juvenile production with Red Bluff Rotary Trap records and its 90% confidence interval (grey area); (b) Time series of simulated juvenile migration numbers compared to observed counts at Knights Landing Rotary Trap and its 95% confidence interval (grey 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, Garrison & Cramer 2013); (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, Garrison & Cramer 2013) of smolt abundance at Chipps Island Midwater Trawl.

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. 2.5). 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).

### 2.3.2. 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. 2.6), 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 experiments 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. 2.6), which agree with existing conditions (i.e., lower prey density). In contrast, Knaggs Ranch was disconnected from the Sacramento River during the

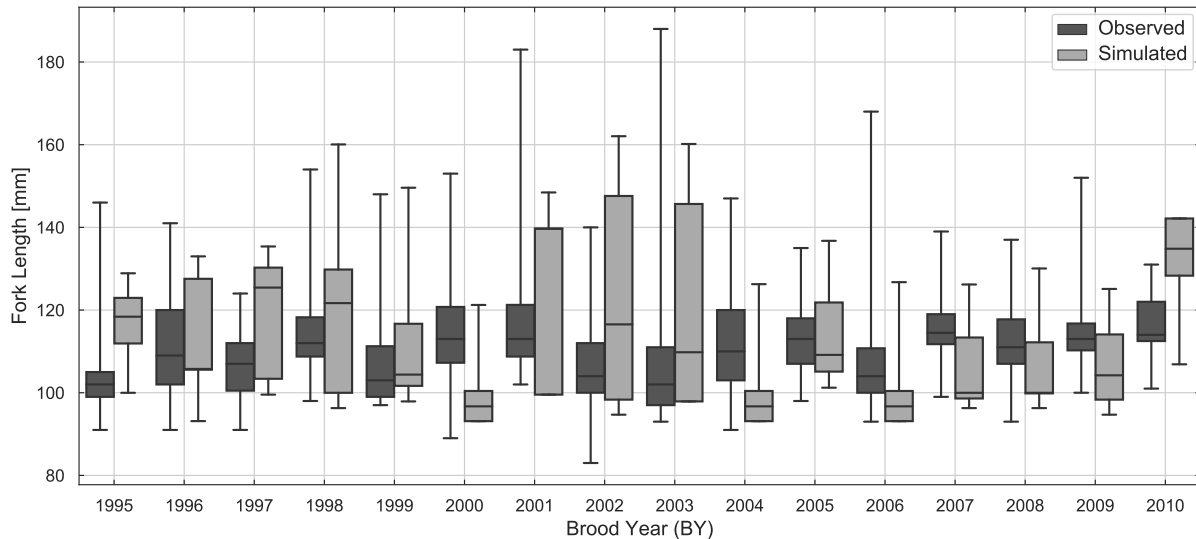


FIGURE 2.5. Observed and simulated fork length distributions at Chipps Island for out-migrating smolts to the San Francisco Bay

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, 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. 2.6). 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.

### 2.3.3. 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 2.4). 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

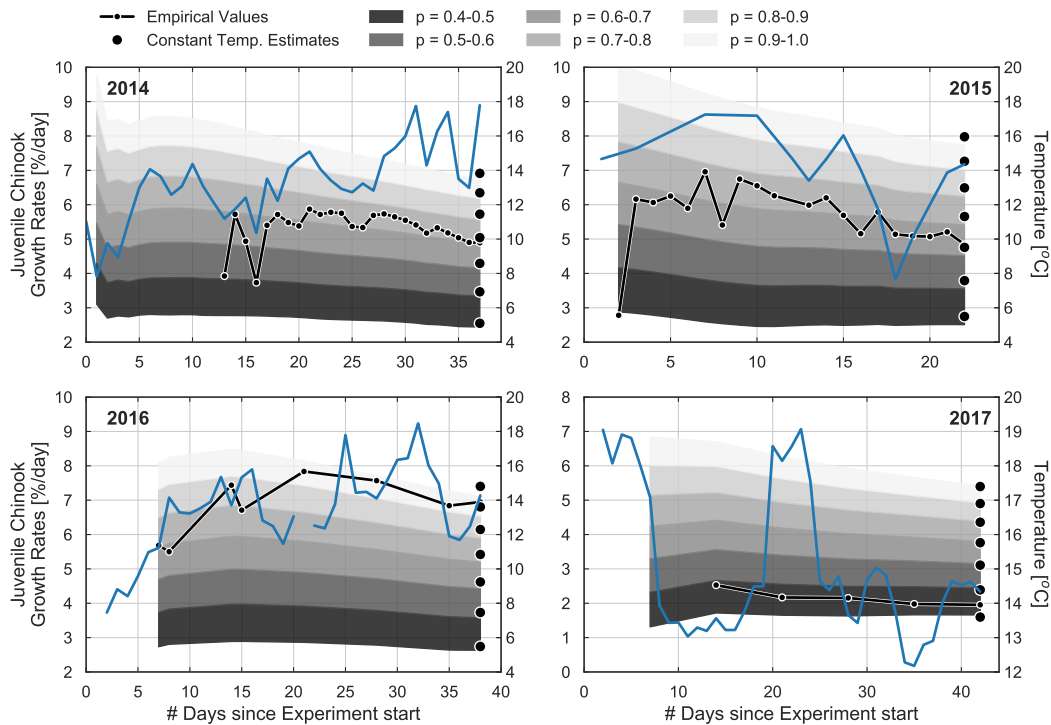


FIGURE 2.6. Observed growth of fall-run Chinook at Knags Ranch for years 2014-2017 (Katz, unpublished data). The blue line represents recorded water temperature.

periods ( $\sim 77\%$  of total rearing time, on average; Table 2.5), 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. 2.2). Such rearing behavior coupled with the positive relationship between fish condition (Fultons  $k$ ) and migration success ( $\beta_M$ ; Eq. 2.7) 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 et al. 1996, Limm & Marchetti 2009). Nevertheless, the latter and off-channel habitat use ( $\gamma_{FLOOD}$ ) 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 2004, 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 ( $d_{FLOOD}^{LS}$ ) 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  $d_{FLOOD}$  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 2.5). 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. 2.7), and smolt numbers (second highest rank for total out-migrants in Table 2.4). 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 et al. 1996, Limm & 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 2.4). As such, its total-effect is nearly two-, four- and ten-fold less than off-channel, mainstem and floodplain areas, respectively.

TABLE 2.4. First order ( $S_{1i}$ ) 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		Param	Range	Avg. Smolt Biomass	
		$S_{1i}$	$S_{Ti}$			$S_{1i}$	$S_{Ti}$
$\beta_{MAIN}$ [%/day]	97.3-98.7	0.505	0.584	$r_{g,FLOOD}$ [%/day]	2.0-8.5	0.120	0.668
Rearing survival at mainstem		(0.001)	(0.0004)	Growth rate at floodplains		(0.004)	(0.067)
$r_{g,MAIN}$ [%/day]	0.5-3	0.103	0.135	$d_{FLOOD}$ [days]	21-90	0.0955	0.562
Growth rate at mainstem		(0.0008)	(0.0001)	Residence time at Floodplains		0.003)	(0.008)
$\beta_{Fry,N}$ [%]	19-38	0.093	0.126	$r_{g,MAIN}$ [%/day]	0.5-3	0.070	0.284
Egg-to-fry survival with no temperature effects		(0.0008)	(0.0001)	Growth rate at mainstem		(0.0054)	(0.0068)
$r_{g,TRIB}$ [%/day]	1-5.5	0.023	0.041	$\alpha_{FLOOD}$ [%]	0-100	0.0084	0.172
Growth rate at tributaries		(0.0024)	(0.0013)	Prop. of juveniles rearing at floodplains		(0.0012)	(0.0104)
$r_{g,OFF}$ [%/day]	2-8.5	0.019	0.040	$r_{g,OFF}$ [%/day]	2-8.5	0.019	0.130
Growth rate at off-channel habitat		(0.0037)	(0.002)	Growth rate at off-channel habitat		(0.0026)	(0.009)
$\gamma_{OFF}$ [%]	0-100	0.015	0.039	$d_{OFF}^{US}$ [days]	10-40	0.0074	0.078
Prop. of juveniles rearing at Upper Sac. off-channel areas		(0.0051)	(0.0024)	Residence time at off-channel habitat along Upper Sac.		(0.0000)	(0.0000)
$d_{OFF}^{US}$ [days]	10-40	0.019	0.036	$r_{g,TRIB}$ [%/day]	1-5.5	0.0045	0.065
Residence time at off-channel habitat along Upper Sac.		(0.012)	(0.011)	Growth rate at tributaries		(0.0011)	(0.0016)
$\beta_{S,Delta}$ [%]	60-100	0.021	0.031	$\alpha_{TRIB}$ [%]	0-100	0.0028	0.036
Outmigration survival through the Delta		(0.0133)	(0.0004)	Prop. of juveniles rearing at Lower Sac. tributaries		(0.0011)	(0.002)
$\gamma_{TRIB}$ [%]	0-100	0.012	0.029	$\gamma_{OFF}$ [%]	0-100	-0.0001	0.022
Prop. of juveniles rearing at Upper Sac. tributaries		(0.0015)	(0.0003)	Prop. of juveniles rearing at Upper Sac. off-channel areas		(0.0006)	(0.0002)
$d_{TRIB}^{US}$ [days]	10-50	0.015	0.025	$\alpha_{OFF}$ [%]	0-100	-0.001	0.020
Residence time at tributaries along Upper Sac.		(0.0013)	(0.0003)	Prop. of juveniles rearing at Lower Sac. off-channel areas		(0.0004)	(0.0001)

## 2.4. Discussion

WRHAP outputs result from mechanistic understanding of fish survival and growth and agree reasonably well with observed records of winter-run abundances (Fig. 2.4). 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 2014). 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 (NRC 2014). 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 ( $S_{Ti}$ ; Table 2.4), 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 & Marchetti 2009) and only three brood years (2004-2006) of otolith growth data were available for estimating tributary rearing (Phillis et al. 2018). 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. 2018). 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 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 & Marchetti 2009). Other modelling 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. 2.7). As summarized in Table 2.5, floodplains contribute the second most to total simulated out-migration biomass, approximately 29% (~30% less than mainstem; Fig. 2.7), 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. 2.7). 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

TABLE 2.5. 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

	<b>Total</b>	<b>Mainstem</b>	<b>Tributaries</b>	<b>Off-Channel</b>	<b>Floodplain</b>
Out-migrants	1,132,364	100% (21.9%)	45.1%	33.9%	17.5%
Biomass [kg]	19303	41.3%	19.9%	9.9%	28.9%
Avg. Rearing Time [days]	167	78.1%	11.2%	3.3%	7.4%

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 2.4). 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. 2.6). 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. 2.7). 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 2.5). However, off-channel habitats are active for shorter durations ( $\sim$  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 2.5). 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 et al. 1996). This tradeoff is also shown by their Sobol total-order indices, ranking off-channel growth and residence time over tributaries (Table 2.4). 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 2.4). 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 2.4). 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 ( $\sim +7\%$ ) 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 2.3.3; Table 2.4), 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 Chipps Island, with longer residence times at the lower Sacramento River producing fewer smolts in better condition and increasing and individuals probability of returning as an adult.

Modelling, 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. 2.4). If these conditions were persistent across several years, warm water releases from Shasta Reservoir (associated with cold

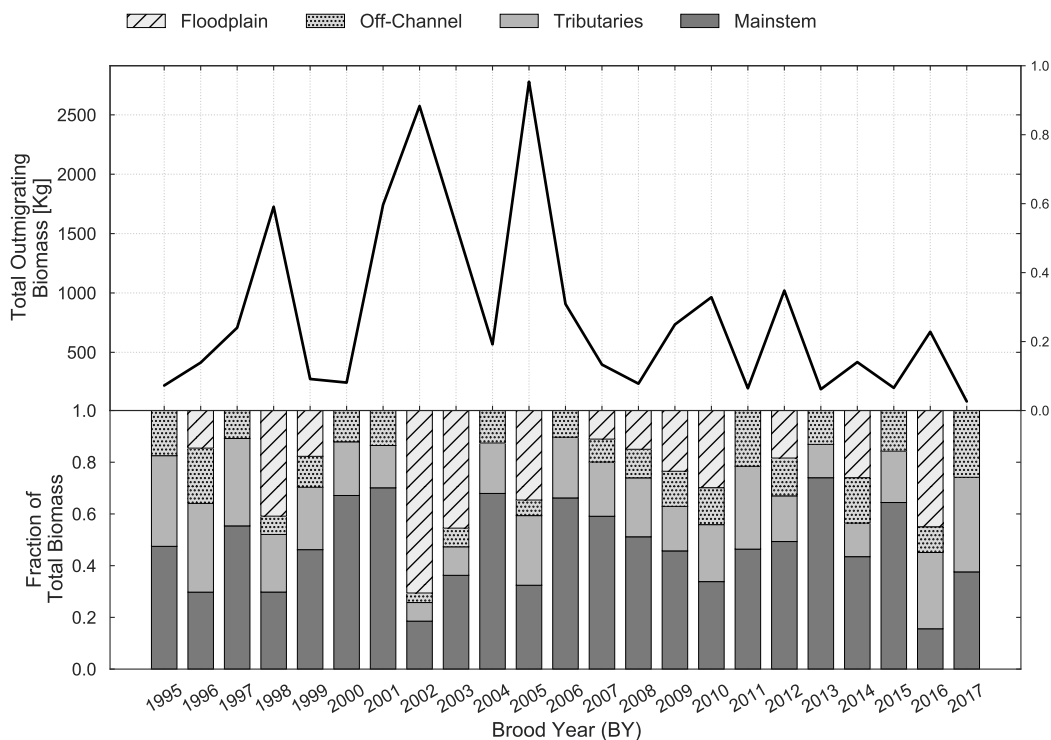


FIGURE 2.7. Simulated out-migrating biomass and fraction generated in each available rearing habitat



pool depletion) significantly increase egg-to-fry mortality (Johnson & 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 2.4). 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 2.2). 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, Pyper, Garrison & Cramer 2013, 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 models behavior was extensively reviewed to avoid errors and unrealistic hypotheses.

WHRAP 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 & 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 (Maurer et al. 2014).

## 2.5. Conclusions

This study developed and tested a simplified freshwater rearing phase simulation model for winter-run Chinook salmon in Californias 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.

## CHAPTER 3

# Optimized conservation and habitat restoration portfolios for winter-run Chinook salmon (*Oncorhynchus tshawytscha*) based on a Life Cycle Simulation Model.

### Abstract

During the last two decades, extensive freshwater restoration efforts have been implemented worldwide to improve degraded ecosystem services (e.g., spawning gravels, nutrient retention, biodiversity), requiring the investment of considerable resources. Optimization frameworks are important to coordinate and structure complex watershed-scale efforts, prioritizing conservation plans before investments are made to maximize the potential to achieve significant ecological benefits. This paper focuses on the federally endangered and endemic Sacramento River winter-run Chinook (*Oncorhynchus tshawytscha*) by developing an optimization framework that defines optimal restoration portfolios which maximize returning adults abundance under alternative investment scenarios. The impact of each considered restoration action on winter-run Chinook was simulated using an expansion on the Winter-run Habitat Based Population Model (WRHAP), denoted as WRHAP-SEA. Additional modules were developed that incorporate hatchery operations, describe reintroduction programs, and define ocean-stage survival based on smolt development along the Sacramento River watershed. Defined optimal portfolios presented promising recoveries in adult spawner numbers, spatial structure, diversity, and growth rate, which could potentially place winter-run Chinook at a low-risk of extinction, according to the Viable Salmonid Population (VSP) guidelines. This effort demonstrates the importance of the reintroduction at Battle Creek, off-channel restoration, and floodplain connection enhancement on advancing winter-run Chinook towards a viable status. The defined framework shows its utility to explore relationships between an ample set of recovery/restoration actions applied on a watershed-scale, and to define optimal portfolios to assist water/environmental management and decision-making processes focused on species recovery.

**KEYWORDS:** Sacramento River, winter-run Chinook salmon, habitat restoration, heuristic optimization, reintroduction programs, endangered species, WRHAP

### 3.1. Introduction

Historically, Pacific salmon in the genus *Oncorhynchus* spawned in rivers and streams from Alaska to California. Their adaptations to diverse local environmental conditions led to the development of unique life history traits (e.g., age and size structure, juvenile and ocean migration patterns, spawning timing), which branched into distinctive salmon ‘runs’ (Waples 1998). Four runs occur in the California Central Valley (CCV) basin, named for the season adults return to spawn (fall, late-fall, winter, and spring). Their geographic and temporal distribution resulted in

the presence of at least one life history form during most seasons and supported inland ecosystems via the distribution of marine derived nutrients. The importance of this annual cycle was included in ceremonies of Native-American communities to celebrate the prominent place of Chinook salmon in their culture (e.g., Patwin, Nisenan, Nomlaki, Maidu, Yana, Achumawi, Winnemen Wintu; Yoshiyama 1999, Houck 2019). This status, as a source of livelihood, was no less important to the immigrant European and Euro-American fishers who came later. Nowadays, its significance continues in several areas with an overall economic impact of \$1.56 billion for the state of California (2012-2016 season aggregate), combining commercial and recreational fisheries (Ransom 2001, PFMC 2017, NMFS 2018). Thus, anadromous Pacific salmonids play crucial roles in the ecology of the CCV, but also in culture, spiritual, and economic activity of indigenous and local communities.

The construction of the CCV's extensive water management system and its operation for agricultural and urban water supply, and hydropower has precipitated strong declines in Chinook salmon stocks (Yoshiyama et al. 1998, Moyle et al. 2017). These changes have affected each run differently. Although fall-run Chinook salmon still support a significant commercial fishery (Jager & Rose 2003), spring- and winter-run Chinook salmon have been extirpated from their historical natal habitat in the San Joaquin River and headwaters of the Sacramento River and its tributaries. Strong declines in these populations have resulted in state and federal listings as threatened and endangered, respectively, under the Endangered Species Act (ESA; California Code of Regulations 1989, Federal Register 1994, Moyle et al. 2017). Winter-run Chinook population declines were initially driven by the closure of Shasta and Keswick Dams, forcing them to spawn in lower-elevation, non-natal habitats between Red Bluff and Keswick Dam (NMFS 2014). This unique, non-natal spawning location drives extinction vulnerability, since winter-run embryos are the most sensitive life stage to water temperature and rely exclusively on cold water releases from Keswick and Shasta Reservoirs. Although temperature-related regulations to govern dam operations were established to protect endangered winter-run salmon eggs (NMFS 2009), such regulations have been insufficient to mitigate critically high temperatures during drought (Adams 2018, NOAA 2021). Additionally, the near elimination of floodplain and off-channel habitat in the lower watershed (due to levee construction and water diversions) further limits development during the winter-run early life history and jeopardizes survival during out-migration and marine stages (Claiborne et al. 2011, Iglesias et al. 2017, Bellido-Leiva et al. 2021).

To address widespread population declines, habitat restoration efforts have become popular across many watersheds to mitigate historical and current habitat degradation (National Research Council 1992; Cowx and Welcomme 1998). For instance, \$14 to \$15 billion were spent on freshwater habitat restoration in the USA since 1990, averaging roughly \$1 billion/year (Bernhardt et al. 2005). To stabilize and recover winter-run Chinook salmon populations, the National Marine Fisheries Service (NMFS) developed a recovery plan with priority actions (NMFS 2014, NOAA 2016, 2021). The latter focused on reintroduction of winter-run Chinook to historical spawning habitat above Shasta Reservoir and along the North Fork of Battle Creek (NOAA 2016, Lusardi & Moyle 2017). The recovery plan included extensive restoration and management actions, based on a threat assessment that targeted habitat quantity and quality specific to winter-run Chinook life stages (Appendix B; NMFS 2014). Sacramento River winter-run Chinook adults migrate during winter and spawn in late spring and early summer below Keswick Dam after reaching maturity typically after two years in the ocean (Moyle 2002). Juvenile rearing and development occur for 5-10 months in freshwater before outmigration to the ocean (Moyle 2002). The latter is triggered by high flows, typically over 400 m<sup>3</sup>/s at Wilkins Slough (del Rosario et al. 2013). Winter-run Chinook exhibit a diverse rearing history, which includes habitats in the Sacramento River mainstem and adjacent off-channel locations (Limm & Marchetti 2009), including Sutter and Yolo bypasses (Jones

& Stokes Associates 1993, Sommer et al. 2001). More recently, otolith microchemistry suggests that winter-run Chinook also rear in non-natal Sacramento River tributaries including Deer, Mill and Battle Creeks, and the Feather and American rivers (Phillis et al. 2018). As such, proposed recovery actions include gravel augmentation to improve existing spawning grounds, Sacramento River side-bank habitat restoration, and re-connection of the Sacramento River to off-channel habitats (NMFS 2014). However, federal recovery plans are guidance documents, with no legal obligation beyond existing legal requirements to implement by any public or private party (NMFS 2014).

Optimization procedures have been widely used in conservation management to support and inform decision-making, improving both efficiency and transparency (Sarkar et al. 2006, Maier et al. 2014, Horne et al. 2016). Although criticism of such analyses arise from the complexity of environmental systems (Rizzoli & Young 1997), many challenges in ecosystem representation (e.g., spatial coverage, randomness, complexity of interactions) also exist in other fields that have benefited from optimization. Further, few studies have combined formal optimization with salmon population modeling to evaluate potential linkages between habitat restoration, recovery actions, and salmon response. Of these, most have focused on reservoir re-operation to benefit salmon (Sale et al. 1982, Cardwell et al. 1996, Jager & Smith 2008, Horne et al. 2016, Adams et al. 2017). Bartholow et al. (1995) and Jager & Rose (2003) proposed the first reservoir optimizations coupled with salmon population models, to better understand tradeoffs among impaired flow regimes, habitat, and population dynamics. Fish population optimization has expanded in other contexts. For instance, Paulsen & Wernstedt (1995) paired simulation and optimization to minimize costs of salmon recovery actions in the Columbia River Basin and analyzed the costs and effectiveness of different restoration alternatives simultaneously, using simulation models to explore impacts on fish survival. Watanabe et al. (2006) optimized riparian vegetation allocation to decrease water temperatures and protect endangered salmonid species under a budget constraint, with the decision space limited to a single restoration strategy. A similar approach was followed by Null & Lund (2012), which maximized the number of out-migrating Coho salmon on the Shasta River in northern California as a response of combined restoration alternatives, subject to budget constraints. This approach combined a simple fish population model with flow and water quality modeling to explore management strategies and enlarged the solution space to a portfolio of restoration activities affecting flow and temperature conditions. Peterson & Duarte (2020) represents the most recent optimization effort for Chinook salmon in the CVV, using a complex life-cycle model to evaluate alternative restoration alternatives. However, an economic analysis was not included, and the authors focused exclusively on population recovery.

Here we describe an optimization model that maximizes winter-run Chinook salmon production as constrained by restoration costs and subject to suitable habitat quantity and quality, where restoration actions improve instream rearing, flow and temperature conditions. We use a modified version of the Winter-Run Habitat based Population model (WRHAP; Bellido-Leiva et al. 2021) to simulate major linkages between restoration actions and smolt production.

## 3.2. Methods

### 3.2.1. Restoration Strategies

Restoration actions focused on Chinook salmon along the Sacramento River Valley normally include flow quantity and temperature during critical periods, minimization of fish entrainment, such as screening water diversions, fish passage improvement to allow access to upstream or side channel habitats, habitat restoration and reintroduction programs (Kondolf 1998, Roni et al. 2010,

Wohl et al. 2015, Peterson & Duarte 2020). The work described here focuses on the latter three, defining a set of candidate management actions that target each freshwater stage of the winter-run life cycle (see Table 3.1). These restoration actions were consistent with the recovery plan and a set of priority actions defined by the National Marine Fisheries Service (NMFS 2014, NOAA 2016). To facilitate comparison between management actions, we compiled information on project costs and anticipated improvements from their implementation, using several sources described as follows, and summarized in Table 3.1.

### 3.2.1.1. Fremont Weir notch

Modification of levees via notching have been implemented in several large rivers to restore river-floodplain habitat connectivity and desirable ecosystem and geomorphic processes (Zhang & Mitsch 2007, Wohl et al. 2015). California’s Department of Water Resources (DWR) has proposed

TABLE 3.1. Summary of candidate actions considered with its associated cost and description. Variable type describes its mathematical representation in the optimization algorithm. Abbreviations used for each action are within square brackets.

<b>Restoration Action</b>	<b>Cost</b>	<b>Description</b>	<b>Var. Type</b>
Fremont Weir Notch [FRE Weir Notch]	M\$136.9	Notch in Fremont Weir to allow juvenile entrainment into Yolo Bypass under low flow conditions	Discrete (binary)
Tisdale Weir Notch [TIS Weir Notch]	M\$66.4	Notch in Tisdale Weir to allow juvenile entrainment into Sutter Bypass under low flow conditions	Discrete (binary)
Reintroduction Plan in Battle Creek [BC Reint. Plan]	M\$13.8	Establish a second population of winter-run Chinook salmon spawning at North Fork Battle Creek	Discrete (binary)
Side Banks Habitat Restoration/Re-connection [Off Rest. US/LS]	\$115K/acre	Increase connectivity between Sacramento mainstem and off-channel habitat Upper Sacramento River: 0 - 400 acres Lower Sacramento River: 0 - 20 acres	Continuous
Tributaries Habitat Restoration [Trib. Rest. US/LS]	\$430K/rmi	Improve tributary habitat. Upper Sacramento River: 0-20 mi Lower Sacramento River: 0-20 mi	Continuous
Reintroduction Plan in McCloud River [MC Reint.]	M\$44.65-214.65	Two-way trap and haul program (TH2) to move returning adults upstream Shasta Dam into historical spawning grounds	Discrete (binary)
Gravel Augmentation [Gravel Aug.]	M\$2.6	Improve spawning substrate quality downstream Keswick Dam and decrease red superimposition	Discrete (binary)

a gated structure to increase inundation frequency and salmon access to the Yolo Bypass floodplain. Six configurations were proposed, with Alternative 6 showing the most promising performance for increasing winter-run Chinook entrainment onto Yolo Bypass (DWR 2017). This alternative includes five gates (14'x40') with a west alignment, a gate invert elevation of 16.1', 200' bottom width and a design flow of 12,000 ft<sup>3</sup>/s. Mean annual increases in the proportion of the total population entrained were estimated at 3,490% during dry and critical water years and 219% during wet and above normal conditions (DWR 2017). These estimates were calculated based on an assumption (with limitations) that juvenile salmon are uniformly distributed across the water column (Acierto et al. 2014, DWR 2017). Regardless, we implemented the reported increases in entrainment in our simulated proportion of juveniles rearing in Yolo Bypass. This management action has an estimated cost of \$136.9 million (\$111.6 million in construction cost and \$1.1 million/year in operation and maintenance costs; USBR 2017).

#### 3.2.1.2. *Tisdale Weir notch*

A Tisdale Weir Notch has not been thoroughly considered in the existing literature, but we assume that its impact on juvenile entrainment into floodplain habitat is similar to Alternatives 1-3 for Fremont Weir (DWR 2017). We selected these described alternatives as they generate an intermediate increase in juvenile entrainment (within proposed alternatives; DWR 2017), similar to maximum changes in entrainment expected on the smaller Tisdale Weir. Thus, mean annual increase in entrainment onto Sutter Bypass was considered as 122% for wet and above normal years and 1,680% for dry and critical years. This management has an estimated cost of \$66.4 million (average cost for Alternatives 1-3, USBR 2017).

#### 3.2.1.3. *North Fork Battle Creek reintroduction*

Reintroduction of winter-run Chinook salmon to spring-fed habitat in North Forth Battle Creek would establish a second population along the Sacramento River Valley, improving spatial structure and population diversity of the winter-run Chinook Salmon Evolutionary Significant Unit (ESU; Waples 1998, McElhany et al. 2000). This action proposes to restore salmon access to 42 miles of habitat in Battle Creek and 6 miles in tributaries through the modification of hydroelectric operations and facilities (NOAA 2016, 2021). This decision has an estimated cost of \$13.8 million, \$3.4 million as one-time cost (e.g., infrastructure, fish transport trucks) and \$350K on annual operations (Action BAC-1.2, NMFS 2014, ICF International 2016). The salmon reintroduction plan includes recolonization, local adaptation, and long-term management phases (ICF International 2016). Each phase is triggered by the number of natural-origin returning adults to North Fork Battle Creek and are different in planned operations to establish a self-sustainable population (ICF International 2016). For instance, recolonization in Phase 1 uses hatchery pre-smolts/smolts from Livingston Stone National Fish Hatchery (LSNFH) broodstock, requiring 120 natural-origin adults from the Sacramento River population, in addition to current operations (USFWS 2012, 2013a). Section 3.2.2.1 describes ecological modeling for a Battle Creek population and its integration into the WRHAP structure (Figure 3.1). Section 3.2.2.3 details modeled hatchery operations.

#### 3.2.1.4. *Winter-run reintroduction over Shasta Dam (McCloud River)*

Two-way trap and haul (TH2) has been proposed as a high-priority action (Level 1) by NMFS (2014) for winter-run Chinook. It consists of capturing returning adults at Keswick Dam and transporting them to historical spawning habitat in the McCloud River, upstream of Shasta Dam. Out-migrating juveniles are proposed to be captured at the McCloud River confluence with Shasta

Lake (head-of-reservoir collection; USBR 2014, Clancey et al. 2017), transported downstream, and released below Keswick Dam (Lusardi & Moyle 2017). Habitat assessments reported 11.6 miles of fair-to-good spawning habitat downstream of McCloud Dam, with optimal instream temperature ( $< 12.7^{\circ}\text{C}$ ; Martin et al. 2017), and fair-to-good juvenile rearing habitat with optimal growth temperatures ( $< 19^{\circ}\text{C}$ ) along 23 miles of the McCloud River upstream of the proposed collection site (USBR 2014). While one-way trap and haul (movement of adults or juveniles) is common for salmonids in the Pacific Northwest (e.g., Snake, McKenzie and Yakima rivers) with mixed success, two-way trap and haul is less common with only five programs in the US (Baker, Cowlitz, Deschutes, Lewis and North Fork Skokomish rivers; Lusardi & Moyle 2017, Al-Chokhachy et al. 2018, Kock et al. 2020). Two-way trap and haul implementation in California is under further study (USBR 2016, Adams et al. 2018) to assess (i) the proportion of adults to be transported; (ii) juvenile growth and development within reintroduced habitats and (iii) the design and efficiency of juvenile trapping. As such, we assumed a reintroduction plan based on progressive phases triggered by the number of natural-origin returning adults hatched at McCloud River and initiated using hatchery broodstock, similar to that for Battle Creek (ICF International 2016). Furthermore, we considered trap efficiency dependent on the characteristics of the collection program, with greater efficiencies for more complex and higher cost collection trap designs. This tradeoff was analyzed by defining five different reintroduction alternatives, with 25%, 40%, 60%, 70% and 80% trap efficiencies and a total cost range of M\$44.65-214.65. Selected trap collection efficiencies include: (i) reported low values for Chinook salmon in systems using floating surface collectors ( $< 40\%$ ; PGE and CTWSRO 2014, 2015, 2016, Lusardi & Moyle 2017, Mendez & Hill 2017, Al-Chokhachy et al. 2018, Kock et al. 2020, PacifiCorp and Cowlitz PUD 2018, 2019, 2020, 2021); and (ii) expected higher efficiencies from the use of head-of-reservoir collection systems (Kock et al. 2020). Such systems could facilitate two-way trap and haul programs at locations where reservoirs are large and operated mainly for purposes other than hydropower (e.g., water storage), such as Shasta Reservoir (Clancey et al. 2017, Kock et al. 2020). Nevertheless, they have rarely been attempted and successful systems have not been developed to date (Kock et al. 2020). Costs are comprised of M\$3.4 for a McCloud River hatchery facility (analogous to reintroduction effort at Battle Creek; ICF International 2016), \$450K in annual maintenance and operation costs (Baker and Lewis River systems average costs; NPCC 2016) and M\$30-200 for juvenile collection traps design, construction and installation. The range is based on reported costs for existing floating surface collectors (FSC) in the Pacific Northwest (\$24-134 million; NPCC 2016) and assuming that (a) a head-or-reservoir collection system cost is lower due to its smaller dimensions, despite a more complex design to adapt to reservoir stage dynamics (Clancey et al. 2017); and (b) higher collection efficiencies are achieved after several iterations on the collection facility design (e.g., FSC designs at Baker River; Kock et al. 2020), incurring in additional costs to achieve the target trap efficiency. Section 3.2.2.2 describes McCloud River population dynamics and its inclusion in WRHAP's structure (Figure 3.1).

#### 3.2.1.5. *Tributaries habitat restoration*

This instream habitat improvement action would alter structural complexity to increase habitat availability and diversity, and provide juvenile refugia from disturbance and predation (Wohl et al. 2015). The management action is divided spatially allowing for different restoration actions along the upper, Deer and Mill Creeks, and lower Sacramento River tributaries, Feather and American Rivers (Phillis et al. 2018). Battle Creek is excluded from this management action, as a restoration program is currently being implemented (Jones & Stokes Associates 2005). A maximum extent



of 20 river miles (rmi), for upper and lower tributaries represent the cumulative available rearing habitat for juveniles reported in literature (ICF International 2016, CDFW 2017*a,b*). Per unit costs of \$430K/rmi were defined from the lower Deer Creek restoration plan (DCWC et al. 2011) that covered the reported habitat used by juvenile winter-run Chinook salmon (from confluence with Sacramento River to SVRIC diversion dam; CDFW 2017*b*). This cost includes a mixture of channel restoration (e.g., levee setback and floodplain restoration), riparian planting and invasive species control (DCWC et al. 2011); being within the reported per unit costs for tributary restoration in other systems (e.g., HR Tables and Yuba River; NMFS 2014, USACE & YWD 2019).

#### 3.2.1.6. *Side bank habitat restoration/re-connection*

Off-channel habitat restoration/reconnection actions increase the inundation frequency and duration of off-channel areas, promoting fluxes of organisms (e.g., *D. pulex* larvae; Corline et al. 2017) and materials between mainstem and side channel habitats (Wohl et al. 2015). Successful implementation of such actions in other river systems (e.g., Chilliwack River, British Columbia; Ogston et al. 2015) and Californias Central Valley (e.g., Cosumnes River; Florsheim & Mount 2002) are reported (Wohl et al. 2015, Roni et al. 2019). As such, restoring and maintaining off-channel ecosystems along both banks of the Sacramento River would expand diversity, abundance, and complexity of riverine habitat. These intermittent wetted areas also provide enhanced rearing opportunities for winter-run Chinook juveniles (Maslin et al. 1996, Jeffres et al. 2008, Limm & Marchetti 2009) and help smolts during out-migration (Bellido-Leiva et al. 2021). This management action is divided spatially, as for tributary restoration, with restoration ranges set by available off-channel area reported in Bellido-Leiva et al. (2021) for the upper and lower Sacramento River. Per unit cost is estimated at \$115K/acre (Action SAR-1.2, NMFS 2014) combining bank protection, acquisitions, restoration efforts and conservation easements. These costs are within the range reported in other systems (Roni et al. 2010, Ogston et al. 2015).

#### 3.2.1.7. *Gravel augmentation*

Gravel placement in winter-run spawning areas is the oldest, most widespread and evaluated instream habitat improvement (Merz et al. 2004, Roni et al. 2019). The effect on egg-to-fry survival, without temperature effects, is adopted from Merz et al. (2004), with an average increase of 24%, associated with an increase in the quality of redds via optimal gravel sizes which facilitate interstitial flow (Windell et al. 2017). This value assumes optimal placement and maintenance of gravel, with optimal permeability, depth, percentage of fines (Merz & Setka 2004) and inter-annual bed mobilization from flushing flows (Wheaton et al. 2004). This decision will be modeled as a binary variable with an estimated cost of M\$2.6 (Action SAR-1.6, NMFS 2014).

### 3.2.2. Winter-run Chinook Salmon Population Dynamics Modeling

Winter-run Chinook salmon juvenile production within the Sacramento River Valley is modeled using the Winter-Run Habitat-based Population Model (WRHAP; Bellido-Leiva et al. 2021). This is a freshwater rearing stage model that includes diverse juvenile rearing habitats including mainstem, tributaries, off-channel areas, and floodplains (Sommer et al. 2001, Limm & Marchetti 2009, Phillis et al. 2018). It also connects rearing habitat availability and quality with hydrologic conditions (flows and temperatures) and impacts to juvenile development and outmigration success (Bellido-Leiva et al. 2021). WRHAP begins with annual numbers of returning adults to spawning areas downstream of Keswick Dam, and estimates the number, fork length distribution, and biomass of

smolts reaching the San Francisco Bay. Biological parameters (e.g., rearing survival, temperature-induced mortality, growth rates) are established from empirical field data (e.g., Poytress et al. 2014, Jeffres 2016), laboratory studies (USFWS 1999), expert knowledge, and from values reported in the literature (e.g., Limm & Marchetti 2009, Martin et al. 2017, Hendrix et al. 2017, Phillis et al. 2018). Growth and survival during juvenile rearing stages are applied on a daily time step. Juvenile growth in floodplains and off-channel areas is simulated using the Fish Bioenergetics Model (Deslauriers et al. 2017), tested against empirical data from Yolo Bypass (Katz, unpublished data). Migration survival towards the Lower Sacramento River is simulated as a function of fish condition (i.e., length-weight ratio) and peak flows during the high-flow event that triggers juvenile movement downstream (del Rosario et al. 2013, Michel et al. 2015, Iglesias et al. 2017). Migration survival through the Sacramento-San Joaquin Delta and Yolo bypass are considered constant across years to avoid additional uncertainty from smolt route selection, defined by natural processes and water management actions (Perry et al. 2010).

However, WRHAP is not a complete life-cycle model as the ocean stage and adult return to spawning habitats was not included (Fig. 3.1, uncolored boxes). The unrepresented population

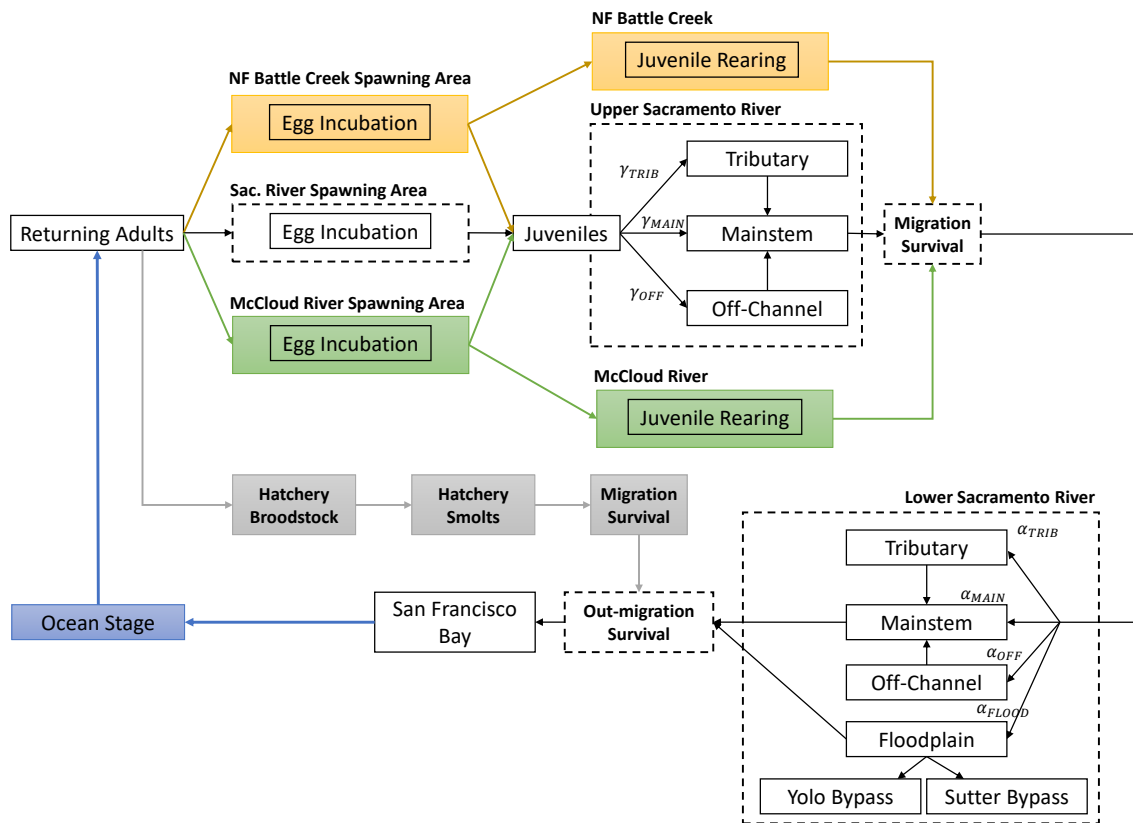


FIGURE 3.1. WRHAP-SEA links between the different spatial discretization areas and considered rearing habitats in them. Colored blocks represent added modules to WRHAP (Bellido-Leiva et al. 2021) structure, represented by non-colored blocks.

persistence (i.e., the lack of connection between simulated out-migrating smolts and future returning adults), hinders its use to evaluate restoration portfolios, as the simulation does not carry the longer-term effects of environmental and hydrological conditions from one time period to future ones (Adams et al. 2017). For instance, model outputs neglect the additional value of restoration actions that mitigate or avoid critical events, such as warm water releases from Shasta Reservoir during embryo incubation, which threaten the winter-run Chinook population (Martin et al. 2017). Furthermore, reintroduction programs require simulating new populations, not initially included in WRHAP structure (see Bellido-Leiva et al. 2021), and their interactions with the existing Sacramento River population. Therefore, additional modules were developed, each representing a coarse discretization in space and time to account for the missing life stages (e.g., ocean-stage, hatchery production) and to follow the rearing movements of reintroduced populations within the Sacramento River Valley (summarized in Table 3.2). This expanded version of the model is called WRHAP-SEA.

### 3.2.2.1. North Fork Battle Creek winter-run Chinook salmon population

Habitat assessments reported spawning habitat at North Fork Battle Creek, with optimal in-stream temperature ( $< 12.7^{\circ}\text{C}$ ; Martin et al. 2017) between Wildcat and North Battle Creek Feeder diversion dams, and a capacity of 1,228-2,457 female spawners (ICF International 2016). Therefore, egg-to-fry survival was computed as a combination of natural ( $\beta_{Fry,N}$ ) (without habitat effects), density-dependent and temperature-induced mortality ( $\beta_{T,MC}$ ) rates over the incubation period,

TABLE 3.2. WRHAP-SEA developed modules description and data requirements. A detailed structure of the module elements and links between them and WRHAP is shown in Figure 3.1

Modules	Spatial Extent	Time Period	Description	Data Requirements
North Fork Battle Creek	North Battle Creek Feeder dam to Sac. River mouth	Mid-April to November/December	Models the re-introduction program at North Fork Battle Creek. Estimates number of natural-origin juveniles reaching the upper and lower Sacramento River	Monthly temperature-related mortality, female fecundity, habitat capacity and flow and temperature at Battle Creek
McCloud River	McCloud Dam to Shasta Lake	Mid-April to November/December	Models the two-way trap and haul program at McCloud River. Estimates number of natural-origin juveniles reaching the upper and lower Sacramento River	Flow and temperature at McCloud River (CDEC; Sahl 2021), trap efficiency
Hatchery Operations	Through Knights Landing	Mid-April/July for collection	Determines number of adults collected from each population for hatchery broodstock. Estimates number of released smolts.	LSNFH Operations (USFWS 2012, 2013a)
Ocean stage	San Francisco Bay to return to freshwater areas	Out-migration to 2-, 3- or 4-year-old adults	Simulates the saltwater stage of winter-run Chinook salmon life cycle and computes number of returning adults to spawning grounds	Annual impact rates (Hendrix et al. 2017), winter mortality (Grover et al. 2004)

analogous to the Sacramento River population (Bellido-Leiva et al. 2021),

$$(3.1) \quad P_{J,0,BC}^{NO} = \frac{\beta_{Fry,N}}{1 + N_{S,BC} r_f / K_{BC,s}} N_{S,BC}^{NO+HO} r_f f \beta_{T,BC} + I_{Phase\ 1B} P_{J,0,SR}^{NO,BC}$$

where  $N_{S,BC}^{NO+HO}$  is the number of natural- and hatchery-origin spawners at North Fork Battle Creek,  $r_f$  is the ratio of females,  $f$  is female fecundity (i.e., number of eggs per female),  $K_{BC,s}$  is the capacity parameter of the Beverton-Holt term,  $I_{Phase\ 1B}$  equals 1 when the reintroduction plan is on Phase 1B, and  $P_{J,0,SR}^{NO,BC}$  are translocated juveniles from the Sacramento River population. Hatchery operation is defined based on the reintroduction program phase, switching progressively from LSNFH to Coleman National Fish Hatchery (CNFH) on Phase 1B and Phase 2, as described in Section 3.2.2.3. Under Phase 3 ( $N_{S,BC}^{NO} > 850$ ), no additional hatchery supplementation is considered (ICF International 2016). Temperature-induced mortality was simulated using daily estimates defined from monthly values reported by USBR (2005) per river reach. Embryo development was modeled with a temperature-dependent maturation function (Zeug et al. 2012, Bellido-Leiva et al. 2021).

After emergence, juveniles that exceed Battle Creek's rearing habitat capacity ( $\sim 550,000$  juveniles; USBR 2005, Appendix H), move downstream to the upper Sacramento River, sharing available habitats with the Sacramento River population. Hence, their complete freshwater stage is simulated using WRHAP equations (Fig. 3.1). The remaining juveniles are assumed to rear along Battle Creek for a period ( $d^{BC}$ ) equal to the Sacramento River population residence time along the upper Sacramento River. Juveniles then migrate downstream towards the lower Sacramento River triggered by the same high flow events as the Sacramento River population (Bellido-Leiva et al. 2021). Therefore, the number of natural-origin juveniles reaching the Lower Sacramento River is provided by,

$$(3.2) \quad P_{J,BC}^{NO} = P_{J,0,BC}^{NO} (\beta_{BC})^{d^{BC}} \left[ 1 - \frac{1}{1 + e^{-b_J(T_{BC} - T_{50,J})}} \right]^{\frac{d^{BC}}{7}} \beta_M [Q_{out}, K_{BC}^{NO}]$$

$$(3.3) \quad \log(\beta_M) = 3.9031 Q_{out}/1000 + 1.8680 K_{BC}^{NO} - 6.1049$$

and their growth by,

$$(3.4) \quad W^{BC} = W_0 (r_{g,BC})^{d^{BC}}$$

where  $\beta_{BC}$  is rearing survival,  $\beta_M$  is migration survival to the Lower Sacramento River (Eq. 3.3; Bellido-Leiva et al. 2021), is the juvenile's body condition (ratio of fish weight [g] to fish length [mm]; Fulton's K),  $W_0$  is the initial weight of juveniles after emergence and  $r_{g,BC}$  is the growth rate at Battle Creek. Due to the lack of field studies documenting juvenile growth and dietary composition along Battle Creek, a 2.1% growth rate is considered, similar to that for McCloud River (Sturgess & Moyle 1978, Mundy n.d.) and tributary rearing (Bellido-Leiva et al. 2021). Parameter values, description and sources are summarized in Table 3.3. Once juveniles reach the lower Sacramento River, their number and development are simulated using modules in WRHAP (Fig. 3.1).

### 3.2.2.2. McCloud River winter-run Chinook salmon population

Reintroduced adults would have access to 11.6 miles of fair-to-good spawning habitat downstream of McCloud Dam, with optimal instream temperatures ( $< 12.7^\circ\text{C}$ ; Martin et al. 2017) and a capacity of 1,200 - 4,200 female spawners (USBR 2014). Egg-to-fry survival was also computed as

a combination of natural ( $\beta_{Fry,N}$ ) (without habitat effects), density-dependent and temperature-induced mortality ( $\beta_{T,MC}$ ) rates over the incubation period

$$(3.5) \quad P_{J,0,MC}^{NO} = \frac{\beta_{Fry,N}}{1 + N_{S,MC} r_f / K_{MC,s}} N_{S,MC}^{NO+HO} \eta_{A,trap} r_f f \beta_{T,MC} + I_{Phase\ 1B} P_{J,0,SR}^{NO,MC}$$

where  $N_{S,MC}^{NO+HO}$  is the number of spawners at McCloud River from natural- and hatchery-origin,  $r_f$  is the ratio of females,  $f$  is female fecundity (i.e., number of eggs per female),  $K_{MC,s}$  is the capacity parameter of the Beverton-Holt term and  $I_{Phase\ 1B}$  equals 1 when the reintroduction plan is on Phase 1B, and  $P_{J,0,SR}^{NO,MC}$  are translocated juveniles from the Sacramento River population. Temperature-induced mortality was simulated using the phenomenological model for winter-run Chinook salmon embryos developed by Martin et al. (2017), with temperature adjusted from MSS station (USGS Gage No. 1136800) using values reported by Sahl (2021).

Fair-to-good juvenile rearing habitat with optimal growth temperatures ( $< 19^\circ\text{C}$ ) exist on 23 miles of McCloud River upstream of the proposed collection site (USBR 2014). Adults successfully moved upstream experience an additional 3.7% pre-spawn mortality ( $\beta_{COLL}$ ) associated to the collection and transport process (observed average over two decades at Yakima River; Kock et al. 2020), assuming safe handling of individuals and suitable collection and release conditions, such as appropriate temperature at McCloud River release site to avoid thermal shock (Hovda & Linley 2000, Al-Chokhachy et al. 2018, Kock et al. 2020). Juveniles are trapped with the selected alternative trap efficiency ( $\eta_{TRAP}$ ), experiencing 98.3% downstream collection and transportation survival,  $\beta_{TRANS}$  (recorded survival in Pacific Northwest programs; Al-Chokhachy et al. 2018). An ideal scenario is assumed in which no further delayed juvenile mortality is considered, despite reported reductions in survival through delayed effects that manifest in subsequent life stages (Budy et al. 2002, Schaller & Petrosky 2007, Anderson et al. 2014). A juvenile daily growth rate of 1.7% ( $r_{g,MC}$ ) is used in the rearing stage, defined from young-of-the-year rainbow and brown trout growth reported values (Sturgess & Moyle 1978, Mundy n.d.). We assume juveniles move from rearing habitats along the McCloud River similarly as for the Battle Creek population, continuing their rearing stage at the Lower Sacramento River, where habitats are shared between populations. Therefore, the number of natural-origin juveniles reaching the Lower Sacramento River is provided by,

$$(3.6) \quad P_{J,MC}^{NO} = P_{J,0,MC}^{NO} (\beta_{MC})^{d^{MC}} \eta_{TRAP} \beta_{TRANS} \left[ 1 - \frac{1}{1 + e^{-b_J(T_{MC} - T_{50,J})}} \right]^{\frac{d^{MC}}{7}} \beta_M [Q_{out}, K_{MC}^{NO}]$$

and their weight by,

$$(3.7) \quad W^{MC} = W_0 (r_{g,MC})^{d^{MC}}$$

where  $\beta_{MC}$  is rearing survival,  $\beta_M$  is migration survival to the Lower Sacramento River (Eq. 3.3; Bellido-Leiva et al. 2021), is the juvenile's body condition,  $d^{MC}$  is the residence time at McCloud River,  $T_{MC}$  is the temperature at McCloud River (MSS station) and  $K_{MC,r}$  is the rearing habitat capacity parameter of the Beverton-Holt term.

TABLE 3.3. WRHAP-SEA model parameters, description, and source. AV indicates values that vary annually.

Modules	Param.	Value	Eq.	Description	Source	Reference
North Fork Battle Creek	$r_f$	0.5	1,5	Ratio of females	Assumption	ICF International (2016)
	$f$	4750	1,5	Female fecundity [#eggs/fem]	Historical average	Poytress & Carrillo (2016); Voss & Poytress (2020)
	$\beta_{FR0,N}$	36.6%	1,5	Egg-to-juvenile survival rate without habitat effects	Fitted parameter	Poytress et al. (2014); Martin et al. (2017)
	$K_{BC,s}$	2457	1	Spawning habitat capacity	Upper limit of estimated values from habitat surveys	ICF International (2016)
	$\beta_{BC}$	98.3%	2	Daily rearing survival along Battle Creek	Assumption	Bellido-Leiva et al. (2021)
	$d_{BC}$	AV	2	Residence time at Battle Creek [days]	Assumption	Bellido-Leiva et al. (2021)
	$T_{50,J}$	20	2,6	Temperature that produces 50% mortality in juveniles [°C]	Laboratory study	USFWS (1999)
	$b_J$	1.8	2,6	Slope of temperature-related mortality for rearing juveniles	Adjusted from laboratory studies	Reed et al. (2011)
	$W_0$	0.420	4,7	Initial weight of juveniles [g]	Field study	Titus et al. (2004)
	$r_{g,BC}$	2%	4	Daily weight increases while rearing in the tributaries	Model input	Bellido-Leiva et al. (2021)
McCloud River	$K_{MC,s}$	4155	6	Spawning habitat capacity considering 6m <sup>2</sup> territories	Estimated value from habitat surveys	USBR (2014)
	$\beta_{MC}$	98.3%	6	Daily rearing survival	Assumption	Bellido-Leiva et al. (2021)
	$\eta_{TRAP}$	20-80%	6	Trap efficiency to collect migrating juveniles	Estimated from reported values in other programs	Al-Chokhachy et al. (2018); PGE and CTWSRO (2014, 2015, 2016); PacifiCorp and Cowitz PUD (2018, 2019, 2020)
	$\beta_{TRANS}$	98.5%	6	Juvenile downstream transportation survival	Estimated from reported values in other programs	PGE and CTWSRO (2014, 2015, 2016); Kock et al. (2020)
	$r_{g,MC}$	1.7	7	Juvenile daily growth in weight [%/day]	Estimated from young-of-the-year rainbow and brown trout growth	Sturgess & Moyle (1978); Mundy (n.d.)
	$J_{HO}$	5,077	8,14	Broodstock female fecundity	Average from reported values by LSNFH	USFWS (2013a); ICF International (2016)
	$\beta_{HO}$	69%	8,14	Egg-to-release survival at hatchery facilities	Average from reported values by LSNFH	USFWS (2013a); ICF International (2016)
Hatchery Operations	$r_{fem}$	50%	8,14	Ratio of females	Re-introduction plan assumption	ICF International (2016)
	$K_{HO}$	1.107	9,14	Hatchery smolts body condition associated to 88 mm Fork Length	Average size of smolts at release	USFWS (2013a)
	$\beta_{DELTA}$	56%	9,14	Migration survival of hatchery-origin smolts through the Sacramento-San Joaquin Delta	Field study	Michel et al. (2015); Iglesias et al. (2017)
	$M_w$	0.2	22, 24,25	Winter mortality	Winter-run cohort reconstruction	Grover et al. (2004); O'Farrell et al. (2012)
	$S_{r2}$	0.08	22	Percentage of age-2 adults in spawner's composition	Historical average	Grover et al. (2004)
Ocean Module	$S_{r3}$	0.96	24	Percentage of age-3 adults in spawner's composition	Historical average	Grover et al. (2004)
	$\beta_{BAY}$	80%	22	San Francisco Bay passage survival	Field experiment; model output	Michel et al. (2015); Hendrix et al. (2017)
	$\beta_{SPAWN}$	0.08	26	Pre-spawn mortality		

### 3.2.2.3. Hatchery operations

Livingston Stone National Fish Hatchery operations were included in WRHAP's structure (Fig. 3.1) as described in USFWS (2012, 2013a). Each brood year, the collection target for winter-run Chinook broodstock, represents 15% of the estimated run size, up to a maximum of 120 natural-origin adults from the Sacramento River population, sufficient to support genetic diversity (USFWS 2013a). A minimum of 20 adults are targeted for capture regardless of run size. Female fecundity ( $f_{HO}$ ) and in-hatchery survival ( $\beta_{HO}$ ) are based on reported values and program planning assumptions reported in USFWS (2013a). So the number of released presmolt/smolt ( $P_{S,0,SR}^{HO}$ ) from the Sacramento River population is given by,

$$(3.8) \quad P_{S,0,SR}^{HO} = \max(\min(0.15 N_{S,SR}^{NO}, 120), 20) r_{fem} f_{HO} \beta_{HO}$$

where  $N_{S,SR}^{NO}$  is the number of natural-origin spawners from the Sacramento River population, and  $r_{fem}$  is the ratio of females. Hatchery-origin smolts are considered to out-migrate directly to the San Francisco Bay after release, without rearing along the Sacramento River and using the Delta migration corridor. Thus, the number reaching the San Francisco Bay is computed as

$$(3.9) \quad P_{S,SR}^{HO} = P_{S,0,SR}^{HO} \beta_M [Q_{out}, K_{HO}] \beta_{DELTA}$$

where  $K_{HO}$  is the smolt's body condition,  $\beta_M$  is migration survival to the lower Sacramento River (Eq. 3.3; Bellido-Leiva et al. 2021) and  $\beta_{DELTA}$  is migration survival through the Delta. Parameter values, description and sources are summarized in Table 3.3.

Reintroduction programs (RP) at Battle Creek and McCloud River require hatchery operations for initial recolonization to establish a population that meets abundance objectives, retains genetic diversity of the Sacramento population and includes a substantial proportion of natural-origin fish (ICF International 2016). To that purpose, each program requires an additional 120 adults from the Sacramento population during Phase 1A, reduced to 60 and 6-24 adults for later phases. In turn, remaining adults to continue a 120 adult broodstock would be collected from reintroduced adults. The preference is to collect natural-origin adults, but if the required number exceeds the 15% target, broodstock would include hatchery-origin fish. Further details are provided in ICF International (2016). The number of adults collected is computed as

$$(3.10) \quad N_{S,SR,H}^{NO,RP} = \begin{cases} \min(0.15 N_{S,SR}^{NO} - N_{S,SR,H}^{NO}, N_{S,SR,H}^{RP}) & = 1 RP \\ \min(0.15 N_{S,SR}^{NO} - N_{S,SR,H}^{NO}, N_{S,SR,H}^{RP}) / 2 & > 1 RP \end{cases}$$

$$(3.11) \quad N_{S,SR,H} = N_{S,SR,H}^{RP} - N_{S,SR,H}^{NO,RP}$$

$$(3.12) \quad N_{S,RP,H}^{NO,RP} = \min(0.15 N_{S,RP}^{RP}, N_{S,RP,H}^{RP})$$

$$(3.13) \quad N_{S,RP,H}^{HO,RP} = N_{S,RP,H}^{RP} - N_{S,RP,H}^{NO,RP}$$

where  $N_{S,SR,H}^{NO,RP}$  and  $N_{S,SR,H}^{HO,RP}$  are the number of natural- and hatchery-origin spawners collected from the Sacramento River population for the reintroduction program hatchery operations (MC-McCloud or BC- Battle Creek),  $N_{S,RP,H}^{NO,RP}$  and  $N_{S,RP,H}^{HO,RP}$  are the number of natural- and hatchery-origin adults collected from the reintroduced population,  $N_{S,SR,H}^{RP}$  and  $N_{S,RP,H}^{RP}$  are the required broodstock size from the Sacramento and reintroduced populations in the current program phase and  $N_{S,SR,H}^{NO}$  is the number of natural-origin adults collected from the Sacramento population for LSNFH normal operations. Female fecundity and egg-to-release survival are based on reported

values for LSNFH (USFWS 2013a, ICF International 2016) and hatchery-origin smolts are also considered to directly out-migrate after release. As such, the number of released presmolt/smolt ( $P_{S,RP}^{HO}$ ) reaching the San Francisco Bay are estimated as,

$$(3.14) \quad P_{S,RP}^{HO} = \left( N_{S,SR,H}^{NO+HO,RP} + N_{S,RP,H}^{NO+HO,RP} \right) r_{fem} f_{HO} \beta_{HO} \beta_M [Q_{out}, K_{HO}] \beta_{DELTA}$$

Parameter values, description and sources are summarized in Table 3.3

#### 3.2.2.4. Tributaries habitat restoration

Responses of habitat characteristics to different management actions and physical variables controlled by water resources are difficult to quantify (Matella & Jagt 2014). Most examples are focused on physical relationships, such as flow versus habitat capacity curves (Matella & Jagt 2014) from hydrodynamic modeling (e.g., HEC-RAS). River restoration may enhance fish numbers by assuring suitable water temperatures through plant shading (Knight & Bottorff 1984, Rutherford et al. 1997), and enhancing habitat carrying capacity and fish survival (Roni et al. 2008, 2010). However, despite the increased emphasis on recording this relationship and new tagging and monitoring techniques, it has not been frequently measured or considered in assessing restoration effectiveness (Wohl et al. 2015, Roni et al. 2019). Thus, given lack of statistically rigorous evidence, assumptions must be made to relate both by using hypotheses based on literature studies for Pacific salmon (e.g., Solazzi et al. 2000, Paulsen & Fisher 2005, Roni et al. 2010) and expert knowledge. A sigmoid expression is used as it is assumed that several miles must be restored before important benefits are achieved, as reported in other systems (e.g., Puget Sound; Roni et al. 2010). Then, the marginal value of additional restored river miles decreases. We also assume that tributary restoration actions increase a greater proportion of suitable rearing area under medium and high flow conditions as a result of levee setback and floodplain restoration (DCWC et al. 2011). An increase in low flows suitable habitat is also assumed, but of a lesser extent. Mathematically it is implemented as,

$$(3.15) \quad \beta_{TRIB} [N_{mi,k}] = \beta_0 - \frac{\eta_{TRIB}}{1 + e^{\sigma_{TRIB}(N_{mi,k} - \theta_{TRIB})}}$$

$$(3.16) \quad \Delta A_{k,TRIB}^Q [N_{mi,k}] = \Delta A_{k,TRIB}^{0,Q} - \frac{\eta_{PROP,k}^Q}{1 + e^{\sigma_{PROP,k}^Q(N_{mi,k} - \theta_{PROP,k}^Q)}}$$

where  $N_{mi,k}$  is the number of restored miles at region  $k$  (upper or lower Sacramento River),  $\beta_{TRIB}$  is the rearing survival at the upper Sacramento area, and  $\Delta A_{k,TRIB}^Q$  is the proportional increase in suitable rearing area at region  $k$  under flow condition  $Q$ , respectively. Improvements in tributary habitat are considered to alter invertebrate density and food availability as well, increasing experienced growth rates. This change is also defined using a sigmoid function,

$$(3.17) \quad r_{g,TRIB} [N_{mi,k}] = r_0 - \frac{\eta_{GTH}}{1 + e^{\sigma_{GTH}(N_{mi,k} - \theta_{GTH})}}$$

where  $r_{g,TRIB}$  is the growth rate at tributaries. The remaining parameters are defined in Table 3.4.

#### 3.2.2.5. Side bank habitat restoration/re-connection

This management action improves off-channel habitat availability due to enhanced transversal connectivity. Similar to tributary restoration, despite billions of dollars spent annually on watershed restoration, the benefits of this investment are poorly documented in terms of the biological response to changes in habitat (e.g., increases in fish biomass or production; Ogston et al. 2015). As such,



we assumed that greater increases in available rearing habitat occur under low flow conditions from enhanced transversal connectivity. For greater flows, habitat capacity also increases from habitat quality improvement, but at a smaller rate and targeted by the last restoration efforts (final restored miles). The mathematical expression used in modeling is analogous to that used for tributaries (sigmoid function),

$$(3.18) \quad \Delta A_{k,OFF}^Q [N_{mi,k}] = \Delta A_{k,OFF}^{0,Q} - \frac{\eta_{OFF,k}^Q}{1 + e^{\sigma_{OFF,k}^Q (N_{mi,k} - \theta_{OFF,k}^Q)}}$$

Where  $N_{acres,k}$  is the number of restored off-channel acres along region  $k$ , and  $\Delta A_{k,OFF}^Q$  is the maximum proportional increase in suitable rearing area at off-channel habitats along region  $k$ , under flow condition  $Q$ . An increase of  $\sim 7$  days on residence time is also considered as enhanced transversal connectivity would extend inundation periods. The remaining parameters are defined in Table 3.4.

### 3.2.2.6. Ocean module

This module gathers output from WRHAP and reintroduction modules (producing numbers and size distributions of smolts reaching San Francisco Bay) and estimates the number of returning spawning adults that renew the population, completing the life cycle. The module formulation for winter-run Chinook ocean stages is based on work by Zeug et al. (2012) and Hendrix et al. (2017). Individuals mature after 1 to 3 years in the ocean, returning to spawn as mixture of 2- (8%), 3- (88%) and 4-year (4%) adults (Hallock & Fisher 1985, Zeug et al. 2012, Satterthwaite et al. 2017). Mortality between each age class is modeled on an annual step and divided into winter mortality ( $M_w$ ), considered as 20% (Grover et al. 2004, Zeug et al. 2012, Hendrix et al. 2017), and ocean harvest ( $H_i$ ). Annual impact rates for age-3 salmon ( $H_3$ ) were computed using a control rule consistent with current fishery management (NMFS 2012, 2018). As such, harvest rates are a function of the projected number of Age-3 natural-origin adults in the absence of fisheries ( $P_{A,3}^{NO,NF}$ , Eq. 3.23) from all existing populations,

$$(3.19) \quad H_3[\%] = \begin{cases} 0.02 P_{A,3}^{NO,NF} & \text{for } P_{A,3}^{NO,NF} < 500 \\ 10 + 0.004 (P_{A,3}^{NO,NF} - 500) & \text{for } 500 \leq P_{A,3}^{NO,NF} < 3000 \\ 20 & \text{for } P_{A,3}^{NO,NF} \geq 3000 \end{cases}$$

Age-4 impact rate ( $H_4$ ) was defined as double the age-3 ocean harvest (Winship et al. 2014, Hendrix et al. 2017). Survival from age-1 to age-2 (for Chinook that remain in the ocean) is computed as

$$(3.20) \quad P_{A,2} = (1 - M_w) (1 - S_{r2}) \beta_{BAY} \left[ \sum_i \sum_k P_{J,P,ki}^O (1 - M_{2,ki} [FL_{ki}]) \right]$$

where  $P_{J,P,ki}^O$  is the number of individuals reaching the San Francisco Bay with origin  $O$  (natural- or hatchery-origin) and from population  $P$  (Sacramento, McCloud or Battle Creek) after rearing in habitat  $k$  and  $i$  at the upper and lower Sacramento River, respectively (WRHAP-SEA output),  $\beta_{BAY}$  is migration survival through the San Francisco Bay, and  $M_{2,ki}$  is the smolt-to-age-2 mortality. As extensively reported in literature, greater growth along the watershed presumably increases early ocean survival by, among others, reducing predation risk at sea (Claiborne et al. 2011, Woodson

TABLE 3.4. Parameters defining changes in population dynamics in WRHAP-SEA due to restoration actions.

Param.	Area	Value	Eq.	Description	Source
$\beta_0$	Upper Sacramento	0.9885	15	Maximum tributary rearing survival reached after restoration	Solazzi et al. (2000)
$\eta_{TRIB}$	Upper Sacramento	$3.5 \times 10^{-3}$	15	Range in rearing survival at restored tributary habitat	-
$\sigma_{TRIB}$	Upper Sacramento	0.65	15	Slope of sigmoid function. Defines value of additional restored miles.	-
$\theta_{TRIB}$	Upper Sacramento	10	15	Restored miles required to achieve 50% increase in survival. Defined from available tributary habitat: $\sim 20$ miles.	CDFW (2017a); CDFW (2017b); ICF International (2016)
$\Delta A_{US,TRIB}^Q$	Upper Sacramento	30%, 60%, 40%	16	Maximum proportional increase in suitable rearing habitat along US tributaries under low, medium, and high flows	-
$\eta_{PROP,US}^Q$	Upper Sacramento	30%, 60%, 40%	16	Range in potential increases in tributary habitat due to restoration under low, medium, and high flows.	-
$\sigma_{PROP,US}^Q$	Upper Sacramento	0.65, 0.85, 0.65	16	Slope of sigmoid function under low, medium and high flow conditions.	-
$\theta_{PROP,US}^Q$	Upper Sacramento	9, 6, 12	16	Restored miles required to achieve 50% of the maximum restoration potential under low, medium, and high flows.	CDFW (2017a); CDFW (2017b); ICF International (2016)
$\Delta A_{LS,TRIB}^Q$	Lower Sacramento	25%, 50%, 10%	16	Maximum proportional increase in suitable rearing habitat along US trib. under low, medium, and high flows	-
$\eta_{PROP,LS}^Q$	Lower Sacramento	25%, 50%, 10%	16	Range in potential increases in tributary habitat due to restoration under low, medium, and high flows.	-
$\sigma_{PROP,LS}^Q$	Lower Sacramento	0.65, 0.85, 0.65	16	Slope of sigmoid function under low, medium and high flow conditions.	-
$\theta_{PROP,LS}^Q$	Lower Sacramento	11, 6, 16	16	Restored miles required to achieve 50% of the maximum restoration potential under low, medium, and high flows.	CDFW (2017a); CDFW (2017b); ICF International (2016)
$r_0$	Upper and Lower Sac.	2.8%	17	Maximum growth rate after full tributary restoration	-
$\eta_{GTH}$	Upper and Lower Sac.	0.7%	17	Potential increase in daily growth from tributary restoration	-
$\sigma_{GTH}$	Upper and Lower Sac.	0.7	17	Slope of sigmoid function	-
$\theta_{GTH}$	Upper and Lower Sac.	9	17	Required restored miles to achieve 50% of potential increase in daily growth	-
$\Delta A_{US,OFF}^Q$	Upper Sacramento	200%, 50%, 20%	18	Maximum proportional increase in suitable rearing habitat along US off-channel areas under low, medium, and high flows	-
$\eta_{OFF,US}^Q$	Upper Sacramento	200%, 50%, 20%	18	Range in potential increases in off-channel habitat due to restoration under low, medium, and high flows.	-
$\sigma_{OFF,US}^Q$	Upper Sacramento	0.04, 0.03, 0.06	18	Slope of sigmoid function under low, medium and high flow conditions.	-
$\theta_{OFF,US}^Q$	Upper Sacramento	120, 200, 300	18	Restored miles required to achieve 50% of the maximum restoration potential under low, medium, and high flows.	CDFW (2017a); CDFW (2017b); ICF International (2016)
$\Delta A_{LS,OFF}^Q$	Lower Sacramento	120%, 60%, 20%	18	Maximum proportional increase in suitable rearing habitat along LS off-channel areas under low, medium, and high flows	-
$\eta_{OFF,LS}^Q$	Lower Sacramento	120%, 60%, 20%	18	Range in potential increases in off-channel habitat due to restoration under low, medium, and high flows.	-
$\sigma_{OFF,US}^Q$	Lower Sacramento	0.85, 0.65, 0.65	18	Slope of sigmoid function under low, medium and high flow conditions.	-
$\theta_{OFF,US}^Q$	Lower Sacramento	6, 10, 12 [rmi]	18	Restored miles required to achieve 50% of the maximum restoration potential under low, medium, and high flows.	CDFW (2017a); CDFW (2017b); ICF International (2016)

et al. 2013, Munsch et al. 2019). Thus, this positive relationship between smolt condition and survival was implemented in  $M_{2,ki}$  definition as a sigmoid function. Mortality values of around 0.86, from winter-run cohort reconstruction (Grover et al. 2004, O’Farrell et al. 2012), were assigned to the historic average out-migrant size of approximately 100-110 mm (del Rosario et al. 2013, IEP et al. 2020).

$$(3.21) \quad M_{2,ki} = 0.6 + \frac{0.36}{1 + e^{0.1(FL_{ki}-120)}}$$

where  $FL_{ki}$  is the fork length of individuals that reared in habitat  $k$  and  $i$  at the upper and lower Sacramento River, respectively. Survival to age 3 is then computed by

$$(3.22) \quad P_{A,3}^{P,O} = P_{A,2}^{P,O} (1 - M_w) (1 - H_3) (1 - S_{r3})$$

and the projected number of Age-3 natural-origin adults in the absence of fisheries

$$(3.23) \quad P_{A,3}^{NO,NF} = \sum_p P_{A,2}^{P,NO} (1 - M_w)$$

where  $P_{A,2}^{P,NO}$  is the number of Age-2 natural-origin (NO) adults from population  $P$ . Survival to age 4 is computed as

$$(3.24) \quad P_{A,4}^{P,O} = P_{A,3}^{P,O} (1 - M_w) (1 - H_4)$$

The complete age-4 population is considered to return to spawning grounds. Additional parameters and values are described in Table 3.3. Returning adults are assumed to have a pre-spawn mortality ( $\beta_{SPAWN}$ ) of 8% (Killam 2006, USFWS 2009, 2011, 2013*b*, 2019), with final numbers given by

$$(3.25) \quad N_{S,P}^O = \left( P_{A,2}^{P,O} \frac{S_{r2}}{1 - S_{r2}} + P_{A,3}^{P,O} \frac{S_{r3}}{1 - S_{r3}} + P_{A,4}^{P,O} \right)$$

### 3.2.3. Optimization Model Formulation

The objective of the candidate restoration actions is to recover winter-run Chinook salmon in the Sacramento River Valley. As such, the optimization model seeks to maximize the end-of-period number of natural-origin returning adults to spawning grounds,

$$(3.26) \quad Z_1 = \max \frac{1}{H} \sum_H \sum_p \sum_{j=T-2}^T N_{RA,P,j}^{NO}$$

where  $T$  is the optimization horizon [years],  $H$  is the number of hydrological scenarios considered, and  $N_{RA,P,j}^{NO}$  is the number of out-migrating smolts from brood year  $j$  and population  $P$  returning as adults to spawning grounds, as described below,

$$(3.27) \quad N_{RA,P,j}^{NO} = F \left[ N_{S,P,j}^{NO+HO}, \mathbf{Z}, \mathbf{X}_j \right]$$

where  $\mathbf{Z}$  denotes the parameters of WRHAP-SEA,  $\mathbf{X}_j$  is the selected selected portfolio of restoration actions, and is the number of simulated spawners from population  $P$  for brood year  $j$  (as in Eqs. 1 and 5). The difference between  $N_{RA,P,j}^{NO}$  and  $N_{S,P,j}^{NO+HO}$  is that the latter is a mixture of 2-, 3- and 4-year individuals spawning on brood year  $j$  (Hallock & Fisher 1985, NMFS 2014) while the first represents the number of out-migrating smolts from brood year  $j$  that successfully return to spawning areas as 2-, 3- and 4-year adults. A 25-year optimization horizon was considered to allow reintroduction programs to develop the initial planned phases and maybe achieve self-sustaining populations.

A maximum budget,  $B$  [\$], limits the feasible extent of applied management actions,

$$(3.28) \quad B \leq \sum_j X_j C_{RD,j}$$

where  $C_{RD,j}$  is the cost of the recovery action  $X_j$  [\$]. The cost of each restoration alternative is summarized in Table 3.1. As the decision variables are a mixture of binary (integer) and continuous (Table 3.1), the optimization algorithm is a Mixed-Integer Non-Linear Program (MINLP), solved using a  $(\mu + \lambda)$  self-adaptive evolutionary algorithm implemented in Python using the package DEAP (Fortin et al. 2012). A maximum of 150 generations were considered with a population size of 120 individuals ( $\lambda$ ) generated from 30 parents ( $\mu$ ) using crossover and mutation probabilities equal to 0.5 and 0.4 respectively. Parent selection was performed using a tournament size of five individuals. Bit-flip mutation and Gaussian mutation were used for binary and continuous variables, respectively.

The optimization included 20 synthetic hydrologic scenarios ( $H$ ), generated from 1967-2020 historical daily records for the Sacramento River Valley using stationary bootstrapping with a 5-year average block size (Politis & Romano 1992, Kreiss & Paparoditis 2011). Water temperatures along Yolo Bypass and temperature-related egg-to-fry mortalities before brood year 1989 were modeled using generalized linear models fitted with a Gaussian distribution and a logarithmic link to 1989-2020 available records. Sacramento River temperatures at Wilkins Slough and air temperatures along the bypass were used as covariates to estimate rearing water temperatures along Yolo bypass. Shasta reservoir storage and average daily maximum air temperatures at Shasta during the incubation period were used as covariates for temperature related egg-to-fry mortality. We seeded WRHAP-SEA for the initial 4 years of the simulations using the average escapement estimates and compositions from 2013-2016 (Azat 2019). This allowed the simulations to begin with a reasonable starting age distribution of adults returning from the ocean (Peterson & Duarte 2020). Generated optimal portfolios were tested under an additional 100 synthetic hydrologic scenarios generated using stationary bootstrapping to test their robustness and performance under novel, unseen hydrologies.

### 3.3. Results

Fish habitat optimization helps quantify tradeoffs between restoration costs and potential winter-run Chinook population benefits, which can inform planning and decision-making. Results should be interpreted not by absolute numbers of fish, as results have only been compared with recruitment data to test the model (Bellido-Leiva et al. 2021), but instead by relative numbers or percent change in returning adult numbers (Null & Lund 2012).

#### 3.3.1. Effect of each Restoration Alternative

##### 3.3.1.1. No Action alternative

For the base case (i.e., no restoration actions in the Sacramento River Valley), an average of 2,810 natural-origin winter-run adults returned to the spawning reach below Keswick Dam at the end of the simulation period (maximized term in Eq. 3.26). Since the average number of returning adults that seeded the model was 3,098 individuals, the No Action base case presents a population decrease, as expected from reported historical abundance estimates (USFWS 2013a, Azat 2019). This, in turn, allows for a clearer interpretation of winter-run Chinook population benefits from each

potential restoration action and their combinations. Simulated hatchery-origin returning adults ranged between 3991024 individuals, consistent with observed numbers from LSNFH operations (Appendix C; ICF International 2016). Simulated freshwater (i.e., egg-to-smolt) and ocean stage mortality ranges, 0.983-0.999 and 0.713-0.960, respectively (Fig. 3.3), and agreed with observed values reported in literature (Hendrix et al. 2017). The highest densities of simulated freshwater-saltwater mortalities for each brood year exceeded the cohort replacement rate (i.e., each spawner produces one offspring), indicating a long-term decline in natural-origin returning Sacramento River winter-run adults (Fig. 3.3). As such, WRHAP-SEA simulations suggest that under most hydrology types, the current population persistence relies heavily on hatchery production, in accordance with the published literature (USFWS 2013a, NMFS 2014) and, thus, does not represent a viable population (McElhany et al. 2000).

### 3.3.1.2. Fremont and Tisdale Weir notches

Increasing floodplain habitat availability greatly benefited returning winter-run Chinook, independent of water year type. For instance, winter-run Chinook exhibited an average increase of ~70% and 45% in end-of-period returning adults, and a maximum of almost 145% and 100% under specific hydrologic scenarios, for Fremont and Tisdale weirs notching respectively (Fig. 3.2). Returning adult increases were achieved through (i) enhanced freshwater survival associated with lower out-migration mortality in the bypass corridor when compared with the Delta (Perry et al. 2010, Takata et al. 2017) and (ii) enhancement of ocean-stage survival, as exhibited by a downward shift in mortality distribution (Fig. 3.3a; Table 3.5). As expected, this shift in returning adults is driven by a higher proportion of better-conditioned smolts during out-migration due to floodplain rearing (Sommer et al. 2001, 2020, Jeffres et al. 2008, 2020, Katz et al. 2017, Holmes et al. 2021). Enhanced conditioning was also associated with greater initial ocean-stage success (i.e.,

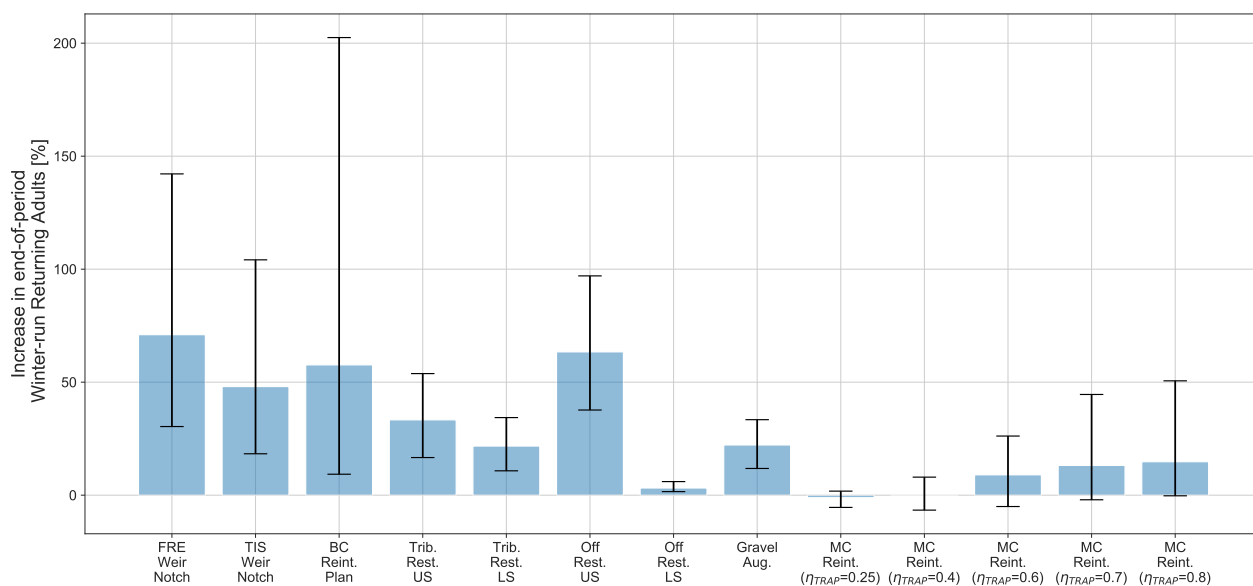


FIGURE 3.2. Simulated increase in end-of-period returning adults [%] for each fully implemented restoration action (Table 3.1).

better smolt-to-Age-2 survival; Eq. 3.21), consistent with observed patterns (Table 3.5; Claiborne et al. 2011, Woodson et al. 2013).

The benefits from notching Fremont and Tisdale weirs were apparent under two distinct scenarios. During low flow years when Sacramento River stage is insufficient to activate floodplains (e.g., BYs 2013-2015), and years when overtopping happens shortly after juvenile migration downstream Fremont and Tisdale weirs (e.g., BY 2001; Bellido-Leiva et al. 2021). These situations preclude juvenile use of warmer, shallow water habitat and its enhanced rearing conditions (Sommer et al. 2001, 2020, Jeffres et al. 2008, 2020, Katz et al. 2017). An average 59% increase in ocean-stage survival was estimated for these conditions in contrast to a 17% increase in wetter years when floodplain habitat was already available (Table 3.5).

### 3.3.1.3. *Gravel augmentation*

For a relatively low cost, gravel augmentation benefitted the entire winter-run cohort each brood year, enhancing natural egg-to-fry survival by ~24% (without habitat effects; Table 3.5). With gravel augmentation, winter-run juveniles experienced greater freshwater survival in all scenarios, since the first source of mortality in deposited eggs was reduced, as shown by the leftward shift in mortality density distributions (Fig. 3.3b). Simulated end-of-period returning adults rose an average 28% from current conditions.

### 3.3.1.4. *Off-channel habitat restoration*

Upper Sacramento River lateral connection enhancement and off-channel habitat restoration showed one of the greatest potentials to increase winter-run returning adult numbers, with an average 60%-70% increase when fully implemented. A larger proportion of juveniles accessing these enhanced rearing habitats experienced lower mortalities during rearing (Limm & Marchetti 2009) and migration through the lower Sacramento, due to enhanced body conditioning (Table 3.5; Iglesias et al. 2017, Bellido-Leiva et al. 2021). As such, freshwater stage mortalities greatly decreased (Fig. 3.3), consistent with reported increases in survival in other systems (e.g., Roni et al. 2010). The greatest benefits occurred in brood years that experienced small high flow peaks which triggered downstream migration and low or non-existent access to productive shallow-water habitats, with up to a 10% increase in migration survival into the lower Sacramento River (Table 3.5). Furthermore, the higher number of better-conditioned juveniles continued rearing along the Lower Sacramento River, so a greater proportion of out-migrating smolts exhibited improved fork lengths. This, in turn, benefitted initial ocean survival ( $M_2$ , Eq. 3.21), as reported in literature (Claiborne et al. 2011, Woodson et al. 2013), with an average 2% decrease in saltwater mortality. Thus, increased usage of off-channel habitats produced multiple benefits for winter-run Chinook returning adults (Fig. 3.3).

On the lower Sacramento River, off-channel restoration exhibited minimal benefits for winter-run Chinook, with an average increase of 4%. This was expected due to heavy channelization of the Sacramento River downstream Colusa, limiting available areas for restoration (Bellido-Leiva et al. 2021).

### 3.3.1.5. *Tributary habitat restoration*

Upper Sacramento tributary restoration benefits are associated with similar mechanisms described for off-channel restoration, i.e., a greater proportion of juveniles rearing under enhanced conditions compared to mainstem habitat (Limm & Marchetti 2009, Phillis et al. 2018). As such,

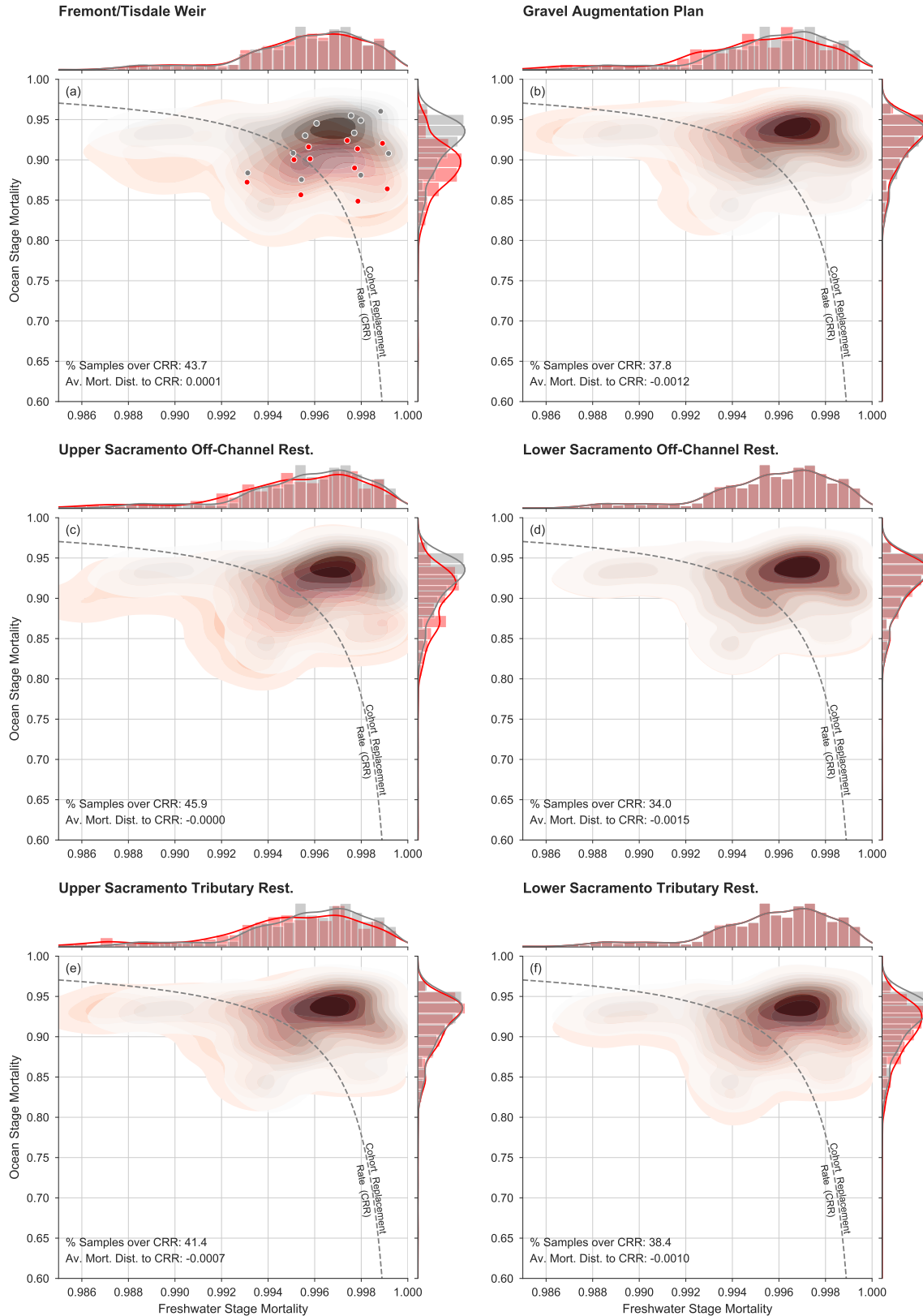


FIGURE 3.3. Freshwater and ocean stage mortality density plots for all 100 hydrologic states considered under no restoration (grey area) and each implemented restoration action (red area) scenarios. The dots on Fig. 3.3a represent a sample of 11 hydrologic scenarios mostly benefited by Fremont/Tisdale weir notching.

mortality was reduced (e.g., Solazzi et al. 2000, Roni et al. 2019) and migration success to downstream locations improved due to improved body conditions (Iglesias et al. 2017). Thus, tributary restoration increased end-of-period adult returns by 45%, on average. Nonetheless, freshwater-stage mortality improvement was less than that for off-channel restoration (Table 3.5; Fig. 3.3), as tributary restoration extent is smaller (Table 3.1), and off-channel rearing is higher ranked (Bellido-Leiva et al. 2021).

Lower Sacramento tributary restoration showed less benefits to returning adult numbers, with an average 18% increase. However, this scenario out-performed the Lower Sacramento off-channel restoration. Lower Sacramento tributary restoration slightly improved initial ocean-stage survival (Fig. 3.3f) by increasing the proportion of juveniles using off-mainstem habitat with better growth conditions (Limm & Marchetti 2009, Claiborne et al. 2011, Woodson et al. 2013).

TABLE 3.5. Average survival (and individual weight) improvement from base case for different isolated actions and optimal portfolios (OP).

Actions	Egg-to-fry	Upper Sacramento	Migration	Lower Sacramento	Initial Ocean Stage ( $M_{2,k}$ )	Returning Adults
Gravel Aug.	24%	-	-	-	-	22%
Trib. Rest. US	-	13% (5%)	2.5%	0% (3%)	5.2%	33%
Trib. Rest. LS	-	-	-	0% (8%)	12%	22%
Off. Rest. US	-	3.8% (19%)	6.2%	0% (13%)	26%	63%
Off. Rest. LS	-	-	-	0% (2%)	2.3%	3%
FRE Weir Notch	-	-	-	2.1% (31%)	42%	71%
TIS Weir Notch	-	-	-	0.6% (22%)	29%	48%
BC Reint. Plan	14%	8% (5%)	2%	5.4% (5%)	9.3%	61%
MC Reint. Plan	19%	4% (-2.2%)	-1%	3.3% (-2%)	-2.4%	15%
[ $\eta_{TRAP} = 80\%$ ]						
\$20 mill. OP	24%	8% (2.3%)	1.4%	0% (12%)	19%	103%
\$80 mill. OP	31%	14% (16%)	14%	8% (27%)	43%	250%
\$110 mill. OP	29%	11% (10%)	3.7%	11% (44%)	64%	330%
\$170 mill. OP	29%	13% (15%)	5.4%	12% (49%)	72%	376%
\$180 mill. OP	28%	10% (10%)	3.7%	15% (53%)	76%	383%
\$210 mill. OP	28%	12% (15%)	5.2%	15% (58%)	83%	440%
\$280 mill. OP	28%	12% (15%)	5.2%	17% (62%)	89%	465%

### 3.3.1.6. Battle Creek reintroduction

Recolonization of historical habitat in North Fork Battle Creek was one of the most promising restoration actions, with an average increase of 55% in returning adults. Two main factors were responsible for the rapid establishment of the Battle Creek population and the subsequent increase in adult returns. First, although temperature-related egg-to-fry mortality was higher than the Sacramento River mainstem for an average brood year (15% versus 7%) (USBR 2005, Martin et al. 2017), it remains low and fairly constant across all hydrologic conditions. This, in turn, avoided high mortality events during warm, dry conditions, such as those experienced in brood years 2014 and 2015 downstream Keswick Dam ( $\sim 94\%$  mortality; Martin et al. 2017), and expected in 2021 (CDFW 2002). Secondly, initial juvenile rearing along the recently restored Battle Creek (USBR 2005) appears superior when compared with the Sacramento River mainstem (e.g., slightly lower rearing mortality and better-conditioned juveniles during outmigration), which improved



downstream survival (Table 3.5). Average survival from emergence to the lower Sacramento areas was 3.7% and 5.2% for Sacramento River and Battle Creek populations, respectively.

As such, the greatest benefits associated with Battle Creek reintroduction (~200%) are related to unfavorable Sacramento River hydrologic conditions, especially once the reintroduced population has successfully been established (Phase 1B or later; ICF International 2016). These are a combination of high egg-to-fry temperature-related mortality, and dry conditions that limit off-mainstem areas' availability along upper Sacramento followed by low flows triggering downstream migration. A marginal increase in abundance was simulated during opposite scenarios (< 5%; Fig. 3.2), when favorable hydrologic conditions occur, and the Sacramento River population has low egg-to-fry mortalities from sustained cold releases from Shasta, and availability of high-flow habitats along the upper Sacramento.

Nevertheless, successful implementation of the Battle Creek reintroduction program depends on Sacramento River returning adult numbers, as an additional 120 natural-origin adults are needed from the 15% run size collection target (USFWS 2012) to initiate the broodstock program that supports the initial Phases of Battle Creek reintroduction (ICF International 2016). As such, to assure the potential availability of natural-origin adults required and reduce the demographic risk to the existing population (Anderson et al. 2014), the reintroduction should be combined with restoration actions directed towards the Sacramento River population.

#### 3.3.1.7. *McCloud River reintroduction*

Benefits from winter-run Chinook reintroduction to historical spawning grounds in the McCloud River via two-way trap and haul program largely depend on the collection efficiency of juvenile traps (Fig. 3.2), as highlighted in previous literature (Lusardi & Moyle 2017, Kock et al. 2020). For lowest trap efficiencies (e.g., 25-40%) and those similar to reported values in the Deschutes River program (PGE and CTWSRO 2014, 2015, 2016), a decrease in returning adult numbers was computed under most hydrologic scenarios (Fig. 3.2). The benefits of repopulating historical winter-run habitat in the McCloud River (e.g., lower temperature-dependent egg-to-fry mortality during critical events and enhanced rearing conditions) are likely offset by precluding juveniles from reaching the Sacramento River mainstem. Higher juvenile trap efficiencies (60%-80%) present small average increases in returning adults (3.5%-13.5%). However, declines persist in winter-run Chinook abundance when favorable hydrologic conditions occur, but of smaller extent than the less efficient cases (-5%, approximately; Fig. 3.2). Under such conditions, offspring from the 120 adults collected annually for broodstock purposes (ICF International 2016) would exhibit a better return success when spawning occurs, instead, downstream of Keswick Dam. Nevertheless, under the driest hydrologic conditions, winter-run Chinook abundance and population growth have a maximum estimated benefit of 25% to 50%, for higher trap efficiencies (60%-80%). Therefore, trap efficiencies over 70% must be assured to minimize the demographic risk to the Sacramento River population during average hydrologic conditions (Anderson et al. 2014), and to achieve impactful recovery of winter-run Chinook during the driest hydrologic scenarios.

As indicated previously, success of the McCloud River restoration action is inherently tied to a robust Sacramento River population, from which to extract additional natural-origin adults in order to initiate recolonization. Therefore, the success of the program may not only depend on high juvenile capture efficiency, but also the implementation of restoration actions that strongly benefit the Sacramento River population.

### 3.3.2. Optimal Restoration Policies

Individual restoration actions reduced freshwater and/or saltwater mortalities, but no single strategy provided enough benefit to overturn the long-term decreasing trend in Sacramento River winter-run Chinook natural-origin returning adults. Even when freshwater-saltwater mortalities were strongly reduced, each successive brood year continue to exceed the cohort replacement line, on average (Fig. 3.3). Hence, restoration portfolios that combine several discrete actions are warranted in an effort to attain conservation objectives guiding winter-run Chinook recovery (McElhany et al. 2000).

Optimal restoration policies differed by available budget and tended to show specific patterns within budget tiers. Restoration efforts under a \$20 mill. tiered budget were focused on management actions that provided the greatest impact on population abundance for each initial dollar invested: off-channel restoration along the lower Sacramento area, gravel augmentation at spawning grounds downstream Keswick and tributary restoration along the upper Sacramento (Fig. 3.4). Despite the low investment, optimal portfolios achieved a 100% increase in winter-run abundance and enhanced each freshwater life-stage. They generated improvements in egg-to-fry survival, upper Sacramento rearing conditions, migration survival, and juvenile development along the lower Sacramento. Hence, ultimately increasing their chances of survival during the marine stage (Woodson et al. 2013) (Table 3.5). The achieved recovery does not signify a self-sustaining natural-origin population, as average freshwater-saltwater mortalities for each brood year still exceeded the cohort replacement rate. Nevertheless, these actions were mostly kept for subsequent optimal portfolios, providing a solid restoration base to which add the benefits of more specific, costly restoration actions.

A rapid increase in returning adults was attained under a tiered budget between \$20-80 million, which encapsulated both the reintroduction program at Battle Creek and a progressive restoration of off-channel areas along the upper Sacramento River. Under such a combined restoration strategy, adult winter-run Chinook salmon returns increased by an additional  $\sim 140\%$  (Fig. 3.4; Table 3.5). Each \$10 mill. budget increment was allocated to off-channel restoration, which also received some additional economic resources from slightly reducing tributary restored miles ( $\sim 10\text{-}20\%$ ; Fig. 3.4). As might be expected, this decrease was focused on the upper Sacramento since both restoration actions target similar stressors on winter-run Chinook freshwater stage (e.g., migration survival). Thus, this budget interval presented a shift to more expensive off-channel restoration actions, due to their enhanced rearing conditions (Limm & Marchetti 2009, Bellido-Leiva et al. 2021) and greater recovery potential (Fig. 3.3c,e). Lower Sacramento tributary restoration was less affected because such restoration aims to improve initial ocean-stage survival (Fig. 3.3d; Table 3.5).

The implementation of the Battle Creek reintroduction program expanded the range of possible benefits to the winter-run Chinook, with maximum increases in returning adults of around 270% and minimums of  $\sim 90\%$ . The optimization algorithm did not select this management strategy until sufficient Sacramento River population recovery was achieved, in order to reduce demographic risk associated with the extraction of additional natural-origin adults for reintroduction purposes (Anderson et al. 2014, ICF International 2016). After initially included for a \$30 million budget, the reintroduction program was kept for each consequent higher-funding optimal portfolio. Thus, the optimization algorithm recognized the value of diversifying the population, key for an Evolutionary Significant Unit (ESU) viability (McElhany et al. 2000). Nevertheless, for McCloud River reintroduction, its high price and demographic risk on the Sacramento River population precluded its selection.

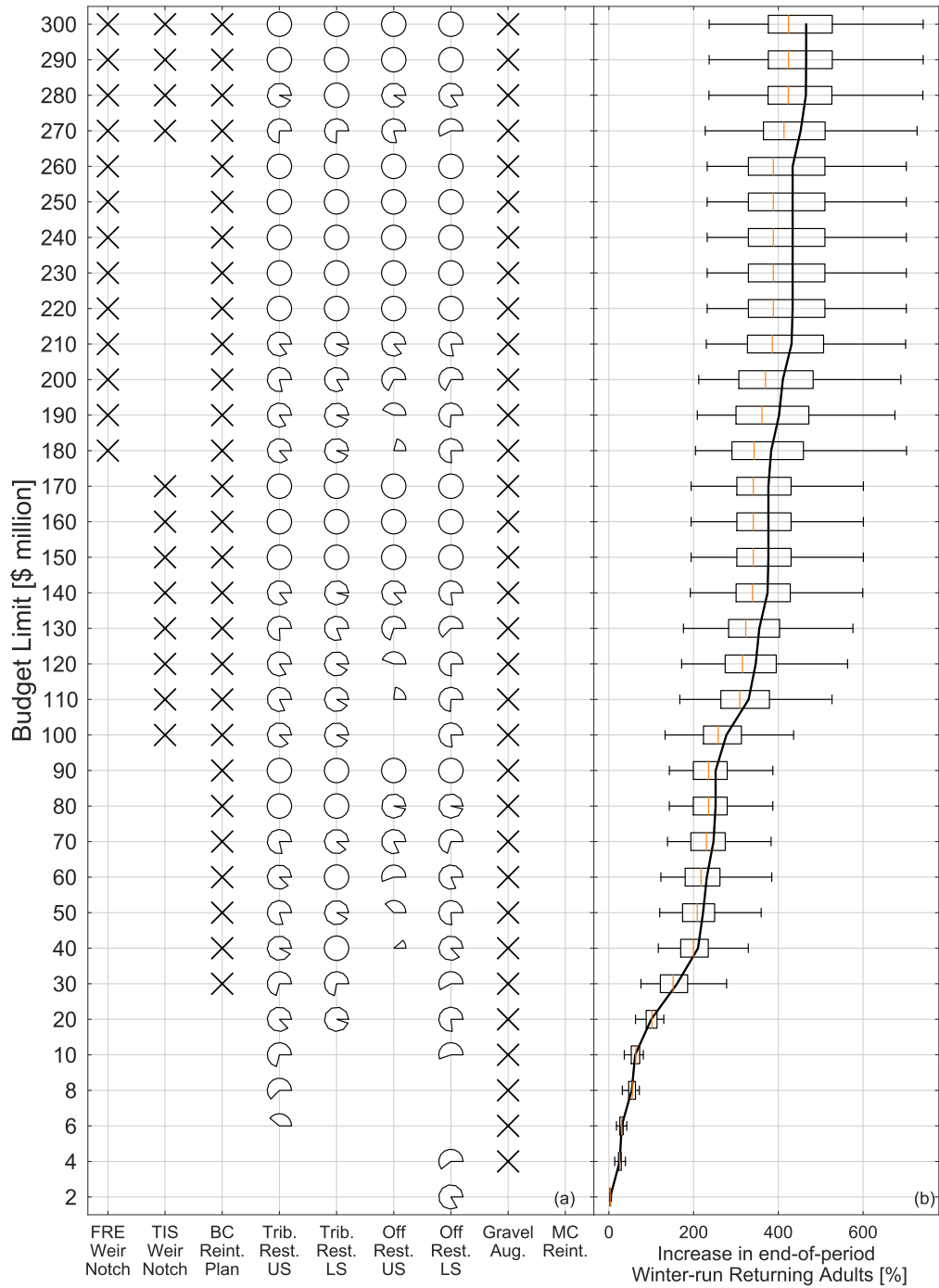


FIGURE 3.4. (a) Defined optimal restoration portfolios for each considered available capital budget. Actions included are reprinted by a cross (binary variables) and a pie chart (continuous variables) depicting the extent of the restoration effort. (b) Restoration tradeoff curve. The box plots show the range in simulated increases in end-of-period returning adults under the different hydrological scenarios considered while the solid black line represents the average increase.

Budget scenarios over \$100 mill. presented enough available funds to increase river-floodplain connectivity through notches at Fremont and Tisdale weirs (Yolo and Sutter bypasses, respectively). This connectivity enhancement produced an effective response in the Sacramento winter-run Chinook population and almost doubled the impact on returning adult abundance (e.g., between ~230% to ~390%, when Tisdale weir notch was added, and up to ~460% when Fremont weir notch was implemented). Such effects were mostly associated with increases in ocean-stage survival (Table 3.5). Three distinct budget intervals were differentiated, each with similar characteristics. These include: (i) \$100 - \$170 million when Tisdale weir notch is considered; (ii) \$180-\$260 million when Fremont weir notch is included; and (iii) \$270-\$300 million when both Fremont and Tisdale weirs are implemented. The initial budget for each interval is slightly greater than the cost of the notching action implemented, suggesting the optimization algorithm eagerness to improve floodplain connectivity, but without losing specific benefits obtained in other locations along the Sacramento River from several restoration actions.

At the start of each interval, the required investment to implement Tisdale/Fremont weir notches removed most off-channel restoration along the upper Sacramento from the optimal portfolios, but kept >75% of tributary habitat improvement. This was an expected outcome, as weir notching provides greater benefits to initial ocean-stage survival of out-migrating smolts than off-channel restoration (42% and 29% versus 26%, Table 3.5; Fig. 3.3a,c); and upper Sacramento tributary habitat restoration effect on freshwater stage survival is ~80% of that provided by off-channel habitat restoration, but for a fraction of the cost (Table 3.5). Then, as additional funding becomes available, a progressive shift from tributary to off-channel habitat restoration occurred, analogous to the previously described for the \$20-\$80 million range. This tradeoff between several actions provides a great flexibility to our decision-making framework. It allows the optimization algorithm to select cheaper, less effective restoration actions for more limited budgets (but still diversifying the areas affected by the optimal portfolio), and then switching to the more impactful and expensive actions when required funds become available (Table 3.5).

Fremont weir notching provided similar benefits to the combination of Tisdale weir notching and upper Sacramento off-channel restoration, highlighting the higher value and importance of Yolo bypass on the life cycle of winter-run Chinook along the highly altered Sacramento River (Sommer et al. 2001, Katz et al. 2017). Nevertheless, enhancing connectivity at both Sutter and Yolo bypasses did not generate enough population recovery (e.g., from 440% to 465%) to justify the increase in investment of an additional \$70 million dollars (Table 3.5). This suggests that other habitat characteristics, such as spawning habitat capacity (9,000 female spawners downstream Keswick Dam and 2,500 for Battle Creek; ICF International 2016, Martin et al. 2017), may be a limiting factor on winter-run adult abundance, and therefore, the considered set of restoration actions must be expanded to achieve further impactful recoveries.

The stepped shape of the trade-off curve (Fig. 3.5b) illustrates several budget intervals where significant benefits to natural-origin adult numbers were achieved, as well as areas where no further increases in abundance were generated with rising funds. The latter was characterized by budget scenarios that increase restoration of habitats which main focus (e.g., boost juvenile development along the Lower Sacramento) was already targeted by another, more impactful recovery action, and before enough funds became available to select a more expensive, effective one (e.g., \$140-\$170 or \$210-\$260 million; Fig 4b). As could be expected, rapid recoveries occurred when the most effective recovery actions, identified on the initial analysis (Fig. 3.2), were included in the optimal portfolios. For instance, \$90-\$110 million interval showed a rapid increase in average returning adults (from 250% to 330%) with the combination of Battle Creek reintroduction plan, increase in floodplain connectivity with Tisdale weir notching and upper Sacramento progressive off-channel restoration

(Fig. 3.4). Similarly, the range \$180-\$210 mill. provided an additional 60% increase in returning adults, based on an analogue combination of actions, but enhancing connectivity to Yolo instead of Sutter bypass. The fastest recovery (from 65% to 210% increase in returning adults) was achieved through \$10-\$40 mill. range. This may seem contradictory, as they represent some of the lowest budgets, but illustrates the population rapidly benefiting to even small improvements in its habitat. Nevertheless, this improvement, as indicated previously, does not imply that a viable population of winter-run could be achieved for very low budgets, as the net growth of the population still falls under the cohort replacement rate, continuing its dependency on hatchery-origin spawners (McElhany et al. 2000).

### 3.4. Discussion

The optimization model described here illustrates an approach to identify promising restoration efforts, combining habitat improvement plans and reintroduction programs for an endangered species by increasing their expected benefits relative to financial costs. This method combines fish population and habitat modelling (WRHAP-SEA), with a heuristic optimization algorithm, able to represent the complex interactions between restoration actions and winter-run population dynamics (Horne et al. 2016), to explore optimal management strategies. WRHAP-SEA outputs result from mechanistic understanding of fish survival and growth across the winter-run Chinook life cycle, providing juvenile production estimates that agree reasonably well with observed abundancies (Bellido-Leiva et al. 2021). However, the model greatly simplifies fish ecology and population dynamics by using a coarse temporal and spatial discretization. It also aggregates several sources of mortality on a single survival estimate, which adapts to the significant lack of explicit monitoring for winter-run Chinook salmon along the Sacramento River (Johnson et al. 2017, Bellido-Leiva et al. 2021). These simplifications were also stipulated as a modeling objective to depart from recent, increasingly complex ecological models with reduced decision-making suitability (Guo et al. 2015, Schuwirth et al. 2019, Peterson & Duarte 2020). Useful ecological models for environmental management must contain only needed elements to characterize the problem of interest (Schuwirth et al. 2019). As such, WRHAP-SEA's flexible, simple conceptual structure, and output interpretability allows more effective communication of underlying processes that govern model results, data used to parametrize the model, and model limitations (Bellido-Leiva et al. 2021). Underlying assumptions can be easily modified with stakeholder input, to reduce distrust in the model and its results (Wohl et al. 2015, Peterson & Duarte 2020).

Our results illustrate population-level effects of individual restoration actions (Table 3.1) and quantify the benefits accrued, under multiple hydrologic scenarios, at freshwater rearing locations and during the marine stage (Fig. 3.3 and Table 3.5). This analysis highlights the robustness of the set of restoration/recovery actions defined by NMFS (2014) and NOAA (2021), as they target every available rearing habitat along the Sacramento River watershed without neglecting any critical threat during winter-run Chinook freshwater stage (NMFS 2014, NOAA 2021). Despite their impact extending to later stages (e.g., dampening stress in marine stages by allowing greater growth in the watershed that presumably reduces predation risk at sea) (Woodson et al. 2013, Munsch et al. 2019), no specific recovery actions were considered along the Delta and the saltwater stage due to their oversimplified representation in WRHAP-SEA's structure. Nevertheless, restoration projects for Chinook salmon will currently be most effective in the river and more connected portions of the Delta (Munsch et al. 2020), while adult returns remain low. Restoration efforts may thus prioritize sites in these areas, as presented in this study, especially to ensure habitat use in years when water

and spawners are scarce. Furthermore, under a warming climate, freshwater conditions have an increasingly role in the interannual variation in salmon abundance, compared to fluctuations in ocean conditions (Ward et al. 2015, Sturrock et al. 2020).

### **3.4.1. Uncertainty in the effect of restoration actions**

Freshwater habitat restoration efforts have been implemented extensively in the USA since 1990, in order to improve degraded ecosystem services (e.g., spawning gravels, nutrient retention, biodiversity) from human activities (Wohl et al. 2015). More than 60% of projects completed during this period were related to salmon and trout habitat restoration efforts in the Pacific Northwest and California (Bernhardt et al. 2005, Katz et al. 2007). Nevertheless, debate continues on the effectiveness of different habitat restoration techniques and the cumulative impact of multiple, poorly coordinated restoration actions (Roni et al. 2002, Kondolf et al. 2008, Roni et al. 2010). Besides, the benefits of these investments are poorly documented in terms of the biological response to habitat change (e.g., increases in fish biomass or production; Ogston et al. 2015). Large-scale studies of restoration effectiveness are rare (Paulsen & Fisher 2005), in part because of substantial costs associated with restoration and monitoring (Ogston et al. 2015). Further, many restoration projects keep poor records of construction and maintenance costs (Bernhardt et al. 2005). Few studies have shown the physical and biological effectiveness of individual restoration actions and most include the placement of instream structures (Slaney et al. 1994, Cederholm et al. 1997, Solazzi et al. 2000, Roni & Quinn 2001), replacement of road crossings that impair fish movement (Glen 2002), and construction and reconnection of floodplain habitats (Morley et al. 2005, Henning et al. 2006, Roni et al. 2006, Ogston et al. 2015).

With this lack of statistically rigorous evidence, there is a dependence on expert opinion and assumptions (Sutherland et al. 2004, Drescher et al. 2013, Ogston et al. 2015). For WRHAP-SEA, the evaluation of restoration actions is based on the increase in quantity and quality of different types of habitats coupled with juvenile density estimates (Bartholow 2004, Hendrix et al. 2017) as predictors of juvenile winter-run abundance and production increase after restoration activities (Reeves et al. 1997, Beechie et al. 1994, Sharma & Hilborn 2001, Roni et al. 2010). Nonetheless, this dependence on assumptions and expert knowledge makes it challenging to accurately assess the benefits of any investment or competing recovery techniques. Nevertheless, the optimization framework presented using WRHAP-SEA provides a good first-order approach for estimating a plausible reasoned range in expected benefits from restored habitat (Fig. 3.5) while (i) increasing understanding of the interactions between physical habitat and factors limiting recruitment; (ii) organizing a complex watershed-scale restoration effort; (iii) developing testable hypotheses; and (iv) comparing estimated effectiveness of many restoration alternatives with expected costs.

### **3.4.2. Do defined portfolios push winter-run Chinook salmon towards viability?**

The expanded conceptual structure of WRHAP-SEA, including hatchery operations and reintroduced individuals to historical habitat, allowed for the analysis of the effect of each defined optimal portfolio on the viability of winter-run Chinook salmon ESU, following the criteria established by Allendorf et al. (1997) and McElhany et al. (2000), and adapted for Sacramento-San Joaquin Basin Chinook salmon by Lindley et al. (2007) (Table 3.6). Several metrics described in Williams et al. (2008) were considered in the analysis, as they appeared in Lindley et al. (2007) (Table 3.7). Abundance criterion was met by all defined optimal portfolios for both populations (e.g., Sacramento River and Battle Creek), as the total population size per generation ( $N_g$ ; Table 3.7) exceeded 2,500 individuals, placing the ESU at a low risk (Fig. 3.5a; Lindley et al. 2007).

The harmonic mean was employed to give greater weight to low returning adult numbers (Williams et al. 2008, Table 3.7). Nevertheless, no restoration portfolio reached the recovery goal of an effective population size of 12,500 females (dotted line in Fig. 3.5a), considered necessary to maintain normal levels of adaptive genetic diversity for reproductively isolated populations as winter-run Chinook salmon (Nelson 1987, Lande 1995, Williams et al. 2008).

The catastrophic population decline criterion was estimated by simulating winter-run population response to a prolonged extreme drought event, i.e., two consecutive brood years with temperature-related egg-to-fry mortalities greater than 90%, similar to estimated values during

TABLE 3.6. Criteria for assessing the level of risk extinction for Pacific salmon. Overall risk is determined by the most limited criterion (modified from Lindley et al. 2007, Williams et al. 2008, NMFS 2014).

Criterion	Risk of Extinction		
	High	Moderate	Low
<b>Population Size</b>	$N_g \leq 250$	$N_g \leq 2500$	$N_g > 250$
<b>Catastrophe Pop. Decline</b>	$\hat{c} > 0.9$	Smaller but significant decline	Not apparent
<b>Population Growth</b>	$C_d < 0$	$C_d \approx 0$	$C_d > 0$
<b>Hatchery Influence</b>	$h > 15\%$ PNI < 0.5	$h < 15\%$ PNI < 0.67	$h < 5\%$ PNI > 0.67

TABLE 3.7. Estimation methods and data requirements for population metrics.

Metric	Estimator	Data	Criterion	Source
$N_{g(t)}$	$N_{g(t)} = \sum_{i=t-3+1}^t N_i$	Simulated natural-origin returning adults for each brood year $i$ ( $N_i$ )	Population Size	Williams et al. (2008)
$N_g$	$N_g = \frac{1}{1/n \sum_{t=1}^n 1/N_{g(t)}}$	4 generations of simulated natural-origin returning adults	Population size	Williams et al. (2008)
$\hat{c}$	$\hat{c} = \left[ 1 - \min \left( \frac{N_{g(t)}}{N_{g(t-3)}} \right) \right] \times 100$	Time series of $N_{g(t)}$	Catastrophic decline	Williams et al. (2008)
$C_d$	$C_d = \frac{1}{n} \sum_i \min \left( \sqrt{(\beta_{FW} - C_x)^2 + (\beta_{SEA} - C_y)^2} \right)$ n: number of simulated brood years $C_x, C_y$ : mortality coordinates of cohort replacement line (Fig. 3.2)	Simulated freshwater- ( $\beta_{FW}$ ) and marine-stage ( $\beta_{SEA}$ ) mortalities for each brood year	Population decline	Developed criteria
$h$	Average fraction of natural spawners from hatchery origin	Mean of 3-4 generations	Hatchery influence	Lindley et al. (2007)
$PNI$	$PNI = \frac{pNOB}{pNOB + pHOS}$ pNOB: proportion of natural-origin broodstock pHOS: proportion of hatchery-origin in-river spawners	Simulated returning adults and hatchery broodstock operations	Hatchery influence	NMFS (2014)

1976-1977 and 2015 Shasta cold pool depletion events (Lindley et al. 2007, CDFW 2002). As expected, the ESU has a high risk of extinction, with declines exceeding 90% over one generation, for budgets under \$30 million, or equivalently, until the Battle Creek reintroduction was included in the optimal portfolios. Re-establishment of a population in the basalt-and-porous-lava region greatly improved the ESU's viability by increasing its resilience to more extreme and frequent droughts expected under climate change (Hanak & Lund 2012), as the spring-fed North Fork Battle Creek is not directly controlled by reservoir operations. This highlights the importance of diversifying winter-run Chinook populations, by lessening their dependence on cold water releases from Shasta Dam. Subsequent reductions in the ESU catastrophic decline were achieved when Fremont and Tisdale weir notches were considered, as these recovery actions greatly increase the chances of surviving juveniles to return as spawning adults and improve population viability (Table 3.5; Fig. 3.5). Nevertheless, even for budgets over \$180 million, generational declines remained significant (~70%), placing the ESU at a moderate risk and highlighting the persistent negative effects of human water mismanagement. Furthermore, the Sacramento River population and proposed reintroduction programs share an alternative catastrophic risk, Mt. Lassen volcanic eruption, as Battle Creek and the entire stretch of the Sacramento River used by winter-run Chinook salmon are within its zone of influence (Hoblitt et al. 1987, Lindley et al. 2007).

To reduce extinction risk from this single catastrophic event, the existing and re-established populations should exceed the Viable Salmonid Population (VSP) guidelines in abundance and growth rates for a plausible rapid recovery (McElhany et al. 2000). As such, optimal portfolios must provide enough ecological benefits to assure population growth under most hydrological conditions. WRHAP-SEA simulations identified such optimal portfolios by computing the average mortality distance to the cohort replacement line ( $C_d$ ) (i.e., the average of the distances of each pair of freshwater- and ocean-stage mortalities experienced by each simulated brood year under each hydrology to the cohort replacement line) (Fig. 3.2). Positive values indicate an expected growth in returning adults for the next generation (cohort replacement rate > 1), on average, with greater values describing faster population growth rates. Negative values represent declines in natural-origin returning adults for the next generation, on average. Sacramento River and Battle Creek winter-run Chinook salmon populations did not reach viable replacement rates until capital funding availability exceeded \$110 mill., i.e., the required amount to include significant floodplain connectivity enhancement in optimal restoration portfolios (Fig. 3.4), highlighting the crucial importance of floodplain habitat on juvenile Chinook development for the ESU.

In order to minimize the risk of genetic introgression, Lindley et al. (2007) recommended that over a four generation span (i.e., 12 years) no more than 5% of natural spawning adults should be of hatchery-origin. Similarly, less than a 15% is recommended to keep introgression at a moderate risk (Table 3.6). None of the defined optimal portfolios reached the low-risk benchmark, placing the ESU at a moderate risk of extinction, but increasing restoration budgets reduced the ratio of hatchery supplementation. From expected high-risk values on base conditions (i.e., ~22% on average), values under 15% were achieved for investments over \$40 mill. (Fig. 3.5), reaching lows of ~7.5% for the largest capital budgets.

Due to LSNFH operation using best management practices, a more appropriate indicator to determine genetic risk could be the Proportionate Natural Influence (PNI) index (USFWS 2013a), a gene flow rate between hatchery and natural populations (Table 3.7). Values must exceed 0.67 for populations considered essential for the recovery or viability of an ESU (NMFS 2014), for the natural environment to be predominant on the genetic constitution of a naturally spawning population. Computed indices exceeded 0.8 on average under all scenarios, in accordance to reported historical values (NMFS 2014), satisfying the guideline for minimizing the genetic effects and defining the



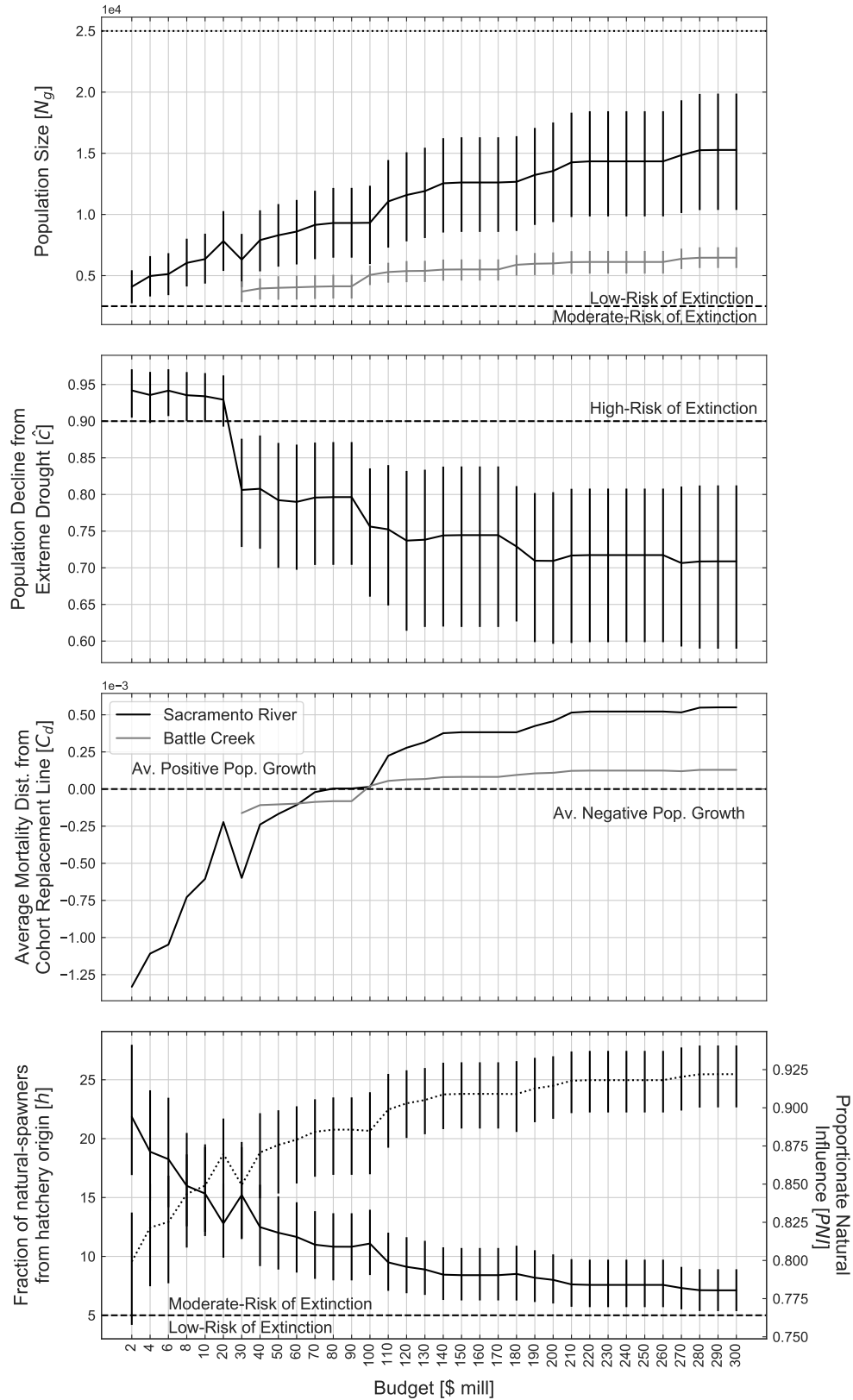


FIGURE 3.5. Winter-run Chinook salmon population metrics (Table 3.7) for each defined optimal restoration portfolio. Dashed lines represent different threshold for population extinction risk classification (Table 3.6).

population at a low-risk, in contrast to moderate-risk from Lindley et al. (2007). However, if ESU's persistence depends on LSNFH operations, despite favorable PNI values, it should not be characterized as having a low risk. This scenario is similar to those explored for catastrophic declines (i.e., the natural-origin population should be able to replace itself under most hydrologic scenarios). Therefore, the ESU could be considered as having a low-risk from hatchery influence for budgets over \$120 million, for which PNI values exceed 0.8, the proportion of hatchery-origin spawners is under 10% and population persistence is not critically tied to LSNFH and/or Coleman National Fish Hatchery operations.

### 3.4.3. Implications for winter-run Chinook salmon management

Winter-run Chinook salmon viability analysis suggested restoration plans with a capital budget over \$120 mill. to generate enough ecological benefits for progressive recovery of winter-run Chinook and, possibly, advance the ESU towards a viable status. Simulated benefits meet or exceeds VSP guidelines (Table 3.6), while simultaneously improving the ESU spatial structure and diversity from a structured restoration program along the Sacramento River watershed. As such, the optimal portfolios defined within this funding range included tributary habitat restoration along the upper and lower Sacramento, restored acres of upper Sacramento off-channel habitat, the reintroduction of a secondary population at Battle Creek and floodplain-mainstem connectivity enhancement through a notch at Fremont/Tisdale weir. Aiming for long-term population resilience, restoration efforts that create large, functional, and connected habitats across the landscape may enable the watershed to capitalize on years when natural conditions and managers facilitate high spawner abundances and flows (Munsch et al. 2020). As commonly shared by CVPIA restoration practitioners, this defined restoration/recovery actions targeting winter-run Chinook would likely also benefit other salmonids (*Oncorhynchus spp.*) or at a minimum, would not harm non-target salmonids, although further analysis should be considered (Peterson & Duarte 2020).

Fremont/Tisdale weir notching exhibit the potential for further benefits to winter-run Chinook salmon viability and abundance through the operation of gates. A minimum flooding period could be determined to maximize growth for entrained juveniles, since recent research has found a positive relationship between water residence time and juvenile Chinook development, from time needed for zooplankton growth and forage abundance (Corline et al. 2017, Katz et al., *in progress*). Similarly, as shown by (Takata et al. 2017), winter-run Chinook juveniles entrained into Yolo bypass delay emigration when flooded habitat is available, and would move out during flood recession. Thus, active floodplain management would help control juvenile rearing period and out-migration timing, expanding life history diversity for the ESU, and offsetting reduced biocomplexity of adult returns due to the increasing synchrony in winter-run populations from hatchery operations (Lindley et al. 2009, Windell et al. 2017, Friedman et al. 2019). Additionally, flood recession timing could be optimized to promote juvenile out-migration when favorable ocean conditions exist (i.e., availability of prey for individuals to maximize early marine-stage growth) (Satterthwaite et al. 2017) and/or when enough primary forage already exists for predators (e.g., California sea lions (*Zalophus californianus*), harbor seals (*Phoca vitulina*), common murre, Brandts cormorants (*Phalacrocorax penicillatus*); Laake et al. 2018, Carretta et al. 2018, Wells et al. 2017, Capitolo et al. 2014) in an effort to reduce predation risk (Friedman et al. 2019).

Floodplain connectivity enhancement and off-channel restoration actions considered in defined portfolios might also be redesigned to simultaneously reduce flooding risks on some reaches of the Sacramento River and provide benefits to both ecosystems and human activities. Although the role of ecosystem-based projects in flood risk reduction has been very limited to date (Colgan

2017, Reguero et al. 2020), some valuations have included their consideration in insurance (e.g., McVittie et al. 2018, Beck et al. 2018, Moos et al. 2018, Whelchel et al. 2018). This combination of ecosystem-based risk reduction projects with flood insurance has introduced a potential new source of funding for restoration projects. Thus, it might decrease the economic pressure on state and federal agencies (Reguero et al. 2020), making these high-cost, high-impact recovery actions more attractive.

#### 3.4.4. Two-way trap and haul considerations

Reintroduction at the McCloud River was not selected for any budget considered, limiting the number of distinct populations of winter-run Chinook to the Sacramento River and North Fork Battle Creek. The optimization algorithm did not select this option due to its high cost for an efficient two-way trap and haul program without an average positive impact on winter-run abundance, and potential demographic risk to the Sacramento River population during implementation (Anderson et al. 2014). Nevertheless, due to the critical importance of additional populations for the ESU viability by providing enhanced spatial structure and diversity (McElhany et al. 2000), the optimization was re-run giving a greater weight to returning adults from reintroduction programs (2-to-1) and considering progressively lower implementation costs. Optimal portfolios did not include the two-way trap and haul program until its cost dropped under \$70 million, as higher expenses would preclude highly beneficial restoration actions in other areas of the Sacramento River Valley. The estimated cost for selection might seem unrealistic when compared to the required investment in other systems (NPCC 2016, USACE & YWD 2019, Kock et al. 2020, \$24-134 million for Pacific Northwest and > 1\$ billion estimated for the Yuba River;), and considering the necessity of extensive feasibility testing of juvenile trap design, management, and optimal placement, since operations and efficiency of top-of-reservoir collection systems represent a current knowledge gap (Kock et al. 2020). The cost estimate could require further discount for selection when more realistic assumptions on adult pre-spawn mortality and juvenile delayed mortality (associated to individuals handling and transport; Al-Chokhachy et al. 2018) are considered following reported findings (Budy et al. 2002, Schaller & Petrosky 2007, Anderson et al. 2014, Kock et al. 2020), in contrast to the ideal conditions simulated with WRHAP-SEA.

Regardless, if selected, our simulations suggest that the reintroduced population would have a cohort replacement rate of 0.84 ( $< 1$ ), and hence, depend on hatchery supplements to assure persistence. For collection efficiencies under 80%, an average  $\sim 15\%$  of naturally spawning adults were from hatchery-origin, placing the reintroduced population at a high/moderate-risk of extinction (Lindley et al. 2007). As such, this will likely threaten the genetic diversity and viability of the reintroduced population (McElhany et al. 2000, Goodman 2005, Kostow 2009). Further, the effect of strays from this population on the Sacramento River population should also be considered and monitored, to reduce risk to the genetic diversity of the original population. Similarly, if transportation effects on individuals are minimized and collection efficiencies  $> 80\%$  are a realistic after extensive testing of top-of-reservoir novel technologies, a sustainable population at McCloud River, dependent on two-way trap and haul, could be achieved (hatchery-origin spawners  $< 5\%$  and cohort replacement rate  $\sim 1$ ), providing further resilience of the ESU to catastrophic events and bolstering its viability with population redundancy at basalt-and-porous-lava regions (Lindley et al. 2007, NOAA 2021).

### 3.5. Conclusions

With billions of dollars being spent on stream restoration worldwide (Roni et al. 2002, Bernhardt et al. 2005), it is important to develop optimization frameworks to prioritize restoration plans before investments are made to maximize the potential to achieve significant ecological benefits. Furthermore, these frameworks allow to structure and coordinate complex watershed-scale restoration/recovery efforts, avoiding isolated and/or disconnected projects (Friedman et al. 2019, Munsch et al. 2020). This is especially crucial for species that demonstrate complex life cycles and long migrations over heterogeneous habitat, such as Chinook salmon (Palmer et al. 2005, Budy & Schaller 2007). This study developed such a framework for winter-run Chinook salmon along the Sacramento River watershed, using an extension of WRHAP (denoted as WRHAP-SEA) to evaluate population-level effects of defined restoration portfolios. Added modules were based on previously published studies, empirical field data, and expert knowledge. They describe hatchery operations, reintroduction programs, and define ocean-stage survival based on smolt development along the Sacramento River watershed. As such, links were developed connecting restored habitat rearing availability and quality with juvenile development, smolt body condition and adult return success.

Considered restoration/recovery actions improve a plethora of ecological services along the Sacramento River Valley including, for instance, instream rearing conditions at tributaries, habitat capacity and residence time at off-channel habitats, floodplain entrainment and reintroduction programs at spring-fed, historical spawning grounds. Viability assessment of defined portfolios showed the prominence of frequent floodplain activation, as average positive population growth was not achieved until their implementation. This, in turn, is crucial to assure a rapid recovery after high-mortality events, and to sever the dependence on hatchery supplementation. In addition, simulated benefits could be exceeded if additional management focuses on defining optimal operation rules for notch gates. For instance, by promoting juvenile residence in the bypass until favorable ocean conditions exist.

The analysis highlighted the critical importance of reintroduced populations to improve the ESU's diversity and spatial structure, increasing its resilience under catastrophic events (e.g., prolonged drought conditions). Despite these benefits, reintroduction at McCloud River, two-way trap and haul program, was not selected for any optimal portfolio, even when considering optimal handling conditions to minimize pre-spawn and delayed mortalities for adults and juveniles, respectively. The high investment required to assure high collection efficiencies (>70%) to minimize the demographic risk imposed to the existing winter-run Chinook population, and the non-viable status of the reintroduced population (dependence on hatchery operations) precluded its implementation.

Due to the uncertain benefits of restoration actions, it is crucial to design monitoring programs to assess whether the proposed optimal restoration portfolios would perform in accordance with the effectiveness evaluated by ecological models. This information would allow to implement an adaptive management approach to correct for any deficiency on expected restoration outcomes and provide robust data on the restoration impact for future similar efforts focused on other areas and/or species. Finally, the defined framework shows its utility to explore relationships between an ample set of recovery/restoration actions applied on a watershed-scale, and to define optimal portfolios to assist water/environmental management and decision-making processes focused on species recovery.

## Quantification of inundated habitat for Pacific Chinook salmon (*Oncorhynchus tshawytscha*) along the Sacramento River, California

### Abstract

Off-channel areas are one of the habitats most impacted by humans globally, as extensive development for agricultural and urban uses has limited their historical extent to roughly 10%. This has been no different for the Sacramento River Valley, where historically frequent widespread inundation has been reduced to just a few off-channel water bodies along the mid-Sacramento River. This remaining shallow water habitat provides crucial ecological benefits to multiple avian and fish species, but specially to floodplain-adapted ones such as Pacific Chinook salmon (*Oncorhynchus tshawytscha*). Characterizing spatiotemporal off-channel dynamics, such as extent and residence time, is essential to better understand their ecological value and inform decision-makers on their potential for restoration. Remote sensing techniques have been increasingly used to map surface water at regional and local scales due to better products at finer resolutions. As such, this study maps off-channel areas inundation and describes its temporal dynamics by analyzing pixel-based time series of multiple water indices, modified Normalized Difference Water Index (mNDWI) and the Automated Water Extraction Index (AWEI), generated from LandSat-8 and Sentinel-2 data between 2013-2021. Quantified off-channel area was similar with each water index and methodology used, but a better performance was found for Sentinel-2 products and AWEI index to identify wetted areas under lower mainstem flows. Results indicate an uneven distribution of off-channel habitat along the study area, with limited inundated areas in upstream reaches (<16% of total area for greater flows). In addition, restricted available habitat exists for flows under 400 m<sup>3</sup>/s, cue for migration of the endangered winter-run Chinook salmon, limiting juvenile access to areas with enhanced rearing conditions. Residence times average 7-16 days, mainly defined by the rate of receding flows, with fast pulses providing marginal off-channel habitat. This study demonstrates the satisfactory performance of moderate resolution LandSat-8 and Sentinel-2 remote sensing imagery to characterize shallow water habitat in higher-order rivers, such as the Sacramento River, and its potential to aid in restoration efforts.

**KEYWORDS:** mNDWI, AWEI, Sacramento River Valley, off-channel habitat mapping, Chinook salmon, LandSat-8, Sentinel-2

### 4.1. Introduction

Geomorphic processes are crucial to form and maintain shallow-water, seasonally inundated habitats on channel margins of actively meandering rivers (Kondolf et al. 2016, Lewin et al. 2018). These habitats, which increase channel complexity, are generated from inundation of former main

channel positions (e.g., oxbow lakes), overbank flows (e.g., floodplains), and point bar dynamics (e.g., scour channels on point bars). They support essential parts of riverine ecosystems that provide habitat and nutrients for terrestrial and aquatic animals (Junk et al. 1989, Sommer et al. 2001, Tockner & Stanford 2002, Opperman et al. 2010). They are among the most biologically productive environments, able to support high biodiversity due to hydrological, topographical, and chemical attributes that promote mixing, enhance trophic resources, and increase residence time compared to mainstem rivers (Junk et al. 1989, Tockner & Stanford 2002, Grosholz & Gallo 2006, Ahearn et al. 2006, Corline et al. 2017). The ecological importance of off-channel sites is reflected in aquatic and terrestrial species developing life history strategies to take advantage of off-channel productivity (Junk et al. 1989, Humphries et al. 1999, Whited et al. 2012, Gallart et al. 2016). For instance, many fish species use off-channel habitats for spawning and rearing to benefit from the productivity of these ephemeral areas.

Off-channel habitats are also highly impacted by humans globally (Roni et al. 2019). Roughly 90% of Europe's and North America's shallow-water areas have been developed for human use, mainly for agriculture and urban areas (Tockner & Stanford 2002). Their disconnection from river mainstems has altered geofluvial processes, riverine productivity, and aquatic community structure, especially for floodplain-adapted species (Sommer et al. 2004). The Sacramento River once flooded the Sacramento Valley frequently, creating extensive seasonal shallow-water habitat ("inland-sea") that benefited multiple fish and avian species (Kelley 1998). California's water infrastructure development has greatly reduced the frequency and extent of off-channel inundation by flow regulation and levee construction. Currently, only 5% of historical floodplains remain, mostly within existing flood bypasses (Yolo and Sutter bypasses; Fig. 4.1) that divert water during high flow events (Hanak et al. 2011). Their occasional flooding provides vast increases in shallow-water habitat in some years; but, these bypasses were developed in the lower Sacramento River valley exclusively. In contrast, the middle Sacramento River, between Red Bluff and Colusa (Fig. 4.1), generally does not provide the same type of periodic expansion of shallow-water habitat, but instead has a mosaic of off-channel habitats such as oxbow lakes, scour channels and side pools, denoted as Off-Channel Water Bodies (OCWB; Kondolf & Stillwater Sciences 2007). They provide critical habitat for Western Pond turtle (*Clemmys marmorata*), Sacramento pikeminnow (*Ptychochelilus grandis*), Sacramento sucker (*Catostomus occidentalis*), and California roach (*Hesperoleucus symmetricus*) (Moyle 2002, USBR 2019). The middle Sacramento River is an important migratory corridor for juvenile salmonids, and OCWB's shallow-water habitats provide important growth opportunities for salmonid fry. Faster growth can promote higher rates of survival for juvenile salmonids during their remaining freshwater life stages (Bellido-Leiva et al. 2021). Furthermore, anadromous salmonids with greater body mass at ocean arrival have higher survival and spawning return rates (Woodson et al. 2013). So enhanced growth conditions in off-channel areas aid native fish populations (Limm & Marchetti 2009, Claiborne et al. 2011, Satterthwaite et al. 2012) and are important to preserve wild Chinook salmon (*Onchorynchus tshawytscha*) populations. This is especially true for the endangered winter-run Chinook salmon, since the seasonality of inundation in these areas generally coincides with fry dispersal between August and December (Yoshiyama et al. 1998, NMFS 2014, Bellido-Leiva et al. 2021). Despite their critical effect on salmonid life cycle, comprehensive, and consistent datasets on the range and availability of OCWBs along the middle Sacramento River are lacking (Limm & Marchetti 2009, Bellido-Leiva et al. 2021). Only Kondolf & Stillwater Sciences (2007) estimated discharge magnitudes needed to activate some OCWBs on public owned land. As a result, it is important to identify ways to estimate OCWB dynamics, expanding our knowledge of their ecological use as a function of mainstem flow, habitat capacity, and residence times. This could help managers and decision-makers develop recovery actions targeting juvenile salmonids in

these areas, such as defining flow pulses and landform changes to expand shallow-water habitat, while reducing stranding risk, during low flow years (Kondolf & Stillwater Sciences 2007). By incorporating this information in juvenile production models (e.g., WRHAP; Bellido-Leiva et al. 2021) and/or decision-making models (e.g., Winter-run DSM; Peterson & Duarte 2020), initial estimates of population response to proposed actions could be made.

Advances in remote sensing imagery and geographic information systems (GIS) provide powerful tools for spatiotemporal analysis of eco-hydrological features in regions and river basins of interest (e.g., North Pacific Rim; Whited et al. 2013). Extensive literature exists on using these technologies for inundation modeling (Chen et al. 2011, Huang et al. 2012, 2013, 2014, 2018, Chen et al. 2014), flood monitoring (Wang et al. 2002, Frazier et al. 2003, Knebl et al. 2005), river geomorphology (Gupta & Liew 2007, Hou et al. 2019), riparian vegetation communities (Johansen et al. 2007, Whited et al. 2007), habitat mosaic shifting (Brennan et al. 2019), and assessment of in-stream and floodplain habitats (Whited et al. 2002, 2013, Gilvear et al. 2004, 2008, Legleiter et al. 2004, Luck et al. 2010, Wirth et al. 2012, Gallart et al. 2016). These analyses have been done on a wide range of resolutions, from fine ( $\leq 5$ -m resolution; Quickbird products) to moderate (10- to 100-m resolution; LandSat and Sentinel-2 imagery), depending on study area extent and required level of detail. Mapping and monitoring river systems from moderate scale satellite remote sensing require piecing together multiple image scenes capturing snapshots of dynamic river and environmental conditions to create desired mosaics of surface conditions over large geographical regions. The interpretation of these river features can be limited by satellite imagery's ability to resolve temporal changes in river features from relatively coarse overpass frequency ( $\sim 8$  days for LandSat; Gorelick et al. 2017). However, the relative abundance and representation of major habitat characteristics in dynamic river systems has been shown to be relatively stable even as the mosaic of habitats changes over time (Ward et al. 2002, Whited et al. 2007). This shifting habitat mosaic (Stanford et al. 2005) of shallow water habitat allows the use of multitemporal satellite remote sensing products to describe and compare the abundance and distribution of riverine features (Whited et al. 2013). Most studies using these products focus on estimating off-channel habitat characteristics such as physical complexity (Luck et al. 2010), extension, width, or type of riverine habitat (e.g., orthofluvial vs parafluvial zones; Whited et al. 2002). For instance, a comprehensive geospatial database based on global Landsat TM imagery (30-m resolution), the Riverscape Analysis Project (RAP), described the distribution and physical characteristics of river basins, floodplains and river networks for catchments draining into the North Pacific, including the Sacramento River Basin (Luck et al. 2010, Whited et al. 2013).

However, these studies and datasets neglect the dynamic behavior of off-channel habitats and do not establish relationships between flow conditions and the extent of inundated shallow habitats over time. Here we present a regional-scale method, focused on the Middle Sacramento River, using moderate scale remote sensing imagery (LandSat-8 and Sentinel-2 multispectral imagery) to construct a database relating Sacramento River mainstem flows with the extent, location and residence time of shallow inundated riparian areas. These areas are key for a variety of species (Moyle 2002, Kondolf & Stillwater Sciences 2007), particularly for juveniles winter-run Chinook salmon (Maslin et al. 1996, Limm & Marchetti 2009, Bellido-Leiva et al. 2021). As such, this database expands on values reported by Kondolf & Stillwater Sciences (2007) and explores the effect of pulse flow actions on off-channel habitat dynamics.

## 4.2. Methods

### 4.2.1. Study area and data

The Sacramento River Valley, in California's Central Valley, is one of the most regulated river systems in the US, with an extensive and complex water management infrastructure that serves two state-wide water projects, the California State Water Project (SWP) and the Central Valley Project (CVP). Sacramento River flows have been greatly altered as a result of reservoir operation, with the least divergence from natural flows during the cool and rainy season (November-March; Shelton 1995), when reservoir storage is drawn down to provide flood protection, and the most during spring snowmelt and dry summers, due to the storage of snowmelt flows and the release of stored water for agricultural and urban water uses (Shelton 1995). High-flows, responsible for off-channel habitat activation, are caused by heavy orographic precipitation along the west slope of the northern Sierra Nevada and the south slope of Mt Shasta-Trinity Alps (Ralph et al. 2016), from landfalling atmospheric rivers and south-southeasterly terrain-locked Sierra barrier jets during the cool-season months of November-March (Kim et al. 2013, Kingsmill et al. 2013, Ralph et al. 2016). Extreme daily precipitation from the period 2001-2011 ranged 43-103 mm, and contributed to ~2-7% of

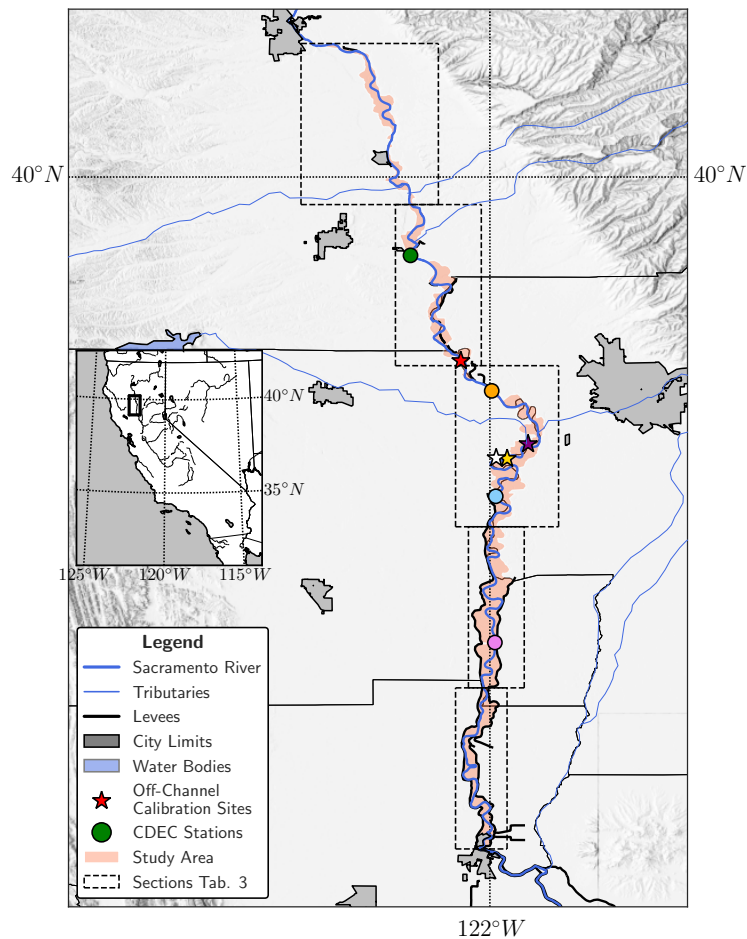


FIGURE 4.1. Middle Sacramento River from Red Bluff to Colusa.



total Water Year precipitation (Ralph et al. 2016). Flood-protection levees has further reduced the extent of shallow water areas under these events and limited fluxes of organisms (e.g., *D. pulex* larvae; Corline et al. 2017) and materials between mainstem and side channel habitats (Wohl et al. 2015), responsible of highly productive ecosystems key in the life history and development of native fish species (e.g., Sommer et al. 2007, Limm & Marchetti 2009). Although inundation at remnant shallow habitats is much less frequent and extensive than it was historically (Opperman et al. 2010), they still provide critically important developing habitats for Sacramento River salmonids, especially the endangered winter-run Chinook salmon (Limm & Marchetti 2009, Bellido-Leiva et al. 2021). The study area stretches along the mid-Sacramento River, from Red Bluff (river mile 244) to Colusa (river mile 144), covering a total of 100 river miles, of which a  $\sim 30\%$  is bounded by flood protection levees. Nonetheless, this river section contains most available OCWBs along the Sacramento River, as the mainstem is heavily channelized downstream Colusa. The extent of the study area was manually defined following existing levees (mainly between Chico and Colusa; Fig. 4.1) and Sacramento River inundated areas on March 3<sup>rd</sup>, 2017, greatest flooding extent captured in remote sensing imagery, to exclude other sources of surface water (e.g., irrigated fields, urban areas) from the area of interest. A total of 1625 points were defined, encompassing an area of 159.7 km<sup>2</sup> (Fig.1).

Two sets of remotely sensed imagery, covering the complete area of interest, were retrieved from Google Earth Engine catalog (Gorelick et al. 2017): (1) Time series of USGS LandSat-8 Surface Reflectance Tier 1 at 30 m resolution over the period 2014-2021; and (2) Time series of Sentinel-2 MSI (MultiSpectral Instrument), Level-2A at 10 m resolution over the period 2018-2021. The band characteristics for both products are listed in Table 4.1. When several images were available for the same date covering different portions of the study area, they were combined and, if overlap existed, composited by selecting the highest-quality pixels, based on the absence of clouds and/or cloud shadows. On average, one image was available each 7-9 and 5-10 days, for LandSat-8 and Sentinel-2 products, respectively. Hydrologic data, observed daily Sacramento River flow [m<sup>3</sup>/s], was retrieved from the California Data Exchange Center (CDEC) for the stations at Hamilton City (HMC), Bend Bridge (BND; green), Vina Bridge (VIN; gold), Ord-Ferry Channel (ORD; cyan) and Butte City (BTC; pink) (Figure 4.1), covering the period of available remotely sensed imagery. Levee spatial data was retrieved from the National Levee Database (<https://levees.sec.usace.army.mil/>).

#### 4.2.2. Estimate of inundation extent

Inundation was extracted from multispectral imagery using the modified Normalized Difference Water Index (mNDWI; Xu 2006) and the Automated Water Extraction Index (AWEI; Feyisa et al.

TABLE 4.1. Characteristics of USGS LandSat-8 and Sentinel-2 multispectral sensors.

Spectral Region	USGS LandSat-8			Sentinel-2		
	Band	Wavelength [ $\mu m$ ]	Pixel Size [m]	Band	Wavelength [ $\mu m$ ]	Pixel Size [m]
Blue	2	0.45-0.51	30	2	0.4966	10
Green	3	0.53-0.59	30	3	0.560	10
Red	4	0.64-0.67	30	4	0.6645	10
Near Infrared (NIR)	5	0.85-0.88	30	8	0.8351	10
Shortwave Infrared 1 (SWIR1)	6	1.57-1.65	30	11	1.6137	20
Shortwave Infrared 2 (SWIR2)	7	2.11-2.29	30	12	2.2024	20

2014). The first was based on NDWI proposed by McFeeters (1996), widely used in the first 10 years of the 21st century (e.g., Chowdary et al. 2008, Hui et al. 2008). Xu (2006) modification replaced the Near Infrared (NIR) band for the Short-wave Infrared (SWIR) band since the latter can reflect subtle characteristics of water and is less sensitive to concentration of sediments and other constituents in the water than the NIR band (Huang et al. 2018), expected during faster, more turbulent flows. This, in turn, makes mNDWI more stable and reliable than NDWI for floodplain delineation. The expression was developed on the basis of a combination of reflectance in the green and shortwave-infrared (SWIR) wavelengths,

$$(4.1) \quad mNDWI = \frac{\text{Green Band} - \text{SWIR1 Band}}{\text{Green Band} + \text{SWIR1 Band}}$$

being bands 3 (Green), 6 (SWIR1) for LandSat-8 and 3, 11 for Sentinel-2 products, respectively (Table 4.1). The use of band ratios enhances the spectral signals by contrasting the reflectance between different wavelengths, reduces many multiplicative noises (illumination differences, atmospheric attenuation, certain topographic variations), and allows comparison between different images through time and space (Ji et al. 2009, Mohammadi et al. 2017).

The AWEI was developed to improve surface water identification from a time series of LandSat-8 imagery, using a wider range of spectral bands, specially from dark surfaces (e.g., shadows and built-up structures) with similar reflectance patterns (Feyisa et al. 2014).

$$(4.2) \quad AWEI_{nsh} = 4 \times (\text{Green} - \text{SWIR1}) - (0.25 \times \text{NIR} + 2.75 \times \text{SWIR2})$$

$$(4.3) \quad AWEI_{sh} = \text{Blue} + 2.5 \times \text{Green} - 1.5 \times (\text{NIR} + \text{SWIR1}) - 0.25 \times \text{SWIR2}$$

being bands 2 (Blue), 3 (Green), 5 (NIR), 6 (SWIR1), 7 (SWIR2) for LandSat-8, and 2 (Blue), 3 (Green), 8 (NIR), 11 (SWIR1), 12 (SWIR2) for Sentinel-2 products, respectively (Table 4.1). The equation coefficients were determined based on the analysis of the reflectance properties of different land cover types (Feyisa et al. 2014). Due to the greater spectral response of water in the green and blue bands respect to NIR and SWIR1 (Mishra & Pant 2020), water pixels should present large positive values. Then, NIR and SWIR2 bands help further differentiate water from other surfaces with similar reflectance characteristics by subtracting their value and forcing non-water pixels to present even larger negative values (Feyisa et al. 2014).  $AWEI_{sh}$  further improve the accuracy of  $AWEI_{nsh}$  to differentiate water pixels from shadow areas. Both indices were computed to determine the importance of shadow pixels in the area of interest.

Thresholding is one of the most crucial issues in using water indices for delineating surface water areas. Generally, mNDWI values range from -1 to 1, with values over 0 representing surface water, based on its reflectance characteristics (Huang et al. 2018). Likewise,  $AWEI_{nsh}$  over 0

TABLE 4.2. Off-channel Water Bodies used for mNDWI threshold calibration. Reference names and coordinates extracted from Kondolf & Stillwater Sciences (2007). Location along the Sacramento River is shown in Figure 4.1.

OCWB	Latitude	Longitude	Sacramento River Flow [m <sup>3</sup> /s]	Color at Fig. 4.1
Site 14 [RM 187R]	39.673	-121.992	>730	White
Site 15 [RM 189.5L]	39.672	-121.980	>650	Gold
Site 17 [RM 191.7R]	39.689	-121.955	>870	Purple
Site 22 [RM 203R]	39.786	-122.034	>650	Red

indicate water features (Feyisa et al. 2014). As such, a threshold of 0 is commonly used to identify surface water pixels (Xu 2006, Zhou et al. 2017). Nevertheless, a slight calibration on the threshold value should be performed to improve result accuracy (Ji et al. 2009), as shown by Chen et al. (2014) and Huang et al. (2018) that defined thresholds of -0.45 and 0.2 for mNDWI, and 0.25 for  $AWEI_{nsh}$ . Four surveyed off-channel habitats between Bend Bridge and Colusa (Table 4.2; Fig. 4.1) were used to calibrate the threshold value for both indices by comparing computed values with periods of known inundation, identified from flow thresholds at Hamilton City station, reported by Kondolf & Stillwater Sciences (2007) and analyzing available images from expected inundation dates. The computed estimates were visually checked and corrected to avoid including misclassified cloud pixels in the analysis. Nevertheless, thresholding a time series of images that cover the same water body is specially complicated as threshold index values might change for different overpass dates, and hence, may need to be fixed for each date independently (Chowdary et al. 2008, Huang et al. 2018). Thus, the defined threshold from the site analysis was compared with an automatic water threshold recognition procedure, Otsu’s binarization algorithm, widely used with good results (Du et al. 2014, Xie et al. 2016, Huang et al. 2018). Google Earth Engine implementation of Otsu’s algorithm was provided by Li et al. (2021).

Cloud and cloud shadow pixels were masked out the composite images using algorithms developed by Earth Engine (Gorelick et al. 2017), based on Landsat-8 QA bands and Sentinel-2 cloud probability collection, before mNDWI and AWEI computation to avoid their misclassification as surface water areas. Images with cloud cover above 20% over the study area were removed from the time series used for the analysis, as the cloud-free image would underestimate existing inundated area. Likewise, Sacramento River mainstem pixels were extracted using the main channel area defined by the Central Valley Floodplain Evaluation and Delineation Program (CVFED) in their HEC-RAS/FLO-2D modelling efforts, to clearly differentiate off-channel areas. Furthermore, other OCWBs and water bodies disconnected to the Sacramento River within the study area were not considered in the inundated area calculations. Total off-channel habitat area for each available date was then computed by summing the area of pixels with indices values greater than the defined threshold. Image processing and computations were performed using the Google Earth Engine Python API.

#### **4.2.3. Estimate of off-channel habitat residence time**

Water residence time within OCWB, after activation during high-flow events, greatly determines the growth potential of Sacramento River Chinook salmon, mainly due to the required time for optimal zooplankton development, and therefore its forage abundance (Corline et al. 2017, Katz et al. *in progress*), and higher water temperatures that boost juvenile growth (Lusardi et al. 2020, Zillig et al. 2021). As such, it is crucial to determine the time availability of OCWBs once they become activated to estimate their impact on the development and population dynamics of Sacramento River salmonids. The change in inundated area within consecutive available images, during high-flow events with suitable cloud cover (<20%), was computed to determine the cut-off point when off-channel habitat was no longer available, considered when less than a 1% of the initial wetted area and/or 100 acres remained, or when inundated areas became disconnected from the mainstem.

## 4.3. Results

### 4.3.1. Indices threshold

#### 4.3.1.1. *mNDWI*

Computed *mNDWI* values at the four off-channel sites listed in Table 4.2 presented a clear differentiation between dry and wet conditions for both LandSat-8 and Sentinel-2 products, especially at site 17, since it requires the highest flows to become active. During certain dry conditions at the OCWBs, for mainstem flows well under activation thresholds (e.g.,  $< 200 \text{ m}^3/\text{s}$ ), *mNDWI* values were consistently under -0.2, much lower than the theoretical 0 threshold (Xu 2006, Ji et al. 2009). Under wet conditions, when threshold flows were exceeded, values over -0.05 were extracted from the remote sensing image collection. Greater *mNDWI* values were obtained for increasing flows (Fig. 4.2), as expected from more prominent and deeper inundated areas, closer in spectral behavior to the mainstem ( $\textit{mNDWI} > 0.4$ ). As such, the range from -0.2 to -0.06 was analyzed in more detail to establish an approximate threshold. Site 14 had the greatest number of *mNDWI* values in this range, with several observations in the -0.10 to -0.16 range during May 2017 (LandSat-8) and June-August 2019 (LandSat-8 and Sentinel-2), when higher flows occurred (400-600  $\text{m}^3/\text{s}$ ), but several weeks after storm high-flow events ( $>14$  days). Additionally, several values were within the -0.2 to -0.15 range for low flows ( $< 300 \text{ m}^3/\text{s}$ ). As such, these slightly higher *mNDWI* values could be from wetted but not inundated conditions at the off-channel area, partially inundated pixels, or a disconnected pool with reflectance properties closer to soil due to its shallow depth (Chowdary et al. 2008, Yagmur et al. 2019). Thus, they were classified as dry or wet but not connected, leading to defining a final threshold for *mNDWI* of -0.08/-0.07, for LandSat-8 and Sentinel-2 products respectively, within range of values defined in literature (Chen et al. 2014, Du et al. 2014, Xie et al. 2016, Huang et al. 2018). Nevertheless, sites 14, 15 and 17 presented wetted conditions for flows under the required threshold (vertical dashed line in Figure 4.2). The analysis of the images represented by each data point (e.g., 17<sup>th</sup> March 2017, and 19<sup>th</sup> February 2019) showed that the off-channel areas were effectively inundated, from high flows 4-11 days before the satellite overpass. This illustrated continued activation of off-channel habitat during receding flows.

The defined threshold was less than the automatic threshold values obtained with Otsu's algorithm for all available images (Fig. 4.3). Data points recognized as inundated by both procedures were highlighted on Figure 4.2 and corresponded to most dates with known wetted conditions (e.g., high flows during March 2019). Sentinel-2 defined thresholds were lower than those for LandSat-8 during overlapping dates (Fig. 4.3), as might be expected from the higher resolution of its Green and SWIR1 bands allowing more precise classification of water/non-water pixels in shallower areas (Table 4.1). Sites 14 and 22 had the highest proportion of misclassified conditions, with a 25-50% of the inundated dates only recognized by the constant threshold. Otsu's algorithm thresholding seems to misclassify wet pixels with a smaller inundation extent and/or shallower conditions, when *mNDWI* values were closer or under 0. This could be expected since the algorithm has been used to identify and delineate extensive surface water bodies (e.g., lakes, reservoirs; Du et al. 2014, Xie et al. 2016), whose optical characteristics might differ from shallow waters. The optical properties of the latter are not determined by water itself, but also by other water components such as phytoplankton, suspended matter and water depth (Zhou et al. 2017, Yagmur et al. 2019), making *mNDWI* values closer to land values than open water. As such, dynamic thresholding might underestimate the total extent of activated side-channel features at certain dates, mainly at shallower areas when  $\textit{mNDWI} \approx 0$ .

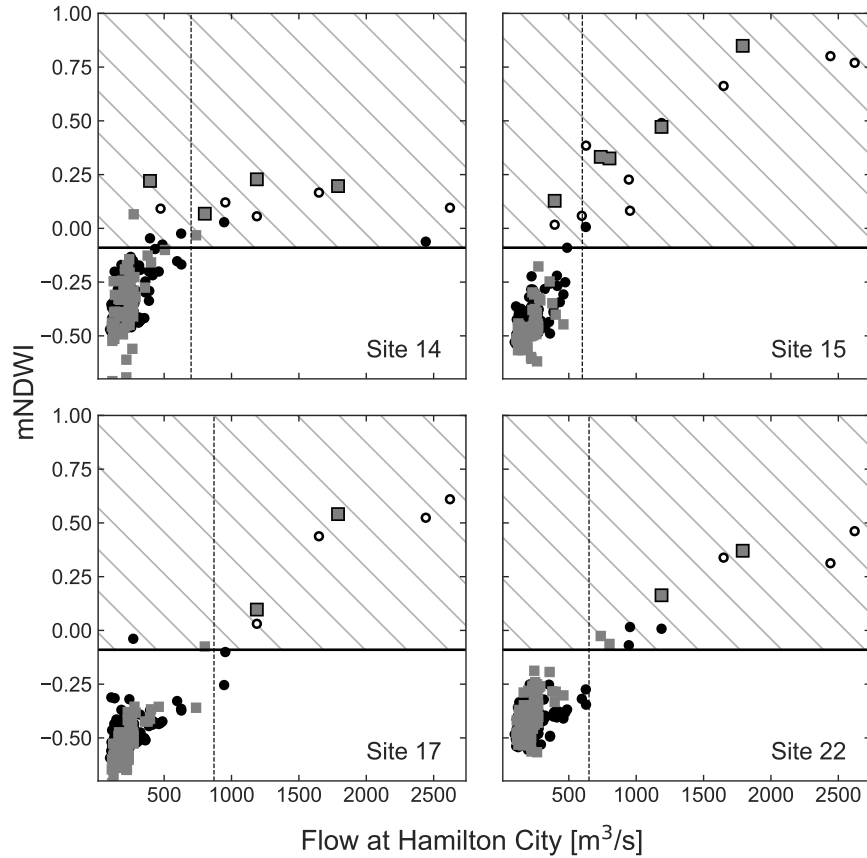


FIGURE 4.2. Computed modified Normalized Difference Water Index (mNDWI) values for surveyed off-channel habitats (Table 4.2) reported in Kondolf & Stillwater Sciences (2007) and existing daily Sacramento River flows recorded at Hamilton City (HMC). The hashed area indicates inundated conditions at the site. The vertical dashed line indicates required Sacramento River flows for off-channel activation (Kondolf & Stillwater Sciences 2007). Highlighted points show dates when both single and dynamic thresholds identified the location as inundated

#### 4.3.1.2. $AWEI_{nsh}$ and $AWEI_{sh}$

Computed  $AWEI_{nsh}$  at the analyzed sites presented a very erratic classification of inundated pixels, with great differences in magnitude between sites. For instance, index values for known inundated date at sites 15 and 22 were much lower than those representing dry conditions at site 14. As such, a single threshold for all sites could not be defined, indicating an important impact of shadowed conditions in our area of interest that greatly reduced the accuracy of  $AWEI_{nsh}$  values. Thus,  $AWEI_{nsh}$  was not further considered and only  $AWEI_{sh}$  was included in our analysis. A similar behavior than mNDWI values was computed for  $AWEI_{sh}$ , considering its difference in magnitude, with certain dry conditions represented by values under -1500 (Fig. 4.4). As for mNDWI, site 14 presented the highest density of data points between this value and the theoretical threshold of 0. Detailed analysis of the -1500 - 0 range led to defining a threshold of  $AWEI_{sh} = -310$ . Dynamic thresholding provided values much smaller than the defined threshold and even the considered

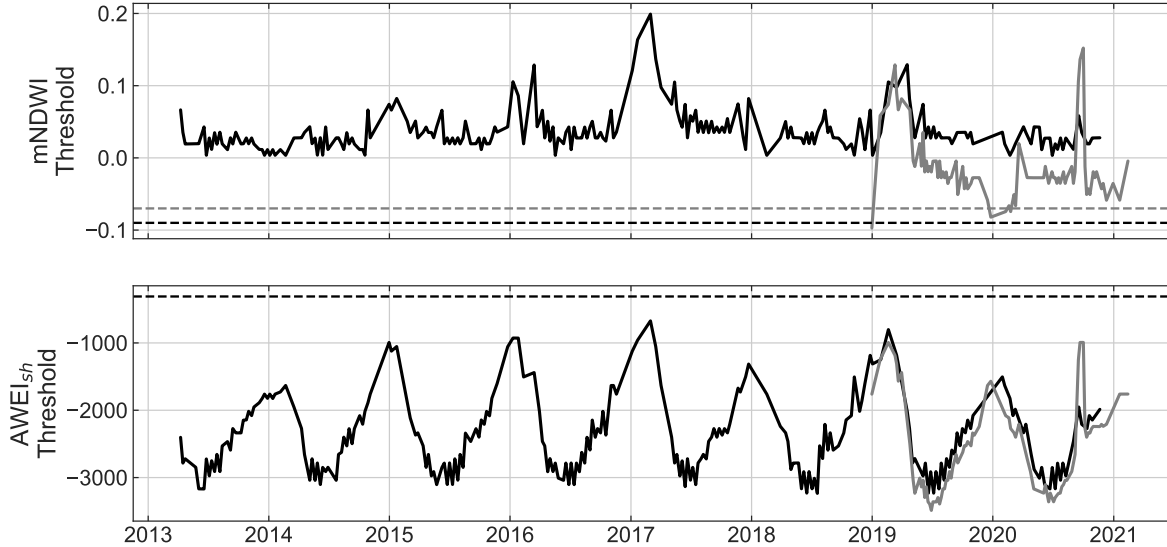


FIGURE 4.3. Computed mNDWI and  $AWEI_{sh}$  threshold values using Otsu’s binarization algorithm. Black line represents LandSat-8 products while grey line represents Sentinel-2 products. Dashed lines indicate defined single thresholds.

land value ( $< -1500$ ; Fig. 4.3). As such, dynamic thresholding was not used to compute total inundated areas because of expected common misclassifications. Nonetheless, AWEI showed to have a relatively stable optimal threshold (Feyisa et al. 2014, Huang et al. 2018), and thus, accurate results could be achieved using a single threshold for the time-series of remote imagery (Xie et al. 2016).

### 4.3.2. Mid-Sacramento River inundated area

#### 4.3.2.1. Computed inundated area using mNDWI and $AWEI_{sh}$

Computed inundation extent was compared with surveyed values reported by Kondolf & Stillwater Sciences (2007) to see if realistic magnitudes were obtained using the proposed method. Due to satellite overpass frequency, images during the peak of high flow events were scarce, and those available presented cloud covers over the 20% threshold. As such, off-channel areas quantification was mainly obtained from remote imagery 2-5 days, on average, after the recorded flow peak. Nevertheless, it is assumed that they are representative of the expected off-channel extent for Sacramento River Pacific salmonids, as their rearing quality is associated to prolonged residence times. Estimates from both indices agreed well with Kondolf & Stillwater Sciences (2007), which values formed a lower bound of available off-channel areas along their reported flow range (Fig. 4.5ab). This was an expected outcome since they represent only a subset of all OCWBs from Red Bluff to Colusa, those located within public land (Kondolf & Stillwater Sciences 2007). Furthermore, they also show a similar increase rate in total wetted area per increase in mainstem flow, with a rapid increase between 200 to 350  $m^3/s$  followed by a slight decrease in the growth rate and, finally, significant gradual increases as flows exceed 700  $m^3/s$ . This suggested that non-surveyed areas present a similar mosaic of OCWBs that become active under a wide range in flows.

Several peak flows showed 2-4 different off-channel area estimates for the same date (e.g., 1,980  $\text{m}^3/\text{s}$  - 2/19/2019), as they were computed using each available product (LandSat-8 and Sentinel-2), and both the single and dynamic threshold procedures. More detailed analysis on the effectiveness and accuracy of each procedure is presented in the following sections. Nonetheless, a byproduct of considering each procedure, when combined with satellite band resolution, is that quantified off-channel areas show some dispersion, especially for low flows and small inundation areas (Fig. 4.5). This was expected as pixels could be classified differently by each procedure, building proportional differences rapidly under low flow conditions (Ji et al. 2009, Huang et al. 2018). Nevertheless, since they represent situations with limited off-channel available ( $<100$  acres), the dispersion does not pose critical differences on their potential for enhanced development of juvenile salmonids (Bellido-Leiva et al. 2021). Flows  $\sim 500 \text{ m}^3/\text{s}$  were required to exceed 100 acres of wetted surface consistently, but a rapid increase in inundated areas was computed subsequently, reaching 1,000 acres for flows  $\sim 1,000 \text{ m}^3/\text{s}$ . Largest off-channel inundation extents ( $> 5,000$  acres) occurred during the greatest

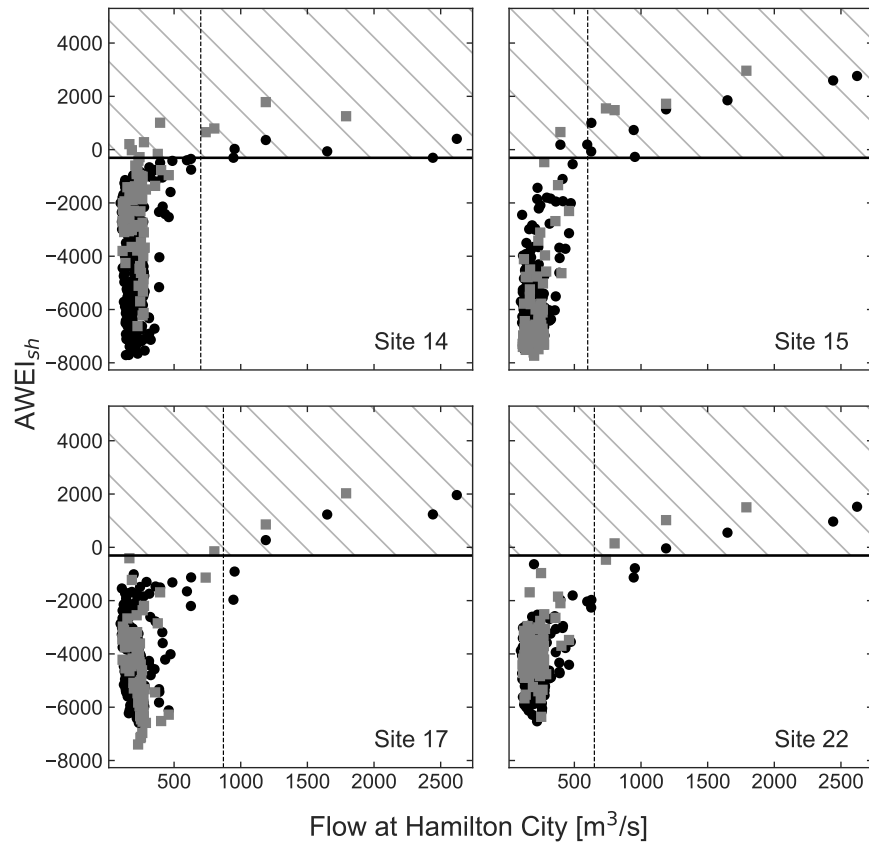


FIGURE 4.4. Computed Automated Water Extraction Index ( $\text{AWEI}_{sh}$ ) values for surveyed off-channel habitats (Table 4.2) reported in Kondolf & Stillwater Sciences (2007) and existing daily Sacramento River flows recorded at Hamilton City (HMC). The hashed area indicates inundated conditions at the site. The vertical dashed line indicates required Sacramento River flows for off-channel activation (Kondolf & Stillwater Sciences 2007).

high flow events on the available remote sensing imagery record (March 2017 and 2019), when flows along the Sacramento River mainstem exceeded 2,000 m<sup>3</sup>/s.

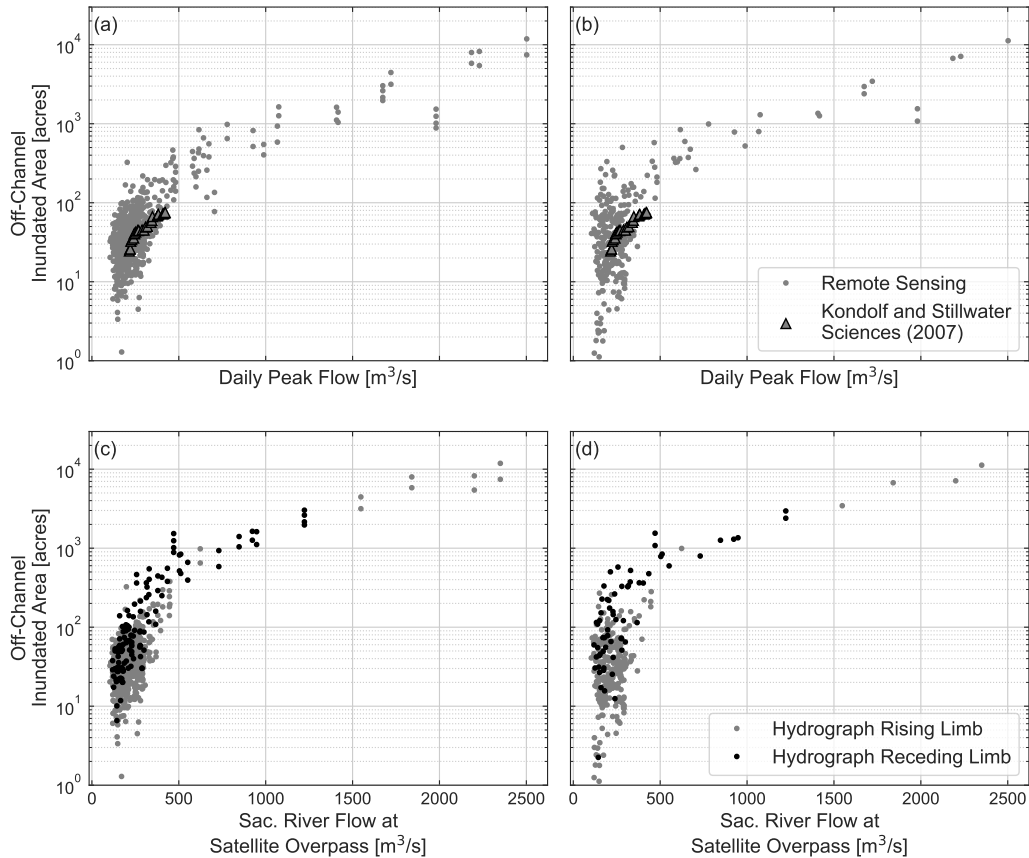


FIGURE 4.5. Computed shallow areas extent along the mid-Sacramento River for each high-flow event peak using (a) mNDWI with single and dynamic thresholds; and (b) AWEI<sub>sh</sub> single threshold. Surveyed estimates by Kondolf & Stillwater Sciences (2007) are also included for comparison. Subplots (c) and (d) show computed off-channel inundated areas against flows at satellite overpass for each water index.

Quantified off-channel areas for 1,980 m<sup>3</sup>/s seemed to be underestimated when compared with the trend of the remaining high-flow data points (Fig. 4.5ab). This might be from the five-day time lag between the available image (2/19/2019) and peak flows (2/14/2019), that led to smaller estimates than expected, most likely occurring shortly after peak flows. Nevertheless, extensive inundated conditions persisted during receding flows at satellite overpass even with 470 m<sup>3</sup>/s daily flow (24% of the peak), as previously analyzed for sites 14, 15 and 17 (Section 3.1.1). When off-channel area estimates are plotted against Sacramento River daily flow at the date of satellite overpass (Fig. 4.5cd), an identifiable pattern arises on the distinct OCWBs behavior during rising and receding flows. This pattern is a result of flood wave propagation and unsteady flows, having for the same stage a higher discharge during rising flows than during the falling stage (Petersen-Øverleir 2006). These effects generate distinctive loops in the stage-discharge relationship for the Sacramento River, referred to as hysteresis (e.g., Chow 1959, Fenton & Keller 2001). Since river



stage is the main driver of off-channel habitat activation, computed inundated area extent also showed this pattern (Fig. 4.5cd). As such, inundation during receding flows showed greater extent for lower flow magnitudes, than rising limb wetted areas, due to the backwater effect of the flood wave (Petersen-Overleir 2006).

#### 4.3.2.2. *mNDWI versus AWEI<sub>sh</sub>*

Both indices led to similar estimates of off-channel inundation ( $r^2=0.94$ ), as reported in other areas (Xie et al. 2016, Mohammadi et al. 2017, Huang et al. 2018, Li et al. 2021), especially for the highest peak flows. The largest differences occurred at the opposite end of the range, with  $AWEI_{sh}$  seemingly classifying inundated areas more accurately for the lowest flows (Fig. 4.6f). This is further suggested by the bigger divergence between estimates from LandSat-8 and Sentinel-2 products (Fig. 4.6e), as improved classification combined with the higher resolution of Sentinel-2 images should increase the difference with the lower resolution imagery of LandSat-8.

#### 4.3.2.3. *Single threshold versus dynamic threshold for mNDWI*

As expected, off-channel extent quantification using a single threshold led to consistent greater estimates of inundated area than those with the defined dynamic thresholds for both LandSat-8 and Sentinel-2 products (Fig. 4.6ab). Estimates averaged 80% and 11% greater, with 5- and 3-fold maximum differences, for LandSat-8 and Sentinel-2, respectively. These larger percent differences in quantification between both procedures were for dates with low mainstem flows and minimal side-channel activation (e.g., 06/18/2016, 8/11/2018, 7/14/2019), for which any additional pixel classified as wet generated a big percent difference. During the highest flow events on available remote imagery (March 2017, 2019), the largest differences in quantified off-channel inundation were computed ( $> 1,000$  acres). This was an expected outcome as thresholds between 0.05-0.2 were defined for these dates (Fig. 4.3), that might misclassify the transition areas of shallow water as dry pixels (Fig. 4.7). Likewise, the single threshold would be able to capture those transition areas, but it may also include other regions only partially wetted (represented by negative  $mNDWI$  values) or poorly connected, very shallow sections (Fig. 4.7), overestimating available off-channel extent. Nonetheless, defined inundation extents using both procedures presented a high correlation between them ( $r^2 = 0.997$  and  $0.998$ ; Fig. 4.6ab), suggesting that the proportion of misidentified pixels stayed consistent across images, and thus, across mainstem flows.

#### 4.3.2.4. *LandSat-8 versus Sentinel-2*

Computed total inundated area agreed well between LandSat-8 and Sentinel-2 products for both water indices, similar to previous analysis in literature (e.g., Zhou et al. 2017, Mishra & Pant 2020, Fig. 4.6cde). As could be expected, biggest differences occurred for dates with smaller inundation extents and from the single threshold procedure ( $mNDWI$  and  $AWEI_{sh}$ ), when LandSat-8 estimates exceeded computed areas with Sentinel-2 images (Fig. 4.6cde). The higher resolution of Sentinel-2 products (20 m versus 30 m pixel size, Table 4.1) allowed for a more precise identification of wet pixels under low flow conditions, as partially wet LandSat-8 pixels might be classified as surface water despite a proportion of its surface being dry. This is especially important for the defined single thresholds since their low values ( $< 0$ ) increase the chance of misidentifying partially wetted pixels as water. Even so, for inundated areas under 200 acres, the difference between both estimates was  $< 30$  and  $< 50$  acres, on average, for  $mNDWI$  and  $AWEI_{sh}$ , respectively. Dynamic thresholding presented very similar estimates using both products ( $r^2 = 0.98$ ; Fig. 4.6d), as could be expected from the described difference in the threshold magnitude during overlapping dates (Fig. 4.3).

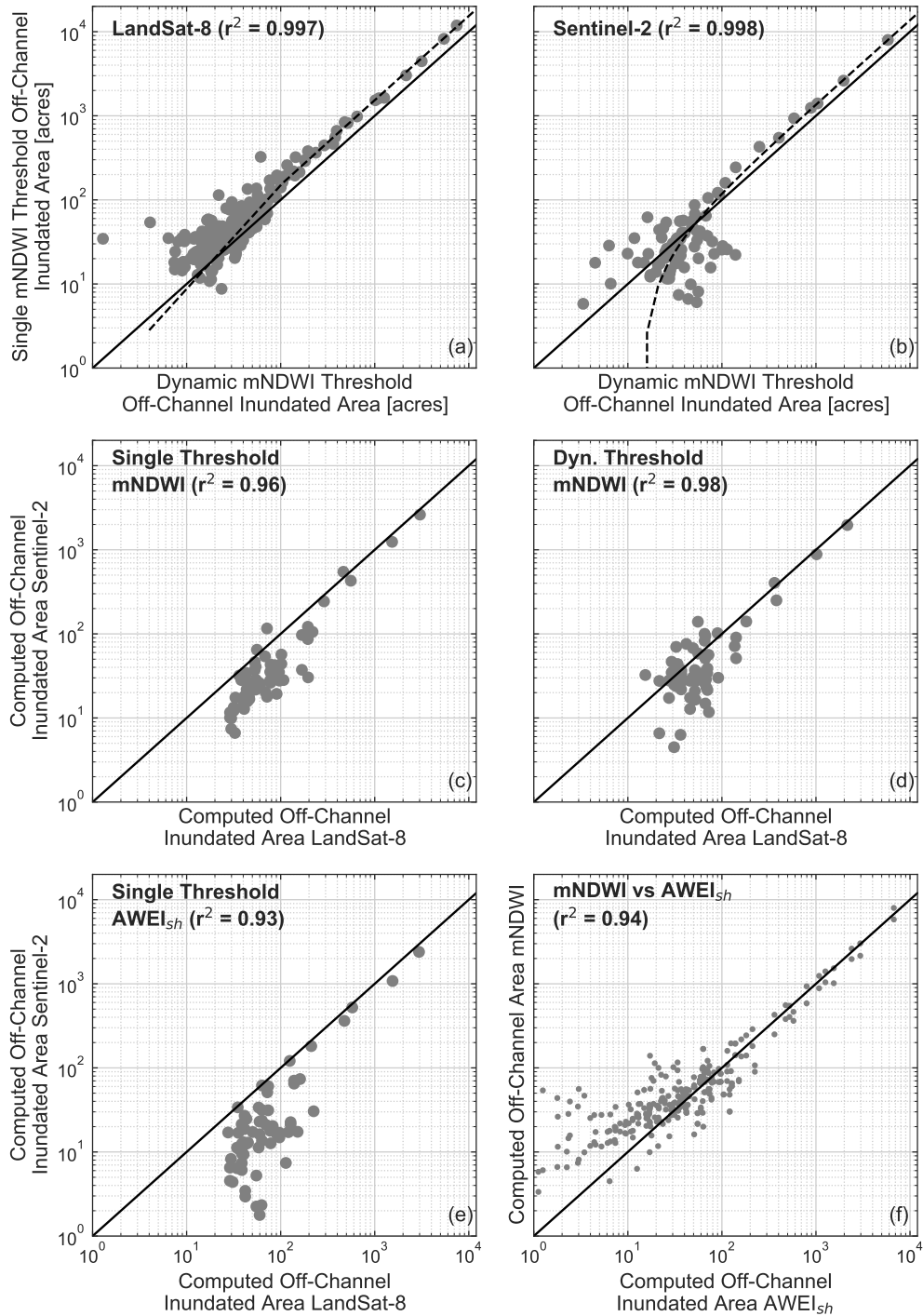


FIGURE 4.6. Comparison of computed inundated areas using the different considered procedures: (a) and (b) single vs dynamic mNDWI threshold using LandSat-8 and Sentinel-2 imagery, respectively; (c), (d) and (e) estimates from LandSat-8 vs Sentinel-2 products from single and dynamic mNDWI thresholding and AWEI<sub>sh</sub> single threshold, respectively; and (f) mNDWI vs AWEI<sub>sh</sub> estimates.

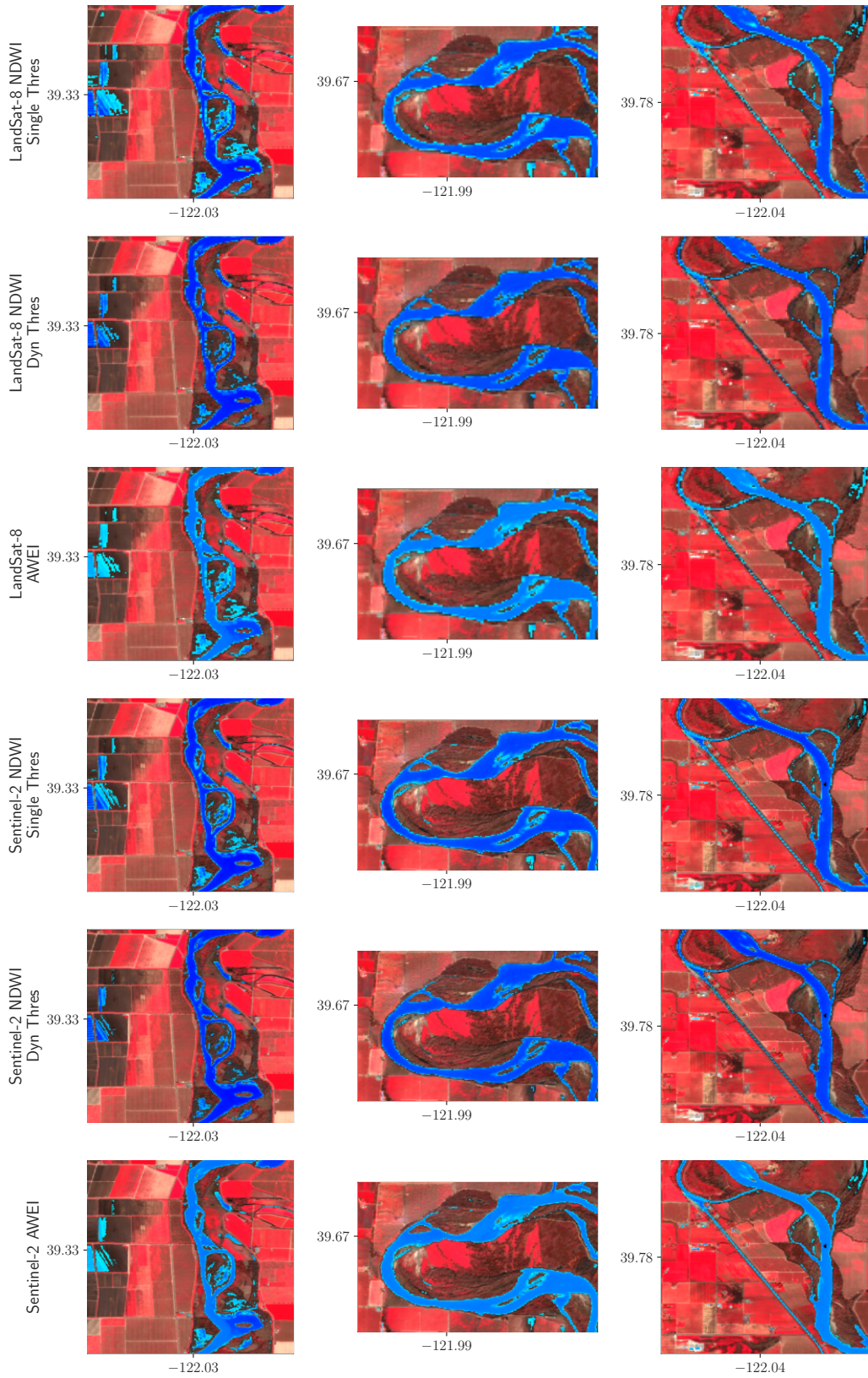


FIGURE 4.7. Identified inundated areas with each product and method used for three areas along the Sacramento River during a high-flow event on 03/16/2019.

Nevertheless, the lack of availability of Sentinel-2 products (end of 2018-present) greatly limited the range of mainstem high-flow events captured by the remote sensing imagery and did not allow for their exclusive use in this analysis.

#### 4.3.3. Off-channel inundation residence time

Cloud coverage during several high-flow events available on the remote sensing imagery record (e.g., February 2017) reduced the number of available storm events for this analysis. Residence time at off-channel areas depended mainly on the extent of the initial inundation and the flow rate of the decreasing limb, as expected from the existence of the hysteresis phenomenon explored previously (Fig. 4.5cd). On average, shallow water areas did not persist over 7-18 days, chiefly

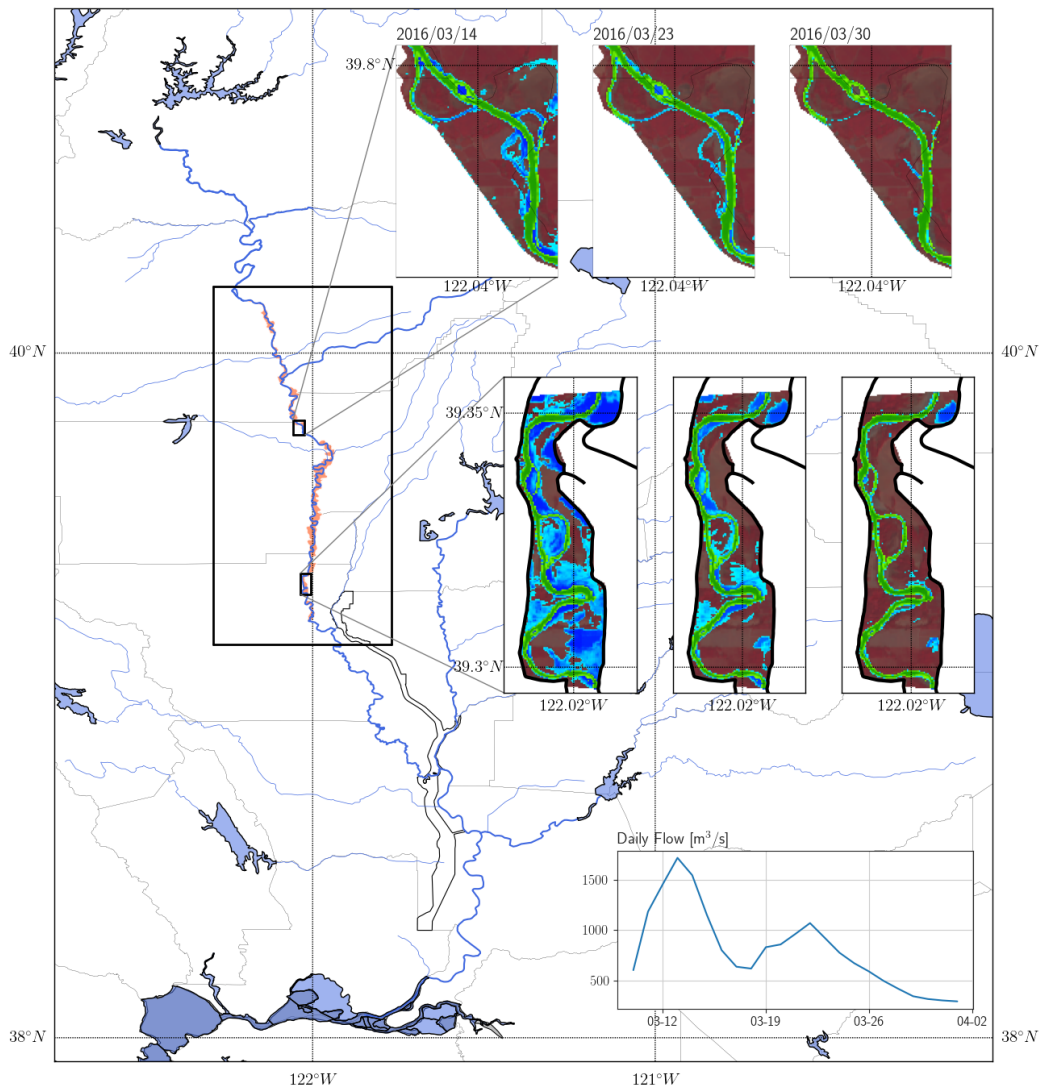


FIGURE 4.8. Off-channel inundated areas after 03/13/2016 storm event (hydrograph at bottom right corner) at two specific locations along the study area (black rectangle).

when storm events were isolated (e.g., Fig. 4.8 and 4.9). Nevertheless, during very wet periods (e.g., January-March 2017, 2019), when mainstem flows exceeded 1,000 m<sup>3</sup>/s for extended periods, extensive off-channel inundation persisted for up to several months (>40 days), giving a small glimpse of historical conditions pre-water infrastructure development (Kelley 1998).

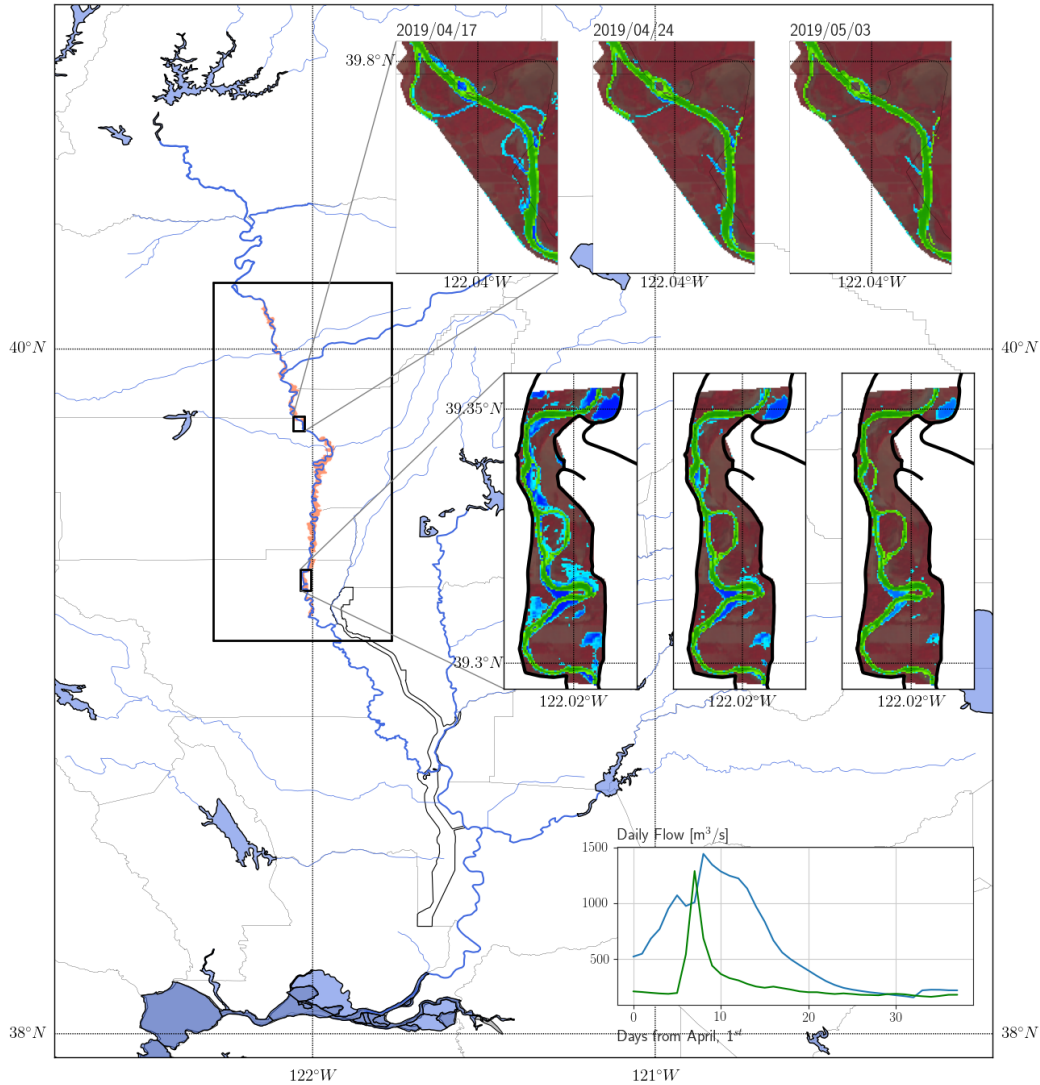


FIGURE 4.9. Off-channel inundated areas after 04/08/2019 storm event (hydrograph at bottom right corner) at two specific locations along the study area (black rectangle). The green hydrograph represents flow conditions during 04/07/2018 high flow event.

A detailed analysis of two events, March 2016 and April 2019 (Figs. 4.8 and 4.9, respectively), illustrates residence time computation. The regions for image comparison were selected based on the differences in off-channel habitat type, with scour channels on point bars for the northern area (location of site 22) and side pools of various depths at the southern area (Kondolf & Stillwater Sciences 2007). In 2016, satellite overpass occurred shortly after peak flows (1 day) showing almost



the total inundation extent for the event, with the second overpass around 10 days after, similar to the first 2019 storm overpass (9 days). For both high flow events, extensive off-channel inundation (blue areas) was still present after one week ( $\sim 40\%$  left in 2016). This persistence was associated to a secondary flow peak in 2016 ( $\sim 1,000 \text{ m}^3/\text{s}$ ) and slow receding flows in 2019, which highlights the importance of the hysteresis phenomenon on off-channel inundation persistence. These generated images also showed a faster dewatering of scour channels for both events, but side pools presented a higher risk of stranding for juvenile salmon due to disconnection from the mainstem. Nonetheless, both events presented nearly dry conditions after 15-16 days after peak flows (Figs. 4.8 and 4.9). The effect of receding flow rates was further illustrated by April 2018 and 2019 storm events. Both had similar peak flows ( $1200\text{-}1400 \text{ m}^3/\text{s}$ ) at almost identical dates (7th and 8th), but they presented distinct receding limbs in their hydrographs (Fig. 4.8). In 2018, the storm generated a narrow flood pulse with fast-receding flows ( $< 5$  days), while 2019 storm had more persistent decreasing flows ( $> 10$  days). As such, satellite overpass on 4/14/2018, only 7 days after the peak, registered almost non-existent shallow water areas ( $< 50$  acres), while more extensive shallow water areas were estimated for 4/24/2019 (250 acres), 16 days after peak flows.

#### 4.4. Discussion

Off-channel habitat's crucial importance for Sacramento River Pacific salmon juvenile development and survival has been brought to the attention of managers and decision-makers during the last two decades (e.g., Maslin et al. 1996, Limm & Marchetti 2009, Bellido-Leiva et al. 2021). However, the lack of literature on the quantitative description of the existing extent and quality of these shallow water habitats might have hindered their explicit consideration in proposed restoration actions along the Sacramento River, especially for the endangered winter-run Chinook salmon (NMFS 2014, NOAA 2021, Peterson & Duarte 2020). Sparse efforts, mostly part of larger spatial coverages, have reported general information such as off-channel area per river km or total extent (e.g., Pacific Rim; Luck et al. 2010, Whited et al. 2013). Nevertheless, these estimates and the omission of the dynamic behavior of seasonal shallow habitat, key in their ecological value (Corline et al. 2017, Katz, *in progress*), might have generated little value to specific restoration efforts. Only Kondolf & Stillwater Sciences (2007) provided a detailed characterization, i.e., required flows for activation and extent, of a subset of OCWBs along the mid-Sacramento River.

This study built on Kondolf & Stillwater Sciences (2007) and developed a region-scale method to identify the extent and persistence of inundated OCWBs along the mid-Sacramento River. We show the potential of remote sensing imagery to quantify shallow water areas and approximate average residence times (not previously found in literature), provide comparisons on the accuracy of the different available remote sensing imagery (LandSat-8 and Sentinel-2; Gorelick et al. 2017) and analysis procedures using spectral water indices (mNDWI and AWEI<sub>sh</sub>; Xu 2006, Feyisa et al. 2014), and distinguish the main drivers of off-channel inundation extent and persistence. Specifically, we found that the moderate resolution of the remote sensing products employed (20 and 30 m; Table 4.1) allowed a satisfactory identification of reduced-sized off-channel habitat (such as scour channels) for higher-order rivers such as the Sacramento River, despite criticism on their coarse resolution to depict detailed shallow water areas (e.g., Whited et al. 2013). These results have important implications for habitat restoration, as they could help managers and decision-makers develop recovery actions targeting juvenile Pacific salmon, such as defining flow pulses from reservoir releases and landform changes to expand shallow-water habitat. By incorporating this information and proposed restoration actions in juvenile production models (e.g., WRHAP-Sea; Chapter 2)

and/or decision-making models (e.g., Winter-run DSM; Peterson & Duarte 2020), initial estimates of population response to proposed actions could also be generated.

#### 4.4.1. Available off-channel habitat

In addition to developing a dataset which describes expected off-channel inundation extent along the mid-Sacramento River for a range in mainstem flows, our objective was to quantify available off-channel habitat to support conservation decisions for Pacific salmon. The difference between off-channel inundation and available habitat extent resides on the combination of its physical characteristics and juvenile salmon bioenergetics (Limm & Marchetti 2009, Lusardi et al. 2020). As mainstem flows increase, the quality of already activated off-channel habitat might decline from optimal conditions, shallow and warmer water promoting zooplankton production and enhanced growth conditions (Jeffres et al. 2020, Lusardi et al. 2020, Zillig et al. 2021), to marginal when higher depths and velocities, and lower temperatures occur. As such, habitat type transitions from high-value off-channel to poorer mainstem habitat (Bellido-Leiva et al. 2021). This expected shift in growth potential is analogous to the reported by Knaggs Ranch empirical experiments at Yolo Bypass (Katz, *unpublished data*), and detailed by Bellido-Leiva et al. (2021). Nevertheless, the described phenomenon does not imply that available off-channel habitat decreases with rising mainstem flows, as new shallow areas become active with greater stages. In turn, a “slowdown” in the rate of increasing habitat is expected after a certain flow threshold (Lyon et al. 2010). Remote sensing imagery is limited to describe water inundation extent, requiring hydraulic modeling to determine water depths, velocities, and temperatures for a detailed representation of available off-channel habitat extent (e.g., Jay Lacey & Millar 2004). As such, a rough approximation was developed by assuming threshold flows were reached at the minimum marginal increase in inundation extent, signaling an increase in river stage with little expansion in surface water area.

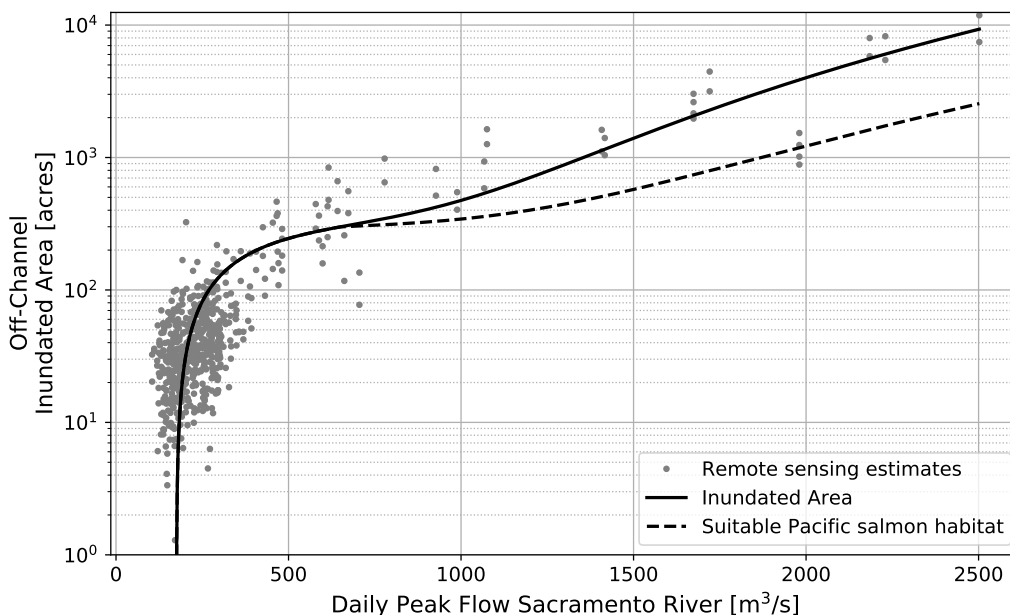


FIGURE 4.10. Fitted flow-habitat curve using Chebyshev polynomials.

A flow-inundation area curve was fitted using Chebyshev polynomials (Mason & Handscomb 2002) to approximate the extent off-channel habitat at each mainstem flow state. All estimates of off-channel inundation computed in this study were used to fit the curve, as each procedure and remote imagery product presented flow ranges with good and poor identification performances. For estimates obtained with single threshold, the possible lack of stability of the threshold among image scenes was a problem (Ji et al. 2009, Huang et al. 2018), making it difficult to decide which value should be used in classification efforts for all image scenes. Our subjective choice of threshold (Section 3.1.1) based on surveyed OCWBs (Kondolf & Stillwater Sciences 2007) might have affected the accuracy of the inundation estimates (Feyisa et al. 2014). This was expected mainly during higher flows, as the threshold’s negative value might have led to the misclassification of dry areas as shallow water. Similarly, Otsu’s algorithm dynamic thresholds seemed to misclassify wet pixels with a smaller inundation extent and/or shallower conditions (mNDWI  $\sim 0$ ), and hence, dynamic thresholding might underestimate the total extent of inundated habitat (Fig. 4.2). By combining both estimates, misclassification errors might be offset and more precise quantification of total off-channel habitat at different mainstem flows could be computed. The obtained flow-habitat curve has the following expression (Fig. 4.10),

$$(4.4) \quad A_{OFF} [Q_{SAC}] = \gamma \sum_{k=1}^4 c_k T_{k-1} \left[ \frac{2Q_{SAC} - (A + B)}{2} \frac{2}{B - A} \right]$$

$$(4.5) \quad T_0 = 1; \quad T_1 = x; \quad T_2 = 2x^2 - 1; \quad T_3 = 4x^3 - 3x$$

where  $c_k$  are the fitted coefficients [5309.17, 8179.62, 3766.79, 1024.39475885],  $T_{k-1}$  is the Chebyshev polynomial of grade  $k - 1$  (Eq. 5), A and B represent the (83.8 and 3002.5, respectively) as Chebyshev polynomials are orthogonal (i.e., [-1,1] domain),  $Q_{SAC}$  represents mainstem flow, and  $\gamma$  is a parameter equal to 1 for  $Q_{SAC} < 648 \text{ m}^3/\text{s}$  and 0.25 otherwise, representing the "slowdown" in the rate of increasing off-channel habitat. The fitted curve is an initial approximation of expected off-channel habitat along the mid-Sacramento River which allows for a primary analysis of their importance on Pacific salmon development and persistence (e.g., Bellido-Leiva et al. 2021). Nonetheless, it aims to motivate more detailed field surveys and hydraulic modeling at river sections of interest, developing a more robust inventory of off-channel habitat location, characteristics, and dynamic behavior.

TABLE 4.3. Average proportion [%] of total off-channel habitat under different mainstem flows along five Sacramento River sections (defined in Figure 4.1).

Flow [ $\text{m}^3/\text{s}$ ]	Section 1	Section 2	Section 3	Section 4	Section 5
<200	12.5	29.5	27	15	16
200-400	24	25	23	13.5	14.5
400-600	24.5	24.5	28	11	11
600-1000	22.5	23.5	28.5	13	12.5
1000-1500	41	20.5	22	8.5	8
>1500	33.5	27.5	24	7.5	7.5



#### 4.4.2. Management implications for Sacramento River Pacific Chinook salmon

The management implications for the described dynamic behavior of off-channel areas and their quantification are extensive. Recently, there has been an increase in the effort by environmental managers to define environmental flow regimes to mimic selected ecologically relevant aspects of the annual natural hydrograph of regulated rivers, such as the Sacramento River (e.g., Yarnell et al. 2015, Horne et al. 2016, 2017, Chen & Olden 2017, Lane et al. 2020). These components of the flow regime sustain important ecosystem dynamics and have documented relationships with ecological, biogeochemical, and geomorphic processes in riverine systems (Yarnell et al. 2015). An important framework that identifies and characterizes these hydrological features is the functional flows approach (Yarnell et al. 2020). The framework recognizes over-bank flows as an important functional flow component (Palmer & Ruhi 2019, Yarnell et al. 2020) that supports a broad suite of physical and ecological processes, including the maintenance of habitat heterogeneity in space and time (Ward 1998), providing cues for fish migration and entrainment in side-channel habitat (Jeffres et al. 2008), and controlling patterns of riparian succession (Ward & Stanford 1995). As such, the fitted flow-habitat curve (Fig. 4.10) and the relationship between off-channel activation period (i.e., residence time) and rate of receding flows are crucial products to assist on the design of optimal environmental pulse flows, i.e., magnitude and duration, to promote Pacific salmon juvenile entrainment in shallow water areas, and hence, providing sufficient habitat with enhanced growing and survival conditions (Maslin et al. 1996, Limm & Marchetti 2009, Bellido-Leiva et al. 2021).

The quantification of shallow water areas also showed little available habitat for flows under  $400 \text{ m}^3/\text{s}$  ( $< 190$  acres), a cue for endangered winter-run Chinook juveniles' peak migration across Knights Landing, downstream Colusa (del Rosario et al. 2013). This suggests that restoration actions should focus on enhancing horizontal connectivity between side-channel and mainstem areas, and increasing off-channel habitat availability for this lower flow range ( $< 400 \text{ m}^3/\text{s}$ ). Such expansions would improve shallow water areas for juvenile development before their migration towards the lower Sacramento River (Bellido-Leiva et al. 2021). As commonly shared by CVPIA restoration practitioners, this defined restoration action targeting winter-run Chinook would likely also benefit other salmonids (*Oncorhynchus spp.*) or at a minimum, would not harm non-target salmonids (Peterson & Duarte 2020).

Once desired restoration extents are drafted, the regional extent of remote sensing imagery allows quantifying the spatial distribution of identified off-channel habitat for a range of mainstem flows. This provides managers with regional information to focus such restoration actions. To this purpose, the study area was divided in five sections, enumerated from south to north (Fig. 4.1), covering the same latitude ranges ( $\sim 0.18^\circ$ ). A significant uneven distribution of habitat was found (Table 4.3), with most available habitat in sections 1-3, specially for higher flows. This has major implications for migrating juveniles, as limited refugia exists that might reduce migration survival across these reaches downstream Red Bluff, sections 4-5 (e.g., BY 2008; Iglesias et al. 2017). These values suggest expanding habitat along these sections might simultaneously address the lack of off-channel rearing habitat for winter-run Chinook (Table 4.3), and improve migration survival for Pacific salmon juveniles. Regardless, the combination of the reported estimates with more detailed studies on juvenile movement along mid-Sacramento River could inform on the river sections for which an increase in habitat quality/extent would most importantly impact Pacific salmon development, and thus, recovery potential.

#### 4.5. Conclusions

This study demonstrated the potential of moderate-resolution remote sensing imagery to characterize the spatiotemporal dynamics of off-channel habitat in higher-order rivers such as the Sacramento River. This method allows to cover a greater spatial extent than physical surveying, while simultaneously avoiding accessibility limitations as reported by Kondolf & Stillwater Sciences (2007), e.g., private land with required permission for entry. Obtained estimates with remote sensing were used to develop a database with which to analyze the distribution and temporal dynamics of off-channel areas along the mid-Sacramento River. The resulting database is not intended to substitute physical surveying, but rather, to provide decision support for the design of effective flow pulses from reservoirs, and the regional assessment and prioritization of river reaches for Pacific Chinook salmon conservation. As such, it aims to motivate and bring focus on detailed field surveys and hydraulic modeling at identified river sections of interest, developing a more robust inventory of off-channel habitat location, characteristics, and dynamic behavior. For instance, limited habitat exists for flows under  $400 \text{ m}^3/\text{s}$ , a cue for migration of endangered winter-run Chinook salmon, precluding juvenile access to areas with enhanced rearing conditions. This scarcity is mainly located along the upper reaches of the area of interest, which also limits juvenile refugia while migrating. Therefore, restoration actions focused on these reaches might provide greater ecological benefits. We hope our results can inform and influence conversations on needed off-channel habitat restoration using the presented rationale, and be useful in refining conservation targets for Sacramento River Pacific Chinook salmon.

## Overall Conclusions and Future Directions

This research has shown the effectiveness of developed valuation, decision-making and characterization tools to structure the complex watershed-scale recovery efforts for winter run Chinook salmon. First, a simple, conceptual freshwater production model (i.e., WRHAP) analyzed the impact of alternative and mainstem habitats on juvenile development and winter-run persistence, while providing realistic estimates of smolt production. This aligned with the conclusions of Lester et al. (2011) in that more complex approaches to representing environmental outcomes do not necessarily improve predictions, but greatly reduce its management effectiveness (Schuwirth et al. 2019). The model was then expanded to a full life-cycle model (adding an ocean-stage module, hatchery operations and reintroduction programs; WRHAP-SEA), and inserted as a valuation tool in the developed optimization framework. The model used linkages between habitat use and juvenile body condition, and information synthesis built in WRHAP-SEA to estimate the population-level response to sets of recovery/restoration actions, allowing the optimization algorithm (Mixed-Integer non-linear Programming) to identify optimal restoration portfolios for alternative financial budgets and hydrologies. Finally, a characterization tool was built to further assist environmental managers in selecting suitable off-channel restoration areas. These findings have important implications for Sacramento River winter-run Chinook management and conservation efforts, and lay out a structured and transparent scientific method, generalizable to other regions for species recovery.

### **Expansion of winter-run Chinook monitoring program**

The development of WRHAP and WRHAP-SEA identified important knowledge gaps in winter-run Chinook freshwater stage due to the lack of explicit monitoring along the Sacramento River (Johnson et al. 2017). Limitations include a poor documentation of juvenile rearing survival and growth along the Sacramento mainstem (high sensitivity parameters), scarce empirical estimates of off-channel areas rearing survival and use, and juvenile residence time at tributaries. New research based on analyzing returning adults eye lenses is starting to map juvenile rearing history along the Sacramento River (Bell-Tilcock et al. 2021), providing a key dataset to understand rearing habitat selection and, hence, to organize detailed monitoring program on areas highlighted by the analysis. The flexible structure of the tools developed in this dissertation would allow incorporating such new knowledge easily, improving the accuracy of the outputs and the effectiveness to inform environmental managers.

### **‘Non-critical’ habitats are crucial for persistence and recovery**

The Endangered Species Act (ESA) only listed the Sacramento River mainstem and some portions of the Sacramento-San Joaquin Delta, i.e., the outmigration corridor, as critical habitat for

winter-run Chinook salmon (Phillis et al. 2018). Nevertheless, WRHAP showed that the contribution of ‘non-critical’ habitats to juvenile development and size at outmigration greatly outweighed mainstem rearing, especially during higher flow years when off-channel and floodplain habitats become activated. As such, since body size at ocean entry is an important, if not the primary, indicator of an individual’s probability of returning from the ocean to spawn (Katz et al. 2017), these habitats are vital for winter-run Chinook salmon persistence. For instance, floodplain habitat contributed to 30% of total simulated biomass (brood years 1995-2017), despite only used by 15-20% of individuals for just 7-8% of total rearing time. Similarly, off-channel and tributary rearing along the upper Sacramento increased simulated migration survival by 60-300% as a result of improved body conditions.

These links between juveniles with diverse rearing histories and adult return success were also shown by WRHAP-SEA outputs. For optimal portfolios mostly comprised by tributary and off-channel restoration actions, rapid recoveries in returning adults abundance were simulated, illustrating the population greatly benefiting from even small improvements in off-mainstem habitat. The results of this dissertation aligns with those of Phillis et al. (2018) and suggest that off-mainstem habitats should be also listed as ‘critical’ by the ESA for their protection, and to open up greater restoration and conservation opportunities for species recovery.

### **Potential for winter-run Chinook recovery**

Defined optimal portfolios improved a wide range of ecological services along the Sacramento River and presented promising recoveries in abundance, even for small investments (>200% increase in returning adults). Nonetheless, viability assessment of identified optimal portfolios showed that a favorable classification in remaining criteria (population growth, hatchery dependence and catastrophic decline) required a combination of floodplain connectivity enhancement, reintroduction at Battle Creek and restoration of a mosaic of tributary and off-channel habitats, and therefore, funds over \$100 million in capital budget.

Frequent floodplain activation arose as a key restoration action since population net growth did not reach positive values until its implementation. This, in turn, is crucial to assure a rapid recovery in numbers after high-mortality events, and to reduce dependence on hatchery supplementation. Weir notching has potential to provide further benefits if weir gate operation is optimized to promote juvenile residence time until favorable ocean conditions exist.

The analysis also showed the importance of reintroduced populations to improve winter-run Chinook diversity and spatial structure, while reducing the impact of catastrophic events associated to drought conditions. Despite these benefits, reintroduction at McCloud River (two-way trap and haul program) was not selected for any optimal portfolio, even when optimal handling operations were considered. Two main issues precluded its selection: (i) the high cost from collection facilities designs to reach high efficiencies (>70%) to minimize the demographic risk imposed on the Sacramento winter-run population; and (ii) the dependence of the reintroduced population on hatchery operations (non-viable status).

### **New technologies to refine proposed restoration actions**

Defined optimal portfolios included specific magnitudes of tributary and/or off-channel habitat to be restored. Nevertheless, these habitats are complex and require more detailed analysis to estimate how proposed restorations can maximize benefits for targeted species. We illustrated the

ability of moderate-resolution remote sensing imagery (LandSat-8 and Sentinel-2 Gorelick et al. 2017) to characterize the spatiotemporal dynamics of off-channel habitats along higher-order rivers as the mid-Sacramento river. This analysis developed a dataset of off-channel habitat, that provided further management implications for winter-run Chinook. It identified mainstem flow ranges of ecological significance ( $<400 \text{ m}^3/\text{s}$ , cue for migration) with marginal habitat availability, and areas with a poorer distribution of activated habitat, located just downstream Red Bluff. This, in turn, allows identification of potential areas to focus the restoration efforts defined by the optimization framework, motivating more exhaustive physical surveys and hydrodynamic modeling. This characterization also suggested an additional alternative to provide enhanced side-channel connectivity, designing pulse flows with slow flow recession rates to promote off-channel activation during desired time periods. These can be included in functional flows management approaches (Yarnell et al. 2015, 2020).

### Future directions

Developed methods and tools gave special focus on effectiveness to inform and assist environmental managers and decision-making processes. Nevertheless, the overall impact of this research is reduced if the developed tools lack accessibility. As such, the next immediate step will develop a simplified tool, web or software based, to facilitate and promote its use in policy conversations.

We assumed in this dissertation, as commonly shared by CVPIA restoration practitioners, that habitat changes focused on winter-run Chinook would also benefit or, at least, not harm other non-target salmonids. Similar tools could be developed for other runs in the Sacramento Valley (fall-, late-fall) following the proposed methods to analyze their relationship with habitat, their viability and the impact of proposed restoration actions on their life-cycle. This could be expanded to include other threatened species sharing the same spatial distribution, as the anadromous green sturgeon (*Acipenser medirostris*), allowing exploration of tradeoffs between species and required habitat characteristics, and mutually beneficial restoration efforts.

Climate change is projected to exert more pressure on California's water system and challenge managers and operators to balance water uses for the multiple and sometimes competing objectives (Cohen et al. 2020, 2021). The developed tools have potential to evaluate winter-run Chinook response to proposed adaptations of reservoir and system operations, providing a more exhaustive ecological measure than simplified indicators. More directly, WRHAP-SEA outputs could be embedded within reservoir re-operation optimization processes to include winter-run Chinook persistence as an additional objective in their non-dominated solution space, allowing to explore tradeoffs with remaining water uses.

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